CENTENNIAL VALLEY ARCTIC GRAYLING ADAPTIVE MANAGEMENT PLAN

6 July 2017

Authors: Jeffrey M. Warren[1] and Matt Jaeger[2]

Planning Team: Bill West[1], Andrew Gilham[1], Kyle Cutting[1], Terrill Paterson[2], Jo Ann Dullum[1] , Andy Brummond[2], Lucas Bateman[2], Austin McCullough[2], David Schmetterling[2], Michael Davis[3], Tom McMahon[3], Travis Horton[2], George Jordan[1], James Magee[1], Glen Boltz[1,5], Jim Mogen[1], Paul Hutchinson[4], Mike Duncan[2]

[1]U.S. Fish and Wildlife Service, [2]Montana Fish, Wildlife & Parks, [3]Montana State University, [4]Bureau of Land Management, [5]Retired.

Introduction

Montana Arctic grayling (grayling) were patchily distributed throughout the Upper Missouri River (UMR) drainage prior to the mid-1850s (Vincent 1962). 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 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 (Warren et al. 2017). Currently, most of the grayling population in the CV 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 contraction and expansion, 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 actions to achieve population goals for CV grayling remain ambiguous and selecting 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. An adaptive management (AM) approach is being undertaken to accomplish this (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.

Adaptive management is an approach to achieve objectives when the outcomes of available management actions are uncertain but decisions must still be made (Walters 1986, Kendall 2001). The central tenet of the AM approach is that systemic knowledge can be gained if management is treated as an ecological experiment. Management actions, e.g., reduction of non-native fish, are *de facto* hypothesis tests that iteratively seek to manipulate an ecological system by altering hypothesized limiting factors and measuring the response. The manipulations in these experiments are the suite of possible management actions available to ameliorate limiting factors and achieve management or conservation objectives for CV grayling. Comparison of population responses among hypothesis tests defines the most effective management actions to achieve population goals. Thus, this plan describes how each implemented management action should be structured, timed, and evaluated to serve as a test of a hypothesized population driver for CV grayling. This plan is unique from all previous research and management efforts in the CV because it seeks to define management actions that most efficiently achieve grayling population goals by linking hypothesized limiting factors to demographic rates, thereby determining which are actual population drivers.

The AMP emphasizes rapid learning through active adaptive management. Due to the initial level of structural uncertainty, and associated agency conflict, the AMP describes a “management by experiment” phase that emphasizes rapid reduction of structural uncertainty (Williams 2011) followed by an iterative phase that uses the information gained to refine management actions and direct their implementation in response to a defined decision threshold (MacNab 1983, Walters 1986, Walters and Holling 1990). The management by experiment phase explores grayling population response to hypothesized drivers that can be influenced via management actions. Active AM by experiment ideally involves synchronous implementation of different management actions on replicates of the resource of interest to maximize the speed of learning (Williams 2011, Allen et al. 2011). Because we have a single replicate (i.e., there is only one Red Rock Lake system) we initiated systemic manipulation across time (8-10 years) rather than space. Models specific to each limiting factor and their associated management action will be simultaneously evaluated by comparing model predictions to observed outcomes throughout this phase. The iterative phase of the AMP will use the information gained in the first phase to determine an optimal policy to inform annual management decisions based on thresholds related to population goals. Although the relative emphasis on learning differs between phases, management will be used to facilitate learning for the purpose of improving future management in both. Emphasis on continued reduction of uncertainty and use of gained information to iteratively make management decisions based on a defined decision threshold differentiate our approach from passive AM (Williams 2011), “AM-lite” (Fischman and Ruhl 2016), or effects analysis (Murphy and Weiland 2011).

Although AM is inconsistently defined and implemented, it is generally characterized by reduction of uncertainty through formulation of 1) a statement of objectives, 2) management actions likely to achieve them based on competing hypotheses about factors that limit the population of interest, 3) identification of models and monitoring plans that allow evaluation of each hypothesis, and 4) decision thresholds that trigger implementation of actions following feedback from monitoring (Kendall 2001, Williams et al. 2009, Allen et al. 2011, Fischman and Ruhl 2016). The first three components occurred as part of a set-up phase undertaken by stakeholders while the last is part of the iterative phase (Williams et al. 2009). The remainder of the AMP describes how we address these components.

Study Area

The CV 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 1). 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 1954, 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 1); however, the AMP applies specifically to the Upper Lake watershed. 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. Mean annual discharge of Red Rock Creek during 1997–2012 was 48.2 cubic feet sec^{-1} (cfs) (SD = 17.3). Annual peak daily discharge varied between 16 May and 26 June during the period 1997–2004, with peak mean-daily discharge varying from 98 cfs (28 May 2000) to 293 cfs (10 June 1997). Elk Springs Creek originates from a series of springs south of Elk Lake and flows southwest, entering Swan Lake along the northeast shore; the latter drains into Upper Lake to the south. Annual peak daily discharge of Elk Springs Creek upstream of Picnic Creek varied between 30 April and 22 October during the period 1999–2004, with discharge ranging from 10.9 cfs in 1999 to 7.6 cfs in 2004. A more recent discharge of 16.5 cfs was measured 7 June 2011, near the confluence with Picnic Creek. Picnic Creek contributes an additional 10.5 cfs at this junction, resulting in a combined discharge of 27 cfs in Elk Springs Creek as it flows toward Swan Lake. A recent (2016) restoration diverted Elk Springs Creek into an historic channel that resulted in the creek entering Swan Lake in the southeast shore, circumventing much of Swan Lake. Pre-restoration data indicate highly variable, but generally suitable, dissolved oxygen entering Upper Lake from Swan Lake during summer (mean July 2016 DO = 8.7 ppm, SD = 4.48 ppm), although lethal levels were recorded (minimum July 2016 DO = 1.31 ppm; J. Marsh, unpubl. data). Future monitoring will help determine changes in dissolved oxygen levels of water entering Upper Lake from Swan Lake during winter. 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.

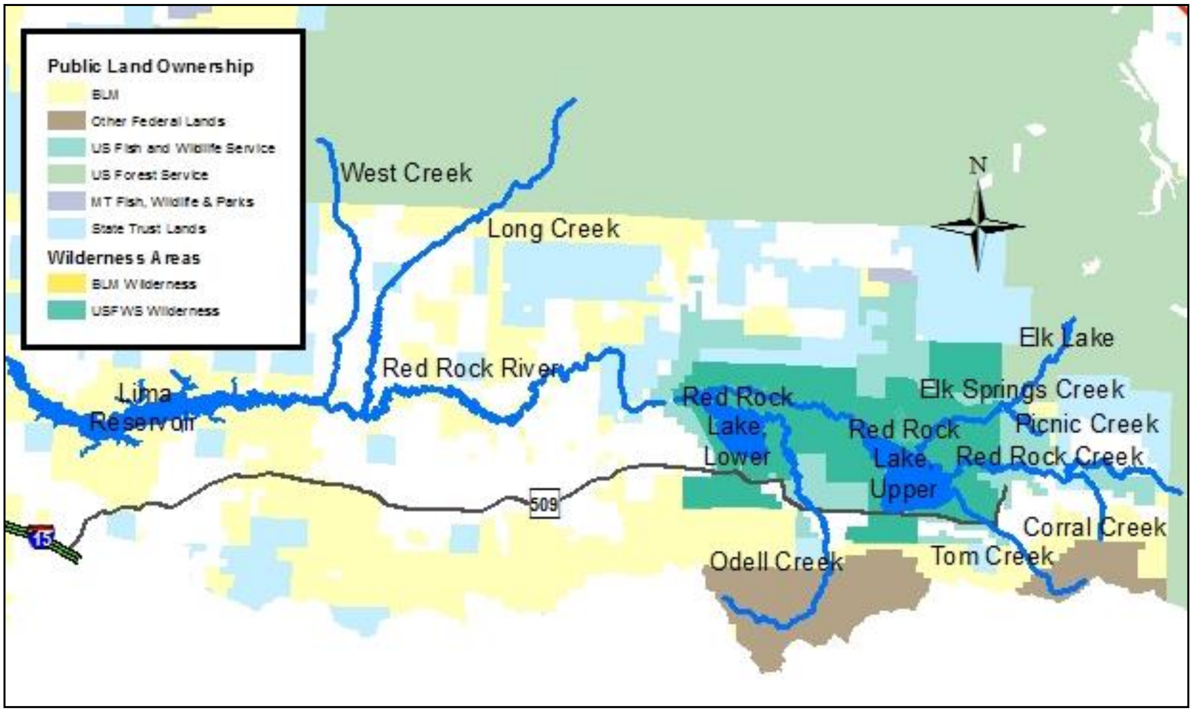

Figure 1. Arctic grayling adaptive management plan study area within the Centennial Valley of southwestern Montana.

AMP SET-UP

A stakeholder group (workgroup) was convened to complete the set-up phase of the AMP. The workgroup was established in 2011 to provide resource managers a forum to discuss management alternatives that could potentially benefit grayling. The workgroup comprises individuals representing agencies that have either direct grayling or land management authority in the CV. Montana Fish, Wildlife & Parks (FWP) has management responsibility for grayling in the CV, the U.S. Fish and Wildlife Service (FWS), Bureau of Land Management (BLM), and Forest Service (FS) manage CV lands that are part of the federal estate, Montana Department of Natural Resources and Conservation (DNRC) manages state-owned lands, and The Nature Conservancy (TNC) owns land in the CV they manage to benefit grayling. The workgroup has no formal governance process and is a voluntary consensus-based management group.

The underlying impetus for creation of the workgroup was resolution of long-standing disagreement among resource managers about what actions would most effectively conserve grayling. Members of the workgroup shared a common goal to conserve grayling, but had not explicitly defined what that meant or developed objectives that would lead to its attainment. Over the past 70 years employees of the respective management agencies had defined a consistent set of potential limiting factors and management actions intended to ameliorate their influence on the grayling population; however, fierce disagreement among agencies about the relative effect of each limiting factor precluded implementation of management actions. Discussions within the workgroup revealed that disagreement was largely due to managers making different assumptions about CV grayling biology and ecology, and therefore the effectiveness of related management actions, often in the absence of empirical data. Hence, selection of management actions to most effectively conserve grayling was precluded by structural uncertainty. The workgroup resolved to take an AM approach to implement management actions while reducing structural uncertainty based on their outcomes, which necessitated creation of the AMP. The remainder of the set-up phase of the AMP was vetted by the workgroup over several years.

Objectives:

The AMP is a tool intended to facilitate achievement of CV grayling management and conservation goals in perpetuity. The species-wide conservation goal for Montana Arctic grayling is described in the Upper Missouri River Arctic Grayling Conservation Strategy (Conservation Strategy; MAGWG, in press) as follows:

Ensure the long-term, self-sustaining persistence of Arctic Grayling in the upper Missouri River Basin (UMR).

Accordingly, the workgroup developed the following objectives to meet the species-wide population goal within the CV:

1) Conserve existing Centennial Valley Arctic grayling genetic diversity.
2) Establish or maintain Arctic grayling spawning and/or refugia in at least two tributaries up and downstream of Upper Red Rock Lake and connectivity among tributaries.
3) Maintain at least 1000 spawning fish in the Upper Red Rock Lake Arctic grayling population.

The AMP was prepared to identify the most effective management strategies to maintain at least 1000 spawning fish in the Upper Lake grayling population. The first workgroup objective can be met by a combination of creating genetic reserve broods and conservation of the extant population. Although it is presently unclear how to best conserve extant populations the general approach to creating a reserve brood is agreed upon and well understood. Similarly, the second objective can be satisfied through agreed upon and routine actions (i.e., establishing new populations by in situ propagation, eliminating physical or chemical barriers to migration, etc.). However, there is considerable uncertainty about how to best achieve or define the third objective, which encompasses conservation of the extant population as implied by the first objective. Therefore, the AMP specifically applies to achievement of the workgroup's third objective while the former two are not discussed further in this document but are addressed in the Conservation Strategy referenced above.

Defining objectives that achieve long-term population viability is a challenging venture that commonly proceeds with uncertainty. The Conservation Strategy defines the long-term self-sustaining persistence of CV grayling to occur when after 5 generations (15 years) a stable or increasing trend in effective population size (N_e) is exhibited. The workgroup developed their three objectives with the belief that, if collectively met, they will satisfy this genetic criteria and resultantly the long term grayling conservation goal. However, the workgroup integrated a demographic (i.e., maintaining at least 1000 spawning grayling), rather than genetic, threshold into their objectives to improve the rate of learning. Successful AM requires objectives that are specific and measurable over a timeframe appropriate for hypothesis evaluation and effective implementation of management actions in response to system state (Kendall 2001, Williams et al. 2009, Allen et al. 2011, Fischman and Ruhl 2016). A lag of about seven years between implementation of a management action and first measurable population response exists when using the genetic metrics described in the species-wide goal because 1) we can't reliably monitor CV grayling until they recruit to the spawning population at age 3, and 2) estimates of effective number of breeders relate back to the parents of the contemporary spawning population rather than the number of spawning fish present at the time of sampling. This feedback lag is reduced to three years or less (depending on the management action) if a demographic threshold is used as an objective. Furthermore, historic monitoring provided multiple estimates of spawner abundance over the past 20 years whose use greatly expedites learning about factors that limit CV grayling; if genetic metrics are used learning is informed only by data collected in future years. However, selecting a spawner abundance threshold that relates to the long-term goal of self-sustaining persistence is an inevitably subjective task because of inherent uncertainty about the range and relative likelihood of future outcomes. To move forward in the face of uncertainty we used the results of an expert elicitation process that was attended by members of the workgroup and other grayling experts to select a spawner abundance threshold that related to the species-wide goal. Experts predicted a grayling population with an initial size of 1000 individuals had a 0.85 to 0.99 probability of persistence over 10, 25, and 50 year timescales (Figure 2; Boyd 2014). Perceived probability of persistence began to decline at lower initial population sizes at all timescales. Because this exercise involved CV stakeholders to functionally define a population size at which long-term self-sustaining persistence of grayling was expected, it presently represents the best available information to inform development of a demographic population threshold. Therefore, maintaining a spawning population of at least 1000 fish was selected as an objective for the Upper Lake population and will serve as a trigger threshold for decision making in the AMP. Our approach to decision making, including how spawner abundances will be forecasted and management alternatives selected, is subsequently described in more detail.

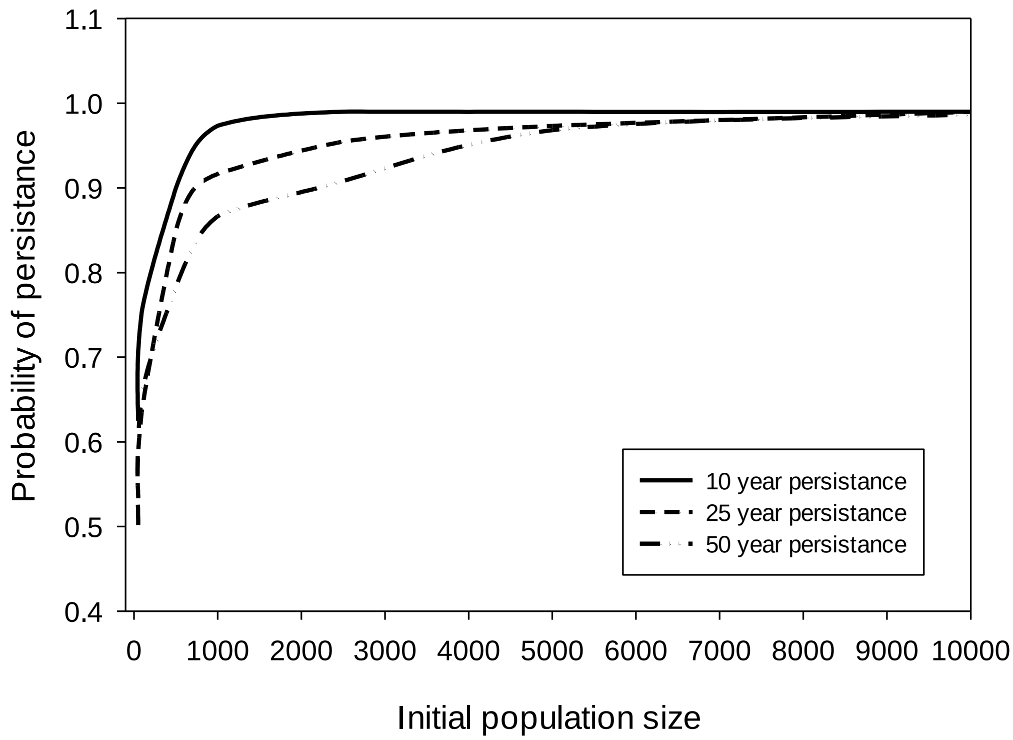

Figure 2. Predicted probability of persistence of Arctic Grayling populations of varying initial size over 10, 25, and 50 year time periods.

Limiting Factor Hypotheses:

Formulation of effective management alternatives requires identification of factors that influence attainment of population goals. Identifying limiting factors, perceived and documented, clarifies uncertainty regarding drivers of the CV Arctic grayling population and the potential management actions that address them, including monitoring approaches required to link the two together. When uncertainty about which factors are most influential to a population exists this process entails developing and testing competing hypotheses about ecological systems. The following hypotheses have been repeatedly suggested over the past 70 years to explain CV grayling distribution and abundance:

1) Quality and quantity of tributary spawning habitat is the primary driver of the CV grayling population.

2) Predation by, and competition with, adult non-native hybrid Yellowstone cutthroat trout is the primary driver of the CV grayling population.

3) Quality and quantity of overwinter habitat in Upper Red Rock Lake is the primary driver of the CV grayling population.

4) Instream conditions during the spawning and early rearing period are the primary driver of the CV grayling population.

Decline of spawning habitat quantity and suitability resulted from changes associated with water, livestock, and wildlife management. Initially used as summer range beginning in 1876, year-round livestock operations quickly became common in the CV; by 1892 21 ranches existed within the present-day Refuge boundary and settlement and grazing was associated with most waters throughout the CV (Vincent 1962, Unthank 1989, Centennial Valley Historical Society 2006). Common impacts of grazing in riparian systems include degradation of woody riparian vegetation and increased fine sediments in the streambed, summer water temperatures, and nutrient levels of streams (see review in Clary and Webster 1989, and citations within). Sedimentation of spawning reaches resulting from grazing has been repeatedly documented in Red Rock, Odell, and Tom creeks, and was reported as the primary threat to grayling persistence for much of the 1900s (Vincent 1962, Myers 1977, Mogen 1996). Manipulation and consolidation of flow among channels of Hellroaring Creek to facilitate irrigation caused erosion and sedimentation on reaches of Red Rock Creek upstream of the most heavily used spawning habitat in the CV. Serial impoundment of the Elk Springs Creek watershed has destroyed or isolated historically important spawning habitats. Elk Springs Creek was diverted into Swan Lake as early as 1908, which may have partially fragmented this formerly heavily used spawning tributary. Spawning habitat in upper Elk Springs Creek was fragmented and destroyed by sedimentation resulting from impoundment of Blair Pond in 1912 and McDonald Pond in 1953. Picnic Creek was first impounded to create Widow's Pool in 1900 (Centennial Valley Historical Society 2006), which was expanded into Culver Pond in 1959, and by the downstream Widgeon Pond in 1964 (Gillin 2001). Finally, fragmentation and degradation of spawning tributaries by beaver dams has been suggested to preclude grayling spawning in CV tributaries to varying degrees (Nelson 1954, Unthank 1989). Recent management direction has likely improved grayling spawning habitats in parts of the CV. A combination of Refuge land acquisition and changes in grazing management on public and private lands has ameliorated this threat on most Red Rock lakes' tributaries (USFWS 2009). McDonald Pond was removed and returned to stream habitat beginning in 2009 and plans are in place to remove at least one of the Picnic Creek impoundments (USFWS 2009).

Competition or predation by native (burbot, white suckers, sculpin) and non-native (Yellowstone cutthroat, rainbow, and brook trout) fishes have been hypothesized to affect CV grayling. Early settlers introduced non-native fishes, followed by decades of agency introductions, largely for recreational fisheries. Stocking of CV waters with rainbow trout (*Oncorhynchus mykiss*) began as early as 1899, followed by brook trout (*Salvelinus fontinalis*) in 1900, and Yellowstone cutthroat trout in 1967 (Randall 1978). Although grayling have persisted with these introduced species in the CV, the degree to which they limit the population remains ambiguous. Early work documented predation of grayling eggs and age-0 grayling by brook trout (Nelson 1954), and more recent work corroborated grayling egg predation (Katzman 1998). Predation on age-0 and age-1 grayling by cutthroat trout has not been documented (Nelson 1954, Katzman 1998, Cutting et al. 2016), but effective sampling has not occurred during winter when predation may be most likely due to lower habitat and food availability. Recent stable isotope analysis identified a greater contribution of fish to the late-winter diet of cutthroat trout in Upper Lake, although no predation of grayling was observed during analysis of stomach contents (Cutting et al.

2016). Stable isotope analysis also indicated that dietary overlap between Yellowstone cutthroat <450 mm and grayling of all sizes in Upper Lake occurs, although it is not possible to determine whether competition for forage items exists because forage availability data were not collected (Cutting et al. 2016). Populations of native fishes, such as burbot and white and long-nose suckers, were experimentally suppressed at various times between the 1960s and 1980s in Upper Red Rock Lake because of their hypothesized effects on grayling, although the effect of these actions were not evaluated (Skates 1985, Unthank 1989). Moreover, no age-0 grayling were found in stomach contents of burbot captured in Upper Lake (Katzman 1998).

Limited winter habitat is another potential driver of observed declines in grayling in the CV. Upper Lake is a shallow (typically <2 m) eutrophic lake that provides the primary winter habitat for grayling in the CV. An early account documented Upper Lake depths >6.1 m (20 ft; Brower 1896, Vincent 1962), although reported maximum depths from the 1950s to present time generally do not exceed 1.8 m (6 ft; Davis 2016). The locations where depths of >6 m were measured are unknown and a single core sample of lake substrate suggests that sedimentation rate has not changed in Upper Lake since pre-settlement times, although changes in water depths cannot be inferred from this sample (C. Whitlock, pers. comm.). Nonetheless, winter dissolved oxygen depletion rates in shallow eutrophic lakes are relatively high (Mathias and Barica 1980), which can lead to high winterkill risk for fish (Barica and Mathias 1979, Fang et al. 2004). Winter hypoxia facilitated by shallow depths and high production of macrophytes presently occurs over large parts of Upper Lake during some years (Randall 1978, Gangloff 1996, Davis 2016, K. Cutting pers. comm.). Suitable winter habitat for grayling in Upper Lake is defined by depths >1 m and dissolved oxygen concentrations in the epilimnion >4 mg/L (Davis 2016). Availability of suitable habitat varies considerably among years, creating the possibility of at least partial winterkills during years when habitat availability is low (Warren et al. 2017). Grayling have persisted in the CV ostensibly under persistent risk of winterkill in Upper Lake; however, the relative significance of winterkill may currently be greater due to lack of connectivity with other Montana grayling populations, which precludes gene flow and a refounding source for the population.

Instream conditions during spawning, incubation, and early rearing periods can influence cohort strength and, ultimately, population abundances in fishes in general (Crecco and Savoy 1984, Mills and Mann 1985, Nunn et al. 2003, Warren et al. 2009) and grayling in particular (Clark 1992, Deegan et al. 1999). Contrasting theoretically ideal hydrologic scenarios exist for adult grayling and eggs or fry. High flows and low temperatures are physiologically favorable for adults and create good spawning habitat (i.e., exposed, flushed gravel beds) whereas low or stable, warm flows are typically better for survival of eggs or fry (Clark 1992, Deegan et al. 1999). The latter of these two scenarios is hypothesized to set year-class strength between spawning and approximately five weeks following emergence. An ideal hydrograph for all life stages would be high flows prior to spawning and a rapidly declining hydrograph and increase in stream temperatures or stable, spring creek-like hydrograph following spawning. Conversely, any peaks in the hydrograph or cool temperatures post-spawning are believed to reduce survival probabilities of eggs or fry. It is presently unknown whether these factors are a driver of CV grayling population and, if so, the magnitude of their influence relative to the aforementioned stressors.

An improved understanding of the relative effect of hypothesized natural and anthropogenic population drivers is necessary to assess the benefits of implementing future management actions.

Anecdotal or observational data that both support and refute each hypothesis presently exists, creating ambiguity regarding true population drivers and, resultantly, which management actions are most likely to result in attainment of population objectives. Our goal during the management by experiment phase is to disentangle the ambiguity by conducting focused empirical tests of these hypotheses via implementation of management actions to ultimately determine the degree to which each hypothesis characterizes CV grayling population dynamics. These results will subsequently dictate the most effective management approaches throughout the iterative phase to achieve CV grayling population goals in perpetuity.

Management Actions:

Implementation of management actions is the mechanism by which hypotheses about limiting factors will be tested. Effective formulation and evaluation of management actions requires placing limiting factors, which constrain population growth of a species, in the context of the demographic rates they affect. The demographic rates influenced by each limiting factor will be the basis of models used to evaluate the relative effectiveness of management actions. Based on existing hypotheses, we've identified four potential limiting factors for grayling, mitigating management actions, and the demographic rates they are hypothesized to affect (Table 1). To improve spawning habitat, management actions on Red Rock Creek will reduce erosion and sedimentation and restore floodplain connectivity and natural processes of habitat formation to upper reaches. Management actions on Elk Springs Creek will restore connectivity and improve spawning habitat quality. Additionally, all beaver dams on Red Rock and Elk Springs creeks will be breached during spawning periods to ensure all suitable spawning habitats are accessible. These management actions are hypothesized to influence abundances of spawning grayling by improving egg and fry survival. To reduce potential predation and competition, management actions will suppress adult Yellowstone cutthroat trout abundances by removing spawning fish from Red Rock Creek via liberalized recreational angling regulations (20 fish daily and in possession) and an agency-operated weir. These management actions are hypothesized to influence abundances of spawning grayling by improving age-0 and age-1 survival. Specific management actions that will directly (i.e., aeration, increasing depth) or indirectly (i.e., snow clearing) increase dissolved oxygen concentrations or suitable depths in Upper Lake have not yet been formulated; however, low amounts of suitable overwinter habitat are hypothesized to influence abundances of spawning grayling by reducing overwinter survival of all ages. Finally, ambient hydrology and temperature during spawning and rearing periods are hypothesized to influence abundances of spawning grayling by affecting egg and fry survival. No management actions are associated with this hypothesis; ambient conditions will be monitored to assess whether they best predict abundances of spawning grayling. If the suite management actions created for the initial hypothesis tests described in this plan do not address actual limiting factors then Table 1 will be revisited to formulate new hypothesis tests and management actions.

Table 1. Hypothesized limiting factors for Arctic grayling in the upper Centennial Valley watershed, Montana. Potential mitigating actions to address each limiting factor and the demographic rates that will be influenced are also provided.

Limiting Factor	Management Actions	Affected Demographic Rate
Spawning habitat	Stream restoration Provide connectivity Reduce beaver abundance	Egg survival Age-0 survival (summer)
Non-native trout	Increase angler harvest Remove non-native trout	Age-0 survival (summer) Age-0 survival (winter) Age-1 survival
Overwinter habitat	Aerate Upper Red Rock Lake Increase Upper Red Rock Lake depth Remove snow from Upper Red Rock Lake	Age-0 survival (winter) Age-1 survival Age-2+ survival
Instream conditions	None	Egg survival Age-0 survival (summer)

Structure, timing, duration, and evaluation of each implemented management action must be carefully defined to ensure it provides the intended test of an established hypothesis during the management by experiment phase. For example, each implemented management action (i.e., hypothesis test) should be temporally or spatially isolated from other management actions to reduce the likelihood of confounded results and each hypothesis test should be of adequate duration for a response to occur and be observed. Because there is a single population of interest, spatial isolation or synchronous implementation of multiple replicates is not possible; management actions will be sequentially implemented to maximize learning. The minimum duration of each management action will be four to five years, which is the approximate generational periodicity of grayling and the soonest a response can be detected. This duration will also reduce the likelihood of cofounded results with potential limiting factors we cannot directly control by implementing management actions (i.e., instream conditions) and provide replicates for each hypothesis test. However, learning about each limiting factor will not be exclusive to the period when its corresponding management action is implemented; data required to update each limiting factor model will be collected annually. Sequence of management actions was initially determined by ease of implementation and availability of funding and data to support management action development at the time of AMP inception (Table 2).

Table 2. Hypothesis testing schedule and approach.

Hypothesis	**Management Action**	**Water Body**	**Timeframe**
YCT competition or predation	YCT suppression	Red Rock Creek	2013-2016
Spawning habitat	Connectivity, restoration	Red Rock and Elk Springs creeks	2017-2020
Overwinter habitat	Unknown	Upper Lake	TBD

The management by experiment phase will use management actions to create a wide range of values for each limiting factor to expedite learning. Understanding the relative effects of a potential limiting factor, and ultimate effectiveness of its associated management actions, on grayling abundance requires observing population response to varying levels of each factor. Passively allowing values of a limiting factor to change or making incremental adjustments through management actions prolongs learning; it may take many years to observe a system state that is beneficial or detrimental to grayling. Actively intervening with management actions intended to elicit relatively large changes in system state over discrete time periods will increase the likelihood of understanding the extent each potential limiting factor drives grayling population. Thus, we structured the management by experiment phase to asynchronously produce high, moderate, and low values of each limiting factor we had the ability to influence through management actions (Table 3). Different expected abundances of grayling will resultantly be predicted by each limiting factor hypothesis in a given year based on hypothesized relationships between limiting factors and demographic rates (Table 3). Creating an array of scenarios with different expectations of grayling abundance allows discrimination among competing hypotheses by comparing observed abundances to those predicted by models representing each limiting factor. Conducting hypothesis tests for multiple years is required to create the range of scenarios needed to discriminate and avoid confounding among limiting factors. Ultimately, the management by experiment phase is intended to maximize the likelihood of identifying management alternatives that will most effectively achieve population goals in the iterative phase. Accordingly, the management by experiment phase of the AMP will be complete when we have successfully elicited the combination of relative values of limiting factors described in Table 3.

Table 3. Relative levels of hypothesized limiting factors in response to planned management actions during AMP phase 1. Hypothesized grayling abundances in response to implemented management actions are shown in parentheses. Winter habitat conditions that cannot be controlled exclusively by planned management interventions are denoted by *.

Year	YCT abundance	Spawning habitat	Overwinter habitat
2013	high	moderate	NA
2014	high	moderate	high (high)
2015	moderate (low)	low	high (high)
2016	moderate (low)	low (moderate)	low (low)
2017	low (moderate)	high (moderate)	low (low)
2018	low (moderate)	high (low)	moderate* (low)
2019	moderate (high)	high (low)	moderate* (low)
2020	high (high)	high (high)	moderate* (moderate)
2021	high (moderate)	high (high)	moderate* (moderate)
2022	high (low)	high (high)	moderate* (moderate)

Potential limiting factors identified in the future will be integrated into the AMP as appropriate. It is our expectation that the AMP will be a living document that is updated if future limiting factors and management alternatives are identified. However, deference will be given to the aforementioned management actions to maximize learning and avoid confounding effects. Inclusion of potential future limiting factors and their associated management actions will be vetted based on their relative likelihood to influence grayling population objectives. For example, the effects of beaver dams, angling, and monitoring (trap and electrofishing) on adult survival have been suggested as possible limiting factors. Survival analyses coincident with planned management actions will be used to assess the relative likelihood that these factors influence adult survival to the extent they limit population size. However, assessment of these factors will be done opportunistically as compatible management actions are implemented with an emphasis on avoiding confounding effects with each other or the intended manipulation of population levels described in Table 3.

Models of System Dynamics:

Learning occurs by discriminating among competing models that represent different hypotheses of system dynamics, thereby reducing structural uncertainty and identifying how a system responds to management actions. 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 limiting factors. To discriminate among models, predictions of grayling abundance will be generated annually from each model (see *Model Prediction and Parameter Estimation* below). Model predictions will then be compared to estimated grayling abundance from mark-recapture sampling, with the model that makes the most accurate prediction receiving more 'weight' than the others. Model parameter estimates will be updated with the current year's data, and updated models will then be used to make predictions for the subsequent year. This process is repeatedly annually; ideally a single model will consistently predict better than the others, resulting in incrementally increasing model weight (i.e., increasing confidence that the model is the best descriptor of system dynamics). If a single model does not separate from the other competing models the hypotheses will need to be revisited and new hypotheses or models created.

Model Prediction and Parameter Estimation—Models representing competing hypotheses of system dynamics will predict grayling spawning population in year $t + 1$ using population size in year t and 1) spawning habitat in year $t - 2$, 2) non-native fish present winters $t - 2$ and $t - 1$, 3) winter habitat conditions in years $t - 2$ through t or 4) spring hydrologic conditions in year $t - 2$, depending on which hypothesis a model represents. Maximum likelihood estimates of model parameters a and b will be updated annually for prediction the subsequent year.

The data structure for fitting models is included in Appendix I. Names and definitions of imported and created variables are provided.

Population of interest – A succinct and precise definition of the population of interest is essential to success in developing models of system dynamics and appropriate monitoring. In the context of this plan the population of interest is defined by our management objective and is the response variable for competing models of system dynamics. Estimated abundance of spawning grayling will be the response variable.

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, excluding a null logistic growth model, share a common balance equation that allows prediction of annual abundance as a function of survival and recruitment processes:

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

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 female fecundity, year *t* – 2,
β_{t-2} – probability of fry emergence (i.e., successful egg fertilization and development), year *t* – 2,
γ_{t-2} – age-0 fish in-stream survival (fry emergence to 5 weeks post-emergence), year *t* – 2,
δ_{t-2} – age-0 fish winter survival (5 weeks post-emergence – 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 every female that participates in the spawning run will successfully spawn. The number of females in the spawning run is calculated as $f_t\widehat{N_t}$, where f_t is the proportion of females captured during the spawning run in year *t*, and $\widehat{N_t}$ 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 by female length category and 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*. Probability of fry emergence was taken from Lund's (1974) work in Elk Lake, which varied from 0.04–0.12; the mean of these values (i.e., 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 4). Maximum and mean survival rates 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 mark-recapture 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}. Mean age-0 in-stream survival was the mean of calculated rates among years and maximum age-0 in-stream survival was the highest annual value calculated.

Table 4. Demographic estimates used for testing competing models of grayling response to winter habitat, spawning habitat, non-native fish, 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 0.75 year	0.43 (0.50) 200–305; 1–3 y 1 year	--

[1]Katzman 1998; [2]Mogen 1996; [3]Paterson 2014; [4]Bowerman and Budy 2012; [5]Achord et al. 2007; [6]Al-Chokhachy and Budy 2008; [7]Dieterman and Hoxmeier 2011.

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 age-0 fish).

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 ≤10% fines is considered suitable, 11–50% fines represent linearly declining suitability, and >50% is unsuitable (Figure 3). Conversely, ≥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 ≤10% fines and ≥20% gravel and rubble.

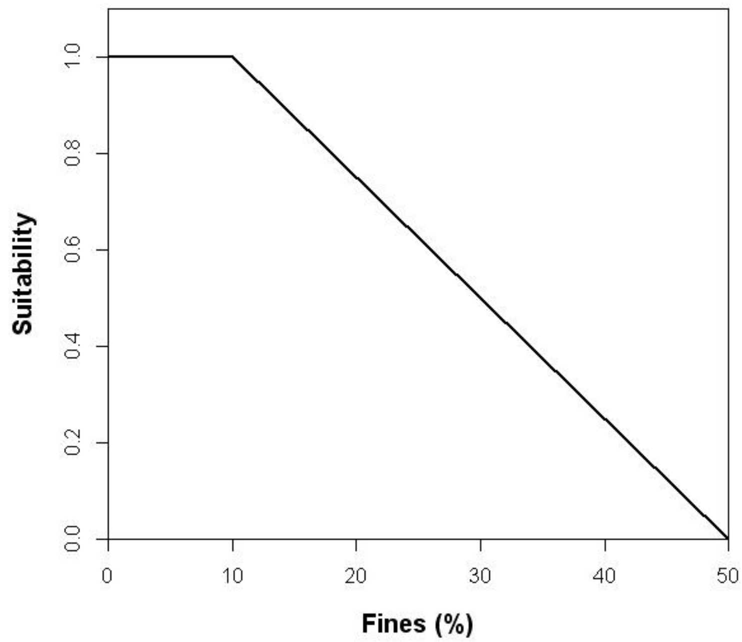

Figure 3. Predicted relationship between suitability of riverine Arctic grayling spawning habitat and percent fines in spawning areas and downstream riffles (from Hubert et al. 1985).

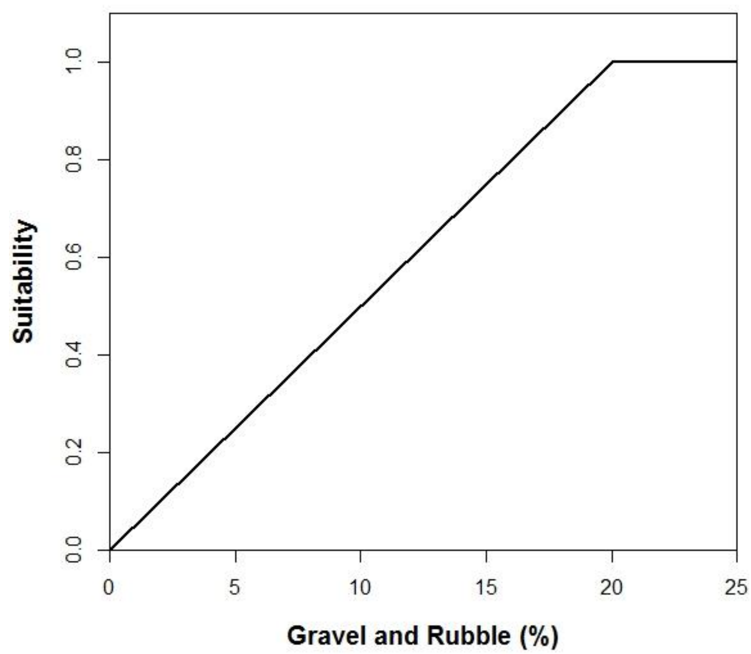

Figure 4. Predicted relationship between suitability of riverine Arctic grayling spawning habitat and percent gravel and rubble (1.0–20.0 cm) in spawning areas (from Hubert et al. 1985).

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 < 2.8 mm) and gravel and rubble (8-180 mm) in riffles will be estimated biennially using pebble count surveys. Each stream of interest was divided into reaches based on gross geomorphological characteristics or changes in land ownership. Sampling sites were randomly selected when reaches were long enough to include multiple sites (i.e., >60 channel widths) and non-randomly selected otherwise (Appendix II). At each sampling site, four separate consecutive riffles are sampled following MT DEQ TMDL Sediment Assessment Methods (Kusnierz et al. 2013). Cumulative percent fines are calculated for each sampled riffle.

Total area of suitable spawning habitat, A_t, is calculated and used in models considering 1) only habitat that has a suitability of 1.0 (i.e., ≤ 10% fines and ≥20% gravel and rubble) and 2) weighted suitability of habitat based on observed percent fines and gravel and rubble following Hubert et al. (1985; Figures 3 and 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 2).

$$\sum_{i=1}^{n} \frac{suitable\ riffle\ area\ (m^2)}{total\ site\ length\ (m)} \times reach\ length_i \qquad (2)$$

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 the probability of upstream passage is reduced then the area of available habitat is similarly reduced up to the point passage is completely prevented and the area of upstream spawning habitat is functionally zero. To correct for the effects of fragmentation, 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. 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. 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. When the cumulative probability of upstream passage reaches zero then all habitat upstream of that point will not be included in calculation of A_t.

Assuming species specific density dependence, the 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,

$$H_t = \frac{A_t}{F_t}. \tag{3}$$

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) by

$$R_t = \frac{aH_t}{b+H_t}. \tag{4}$$

The parameters *a* and *b* determine how survival of eggs and age-0 fish are related to spawning habitat conditions (Figure 5). Maximum survival is *a*, and *b* represents the value of suitable spawning habitat when survival is 50% of *a* (Hilborn and Mangel 1997).

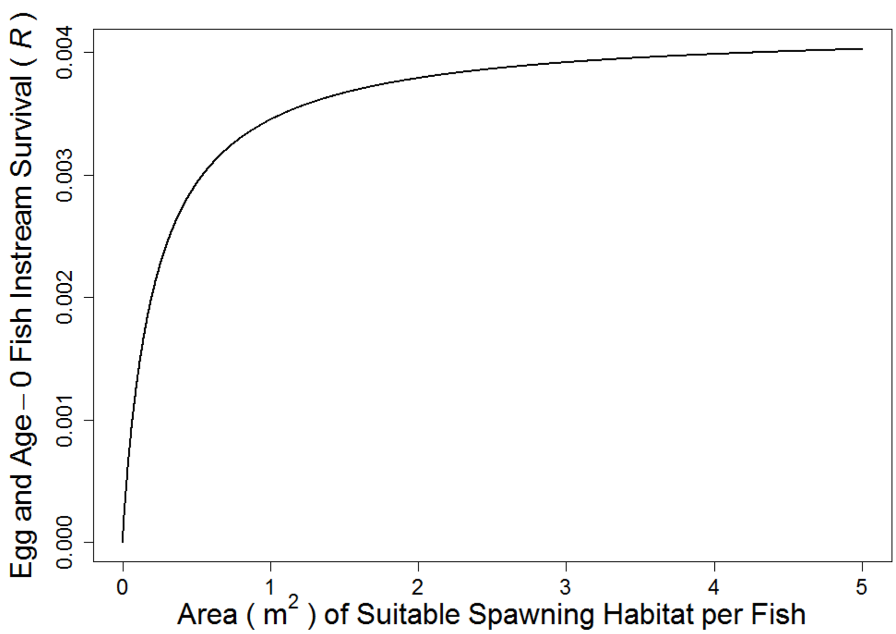

Figure 5. Hypothetical relationship between egg and age-0 fish instream survival (*R*) and the area of suitable spawning habitat per fish (m^2) in Red Rock and Elk Springs creeks based on a Holling type-II functional response (see above). Maximum survival (*a*) is 0.0042, and the value of spawning habitat when survival is 50% of *a* (*b*) is 0.217 (Warren et al. 2017).

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

$$N_{t+1} = N_t S_t + F_{t-2} \alpha_{t-2} R_{t-2} \delta_{t-2} \varepsilon_{t-1} \theta_t \quad (5)$$

$$N_{obs,t} = N_t V_t. \quad (6)$$

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., ≈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.

We used simulated data to explore the spawning habitat model. The area of available spawning habitat (ha) each year was randomly generated using a normal distribution with mean = 12 and standard deviation = 3 (*N*(12,3)). Survival of eggs and age-0 fish in-stream, R_t, and abundance of spawning grayling were subsequently calculated using the spawning habitat model and fixed demographic rates $\alpha = 8628$ eggs female^{-1}, $\delta = 0.25$, $\varepsilon = 0.44$, and $\theta = 0.74$ (see Table 1 for explanation of each parameter). Observation error for predicted grayling abundances was included, assuming $\sigma_v = 0.01$. Maximum survival of eggs and age-0 fish in-stream, *a*, was 0.10 for simulations. Two values for *b*, the relative importance suitable spawning habitat, were used in simulations (*n* = 1000) to compare scenarios where spawning habitat minimally influences R_t (*b* = 0.10; Figure 6), or was a primary driver (*b* = 15; Figure 7).

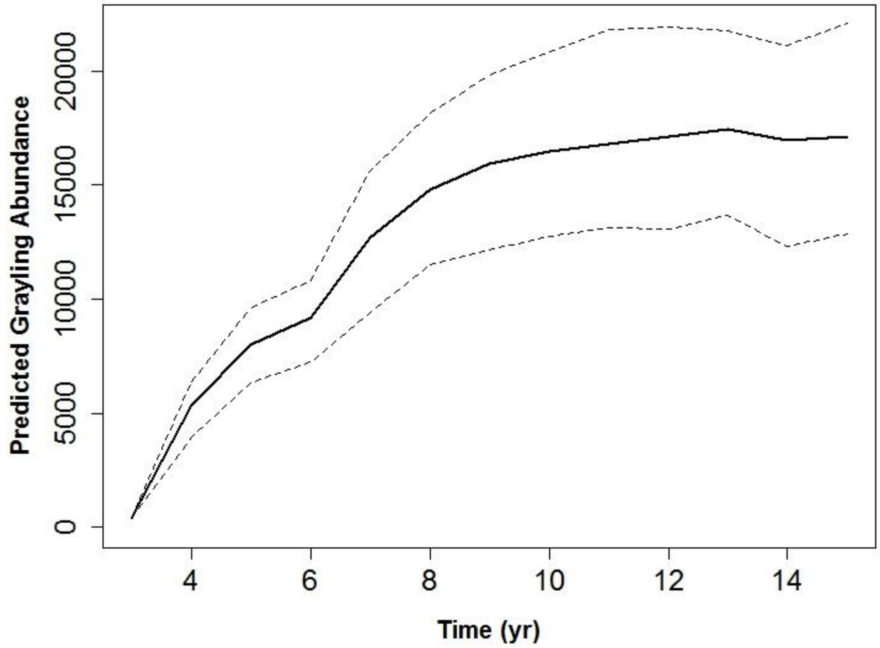

Figure 6. Simulation results (n = 1000) for spawning habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum survival of grayling eggs and age-0 fish in-stream, a, is 0.10, and b, the value of suitable spawning habitat to an individual when survival is 50% of a, is 0.1. Dotted lines represent the 90% confidence interval for the simulations.

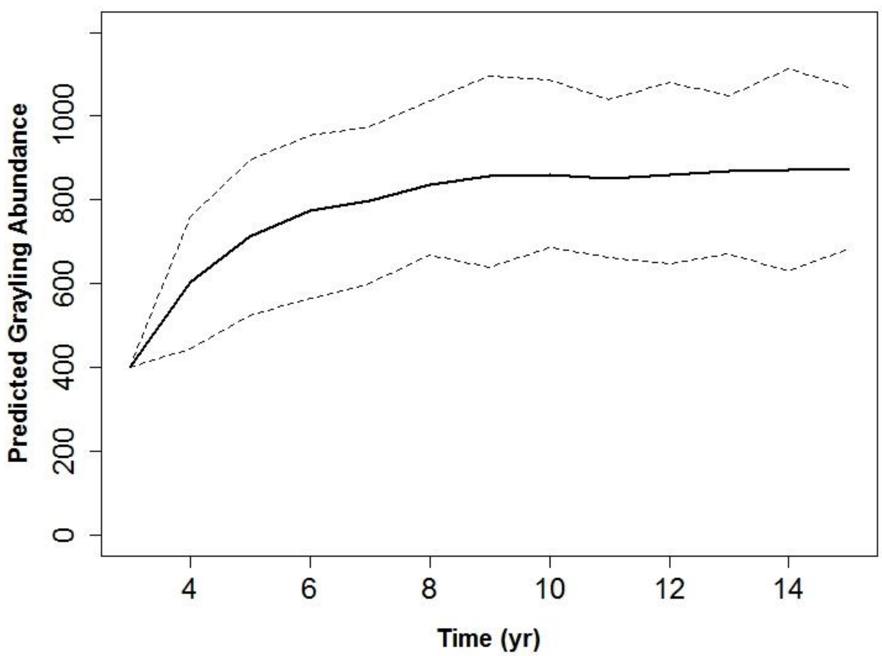

Figure 7. Simulation results (n = 1000) for spawning habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum survival of grayling eggs and age-0 fish in-stream, a, is 0.10, and b, the value of suitable spawning habitat to an individual when survival is 50% of a, is 15. Dotted lines represent the 90% confidence interval for the simulations.

Non-native Fish Model—Non-native hybrid 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 - 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. Mortality of cohort *i* from hatching to age-1, $Z_i\ (1-\gamma_{t-2}\delta_{t-2}\varepsilon_{t-1})$, was asymptotically related to the mean abundance of adult trout during the cohort's first two years (Figure 8). 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

$$Z_t = \frac{aC_t}{b+C_t}. \tag{7}$$

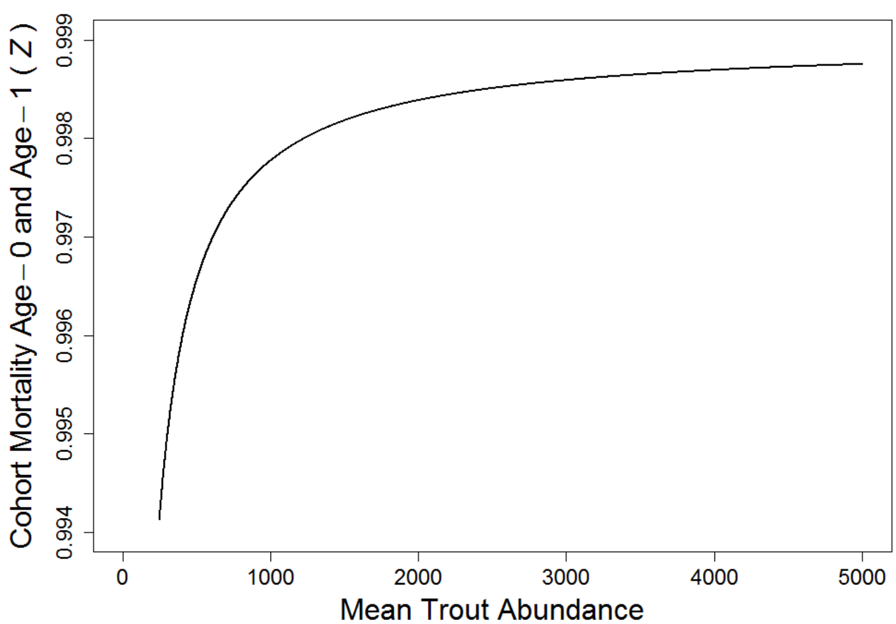

Figure 8. Hypothetical relationship between grayling cohort mortality up to age-2 (*Z*) and mean abundance of non-native trout in Upper Red Rock Lake during a cohort's first two years of life, based on a Holling type-II functional response (see above). Maximum mortality (*a*) is 0.999, and the influence of trout abundance when mortality is 50% of *a* (*b*) is 1.225 (Warren et al. 2017).

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

$$N_{t+1} = N_t S_t + F_{t-2}\alpha_{t-2}\beta_{t-2}Z_i\theta_t. \tag{8}$$

Adult trout abundance will be annually estimated during spawning in Red Rock Creek. During trout reduction efforts, abundance will be estimated as the sum of fish 1) harvested by anglers, 2) removed at the fish weir, and 3) remaining in the system. Adult trout will be 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 will be estimated from catch cards corrected for non-reporting (Appendix III). Most trout encountered at the weir will be enumerated, euthanized, and transported to area food pantries. The number of trout in the spawning run not removed at the weir or by angling will be estimated annually. Approximately 100 trout captured at the weir will be 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 will be recorded and used to estimate detection probability (i.e., capture efficiency). The number of trout encountered during electrofishing will then be corrected for imperfect detection to estimate the number of trout not removed from the system. This number will be added to the number of trout removed at the weir and by angler harvest to estimate the total number of trout in a spawning run. 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.

Estimation of adult trout abundance after the initial reduction experiment will be accomplished using two-pass electrofishing (Vincent 1971, Peterson and Cederholm 1984). Trout will be uniquely marked during late April and recaptured during the first grayling electrofishing survey in May. Angler harvest prior to the recapture survey will be summed with the abundance estimate from electrofishing to provide an annual total adult trout estimate.

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 also likely that some adult trout, 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 (Cutting et al. 2016). Removal of spawning trout reduces the abundance of 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. However, evidence for bottom-up regulation, e.g., low condition factor for either species observed during spawning, is lacking. Resultantly, this management action and associated model realistically provide a better assessment of grayling response to reduced predation than competition.

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 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 temporal and spatial extent of hypoxia in Upper Lake is influenced by several factors, including 1) lake level (i.e., depth), 2) area, 3) trophic status, 4) ice thickness, 5) and snow cover (Mathias and Barica 1980, Gangloff 1996, Fang and Stefan 1997, Fang et al. 2004). Measuring depth and dissolved oxygen levels throughout Upper Lake during winter is the most direct means to determine the extent of hypoxic conditions (Davis 2016). Models to retrospectively predict winter dissolved oxygen conditions in Upper Red Rock Lake are available (e.g., Fang and Stefan 1997, Fang et al. 2004), which would allow use of historic data.

The influence of winter habitat conditions on grayling will be quantified based on the amount of winter habitat available between January and March, the period of hypoxic conditions experienced during the winters of 1994–1995, 2015-2016, and 2016-2017 (Gangloff 1996, Warren et al. 2017). Available winter habitat is defined as the area (ha) of water in Upper Lake from January to March with ≥4 ppm dissolved oxygen and ≥ 100 cm 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.

$$W_t = \frac{A_t}{N_{w,t}} \tag{9}$$

The estimated number of spawning fish in Red Rock Creek in year t - 1 will be used as an index for $N_{w,t}$ (i.e., the prior spring's grayling spawning population will be used for the subsequent winter's $N_{w,t}$) . 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

$$P_t = \frac{aW_t}{b+W_t}. \tag{10}$$

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. Figure 9 shows a hypothetical situation where a = 1, b = 0.0185, and W_t varies from 0 to 0.5 ha fish^{-1}.

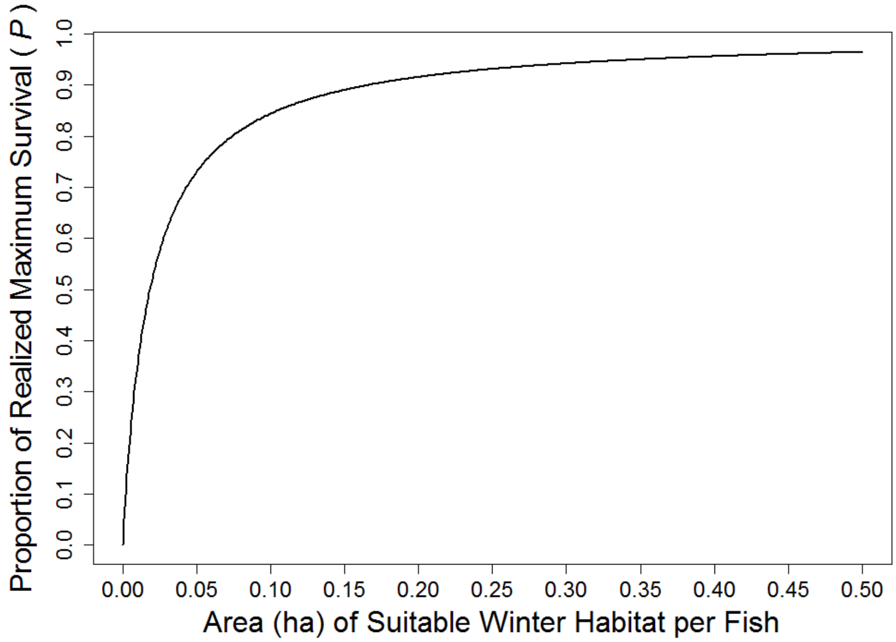

Figure 9. Hypothetical relationship between the realized proportion of maximum grayling survival (*P*) and the area of suitable winter habitat per fish in Upper Red Rock Lake based on a Holling type-II functional response (see above). Maximum proportion of realized survival (*a*) is 1, and the value of winter habitat when the realized proportion of survival is 50% of *a* (*b*) is 0.0185 (Warren et al. 2017).

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

$$N_{t+1} = N_t S_t P_t + F_{t-2} \alpha_{t-2} Y_{t-2} (\delta_{t-2} P_{t-2})(\varepsilon_{t-1} P_{t-1})(\theta_t P_t), \quad (11)$$

$$N_{obs,t} = N_t V_t. \quad (12)$$

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 deposited in year $t - 2$ surviving until its first winter, Y_{t-2}, (the combined probabilities of fry emergence (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.

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.

We used simulated data to explore the potential utility of the winter habitat model. The area of available winter habitat each year was calculated as

$$A_t = U_t mAr \tag{13}$$

where U_t was a uniformly distributed random variable between 0 and 1, *m* was the number of winter months (i.e., 4), and *Ar* was the total area of Upper Lake (1198 ha). Annual survival and population was subsequently calculated using the winter habitat model. We also included observation error for predicted grayling abundances (i.e., *V*, see above), assuming σ_v = 0.01. The relative importance of *b*, the value of suitable winter habitat to an individual when survival is 50% of *a* (Hilborn and Mangel 1997) can be easily demonstrated using the simulations. For example, we can compare simulations from two time series that differ only in the value of *b*; one with a low value (0.1; Figures 10 and 11), and a second with a greater value (2.0; Figures 12 and 13). It quickly becomes obvious that as the relative 'value' of winter habitat increases so does the influence of winter conditions on grayling population.

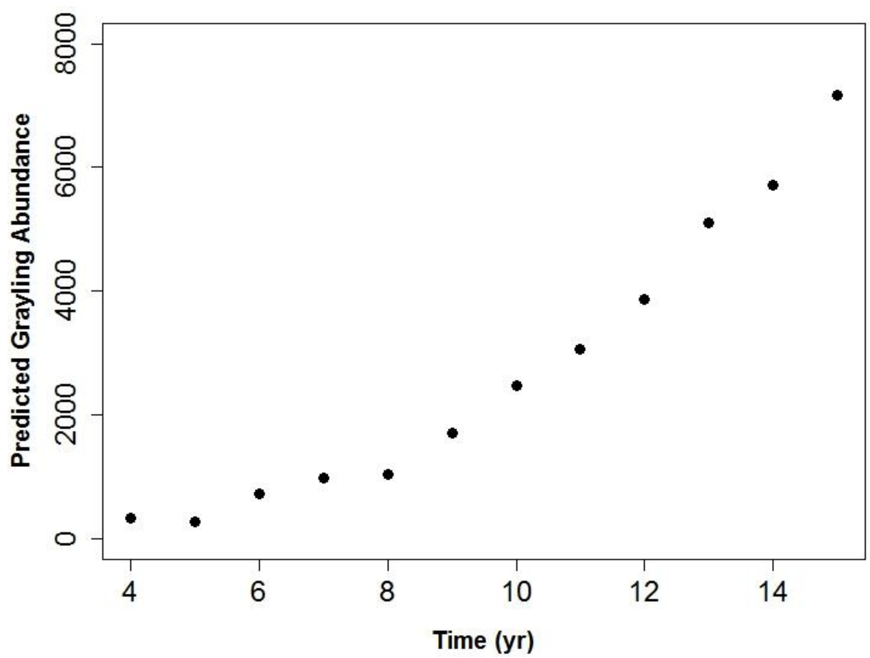

Figure 10. Simulation example for winter habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum grayling survival, *a*, is 1, and b, the value of suitable winter habitat to an individual when survival is 50% of *a*, is 0.1.

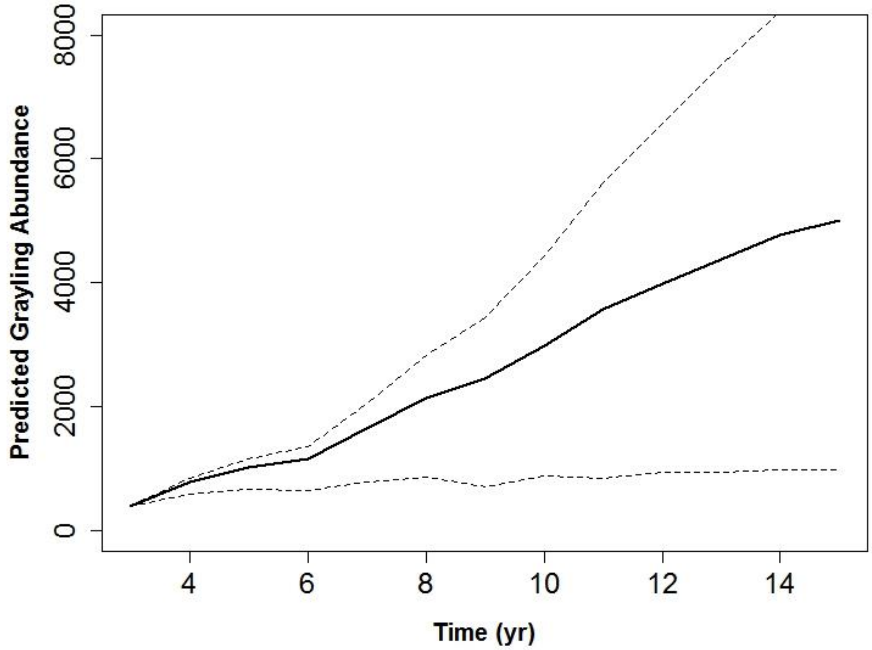

Figure 11. Simulation results (n = 1000) for winter habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum grayling survival, a, is 1, and b, the value of suitable winter habitat to an individual when survival is 50% of a, is 0.1. Dotted lines represent the 90% confidence interval for simulations.

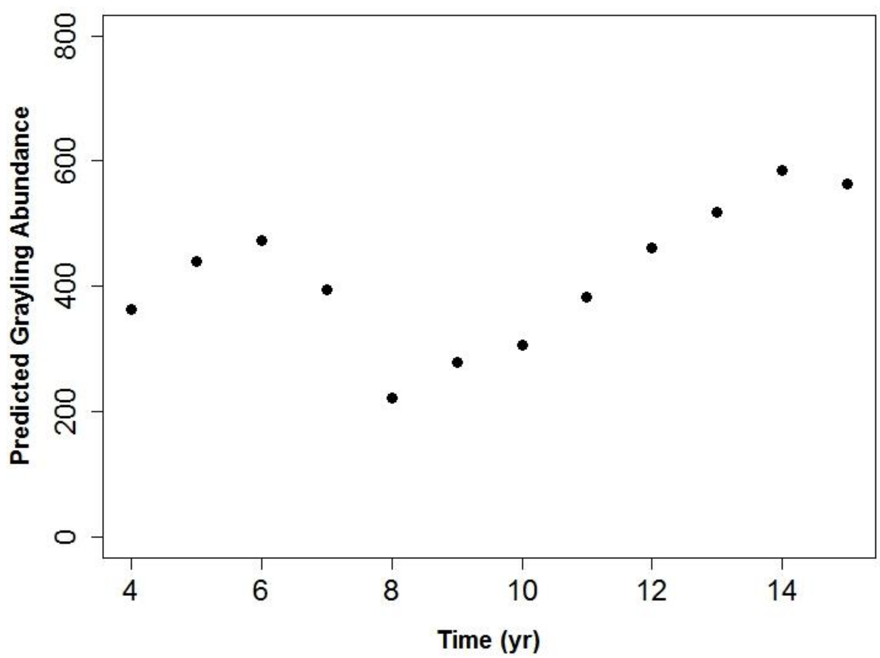

Figure 12. Simulation example for winter habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum grayling survival, a, is 1.0, and b, the value of suitable winter habitat to an individual when survival is 50% of a, is 2.0. Simulation years 6–8 demonstrate the response of grayling population to a series of winters with low habitat suitability.

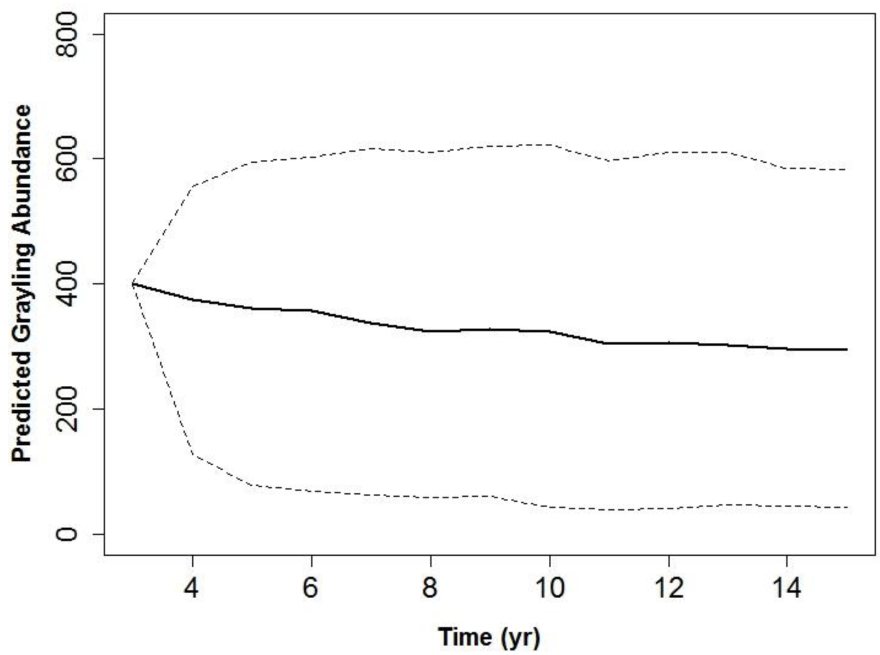

Figure 13. Simulation results (n = 1000) for winter habitat model (see text) with an initial starting population of 400 grayling projected for 15 years. Maximum grayling survival, a, is 1.0, and b, the value of suitable winter habitat to an individual when survival is 50% of a, is 2.0. Dotted lines represent the 90% confidence interval for simulations.

Instream Conditions Models—Instream conditions during egg deposition and incubation, and fry emergence and development, may be a primary driver of grayling year class strength. Influential conditions are likely a combination of density independent variables related to stream temperature and discharge. Year class strength and growth in grayling is negatively correlated with high flows or flooding and positively correlated with warm temperatures during critical periods of fry development (Clark 1992, Deegan et al. 1999). Thus, years with low, stable flows and warm temperatures would be expected to produce strong cohorts and years with high or flashy flows and cold temperatures would be expected to produce weak cohorts. We defined the "critical period," during which variability of flow and temperature will likely have the largest influence on cohort strength, to range from spawning through early fry development. Based on hypothesized effects of hydrology this period can be divided into two ontogenetic phases: 1) egg incubation and 2) early fry development. Survival of incubating eggs can be negatively affected by hydrologic scenarios that mobilize riffle substrate, thereby crushing or transporting eggs to less favorable habitats, or depositing sediment on gravels, which may smother incubating eggs. Temperature is also a potential driver during this phase of the critical period because it sets incubation duration; during cool years eggs take longer to hatch, which increases the amount of time they are susceptible to unfavorable hydrologic scenarios. Following hatching, grayling fry have limited mobility and typically aggregate in areas of low velocity along stream margins. The occurrence of hydrologic scenarios that potentially redistribute and strand grayling in off-channel habitats may reduce year class strength. Temperature similarly affects fry by driving development rate. Warmer temperatures would increase development rate, resulting in a shorter period before grayling fry are able to negotiate high or flashy flows. Thus, spring hydrology models were developed to both examine general effects of cool, high versus warm, low stream flows over the entire critical period and more specific flow and temperature metrics during each phase.

Timing and duration of the critical period will be empirically determined each year. The beginning of the critical period is defined as the day of peak spawning activity. Peak spawning will be estimated using the observed relationship between grayling spawning and stream discharge and temperature. Peak spawning is believed to occur five days after the date of peak capture in the upstream fish weir and coinciding with grayling capture in the downstream weir (M. Jaeger, unpubl. data). During years when the weir is not operated, peak spawn will be predicted based on Red Rock Creek water temperature and flow. A generalized linear model with Poisson-distributed errors will be fitted to legacy weir data, using a panel data approach to account for the longitudinal aspect of the data, and an offset of predicted grayling population. This model will be used to predict timing of peak grayling movement to Elk Lake Road in Red Rock Creek. Similar to when the weir was in operation, peak spawn will be calculated as five days after peak movement of grayling to Elk Lake Road. Duration of incubation is 188 degree days following peak spawning date, which is the upper 95% confidence interval of mean time to hatch and swim up of fry in CV remote site incubators (FWP and FWS unpubl. data). Fry emergence, i.e., *peak spawning* + 188 *degree days*, will be estimated annually using stream temperature data collected at the USGS gaging station on Red Rock Creek upstream of the Refuge. The period of early fry development is defined as the five weeks immediately following fry emergence. This duration was based on empirical observations of fry development in the CV and the period over which streamflows influenced cohort strength of other grayling populations (Clark 1992).

Four models were created to test hypotheses about effects of instream conditions on cohort strength. Variables calculated during the defined critical period include: 1) Mean daily stream discharge (*mdd*); 2), Cumulative degree days from peak emergence to 5 weeks post-emergence (*cdd*); 3) Count of days with *mdd* above bankfull discharge (*cbf*); 4) Count of days with *mdd* above 67% of bankfull discharge (*c67bf*; 95.6 cfs); and 5) a synthetic variable that quantifies temperature and discharge conditions along a single axis from cold, high flow springs to warm, low flow springs (*pca*). Stream discharge greater than 67% of bankfull was selected as it identifies a threshold above which bed load larger than sand and granules are mobilized (Mueller et al. 2005), which could disperse grayling eggs and reduce the likelihood they will hatch. Mean daily discharge (*mdd*) and bankfull discharge for Red Rock Creek were estimated using data from the USGS gauging station 06006000 located on Red Rock Creek upstream of Elk Lake Road (1994-2014), and weekly readings by Refuge staff (1994-1996) were interpolated to provide daily data. Recurrence interval was estimated as the inverse exceedance probability ($^{rank}/_{n+1}$) using ranked annual peak flow data (1994–2014 excluding 1997 when no data were available). Bankfull discharge was estimated as 142.7 cfs using a return interval of 1.5 years (Dunne and Leopold 1978), which is most representative of high elevation snowmelt dominated systems (Lawlor 2004). Temperature data will be collected annually using USGS gauging station 06006000 or thermographs deployed in Red Rock Creek.

Survival of grayling eggs and age-0 fish within the natal stream were hypothesized to reach a maximum at intermediate values of mean daily discharge, with low survival during extreme low or high water years. The Ricker function (Ricker 1954, Bolker 2008) was used to relate survival to mean daily discharge, where

$$R = a \cdot (mdd - 20) \cdot e^{-b \cdot (mdd-20)}. \tag{14}$$

The location parameter was set at a value 62.5% of the minimum mean daily discharge observed 1994–2013 (32 cfs), which results in R = 0 at 20 cfs. The instream conditions model for grayling population dynamics and observation error, linking recruitment to mean daily discharge, takes the same form as the spawning habitat model (Equations 5 and 6)

$$N_{t+1} = N_t S_t + F_{t-2}\alpha_{t-2}R_{t-2}\delta_{t-2}\varepsilon_{t-1}\theta_t \tag{15}$$

$$N_{obs,t} = N_t V_t. \tag{16}$$

Using data from 1994–2013, excluding 1997 (Figure 14), a fixed hydrology window (15 May – 31 July), and mean grayling abundance during 1994–1995 as an estimate for 1996 grayling abundance, we fit the above model to obtain estimates of *a*, *b*, and *R* (Figure 15). Estimates were 0.0035 and 0.0807 for *a* and *b*, respectively. Maximum survival of grayling eggs and fry was 0.0156, attained at a mean daily discharge of 32 cfs.

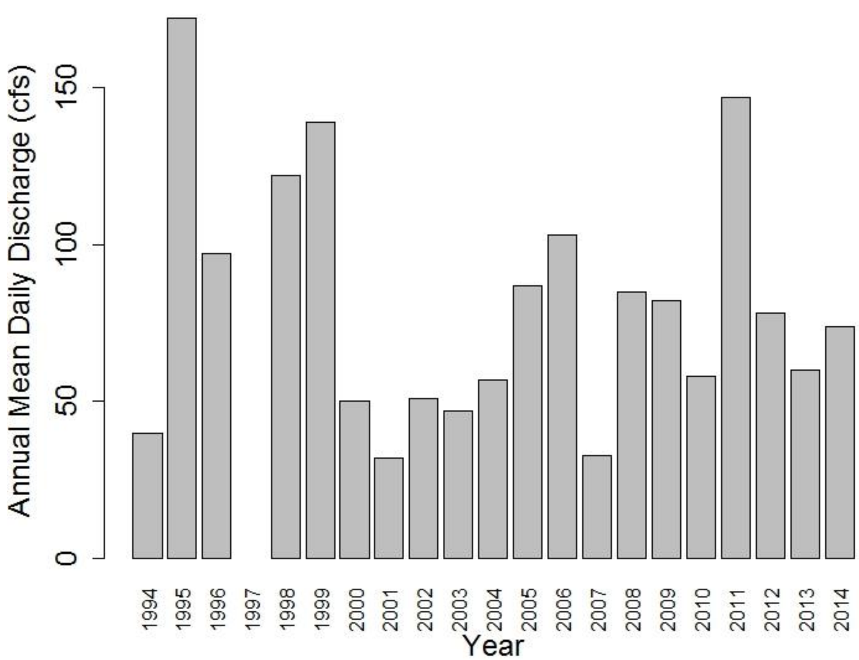

Figure 14. Annual mean daily discharge in cubic feet second^{-1} (cfs) for Red Rock Creek 15 May – 31 July, 1994–2014, as measured at the US Geological Survey gaging station 06006000 upstream of Elk Lake Road.

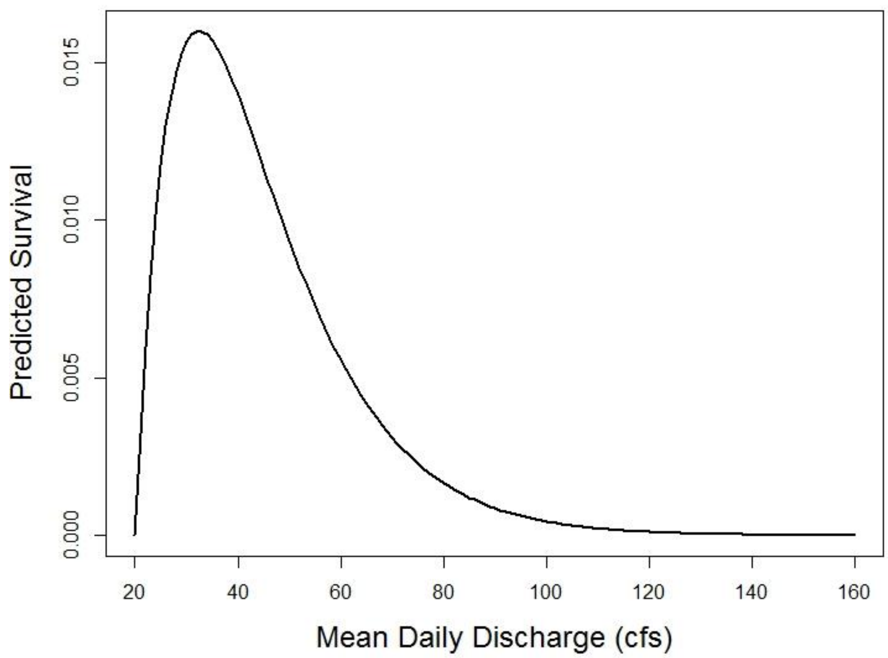

Figure 15. Predicted relationship between egg and age-0 fry survival post-emergence until reaching Upper Red Rock Lake (*R*) and Red Rock Creek mean daily discharge (cfs).

The second instream conditions model tests the hypothesis that grayling egg and age-0 in-stream survival would be most influenced by extreme runoff events. A negative exponential relationship between *R* and discharge days above bankfull discharge was predicted based on this hypothesis, where

$$R = ae^{-b\cdot(cbf)}. \tag{17}$$

We similarly fit the instream conditions model above to existing data using this hypothesized functional form of the relationship between *cbf* and *R*. Most years with high *cbf* values occurred during 1995–1999, which coincided with only a single year with an estimate of grayling abundance (Figure 16). This led to a predicted relationship between *cbf* and *R* with a steep slope, i.e., *R* quickly declined to near zero at *cbf* values > 0. Estimated values of *a* and *b* were 0.0124 and 1.627, respectively. Maximum survival was estimated as 0.0124 at 0 *cbf*, declining to a survival rate of <10 individuals per one million eggs surviving (*R* = 7.75×10-6) at 8 *cbf* (Figure 17).

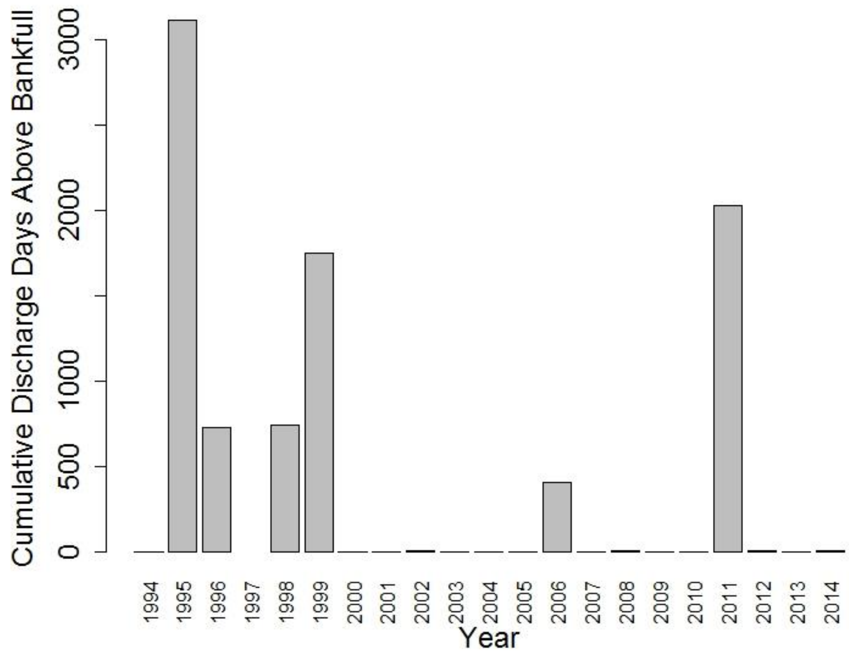

Figure 16. Cumulative discharge days above bankfull (*cbf*) for Red Rock Creek 15 May – 31 July, 1994–2014. Bankfull discharge was estimated as 141 cfs (see text above).

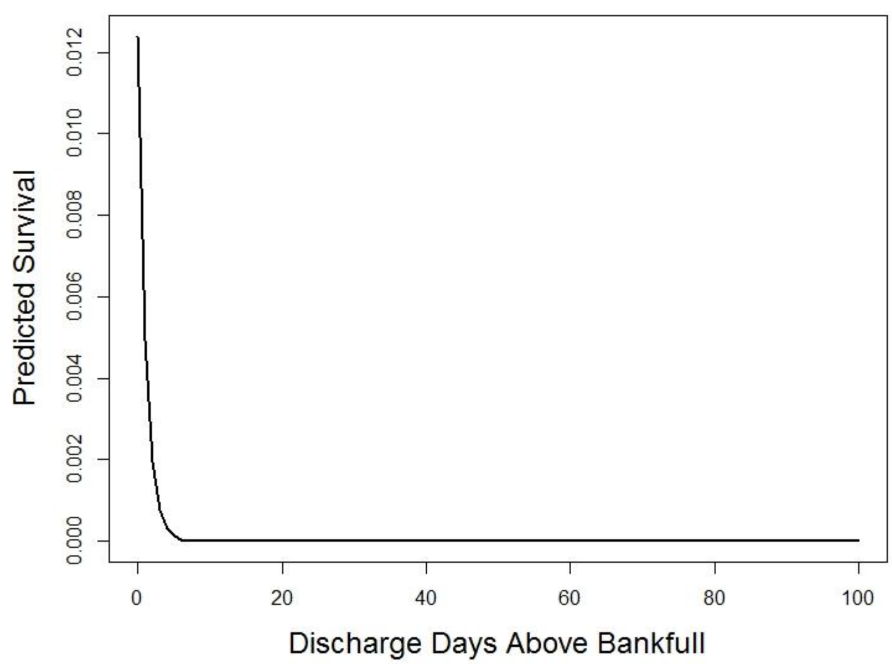

Figure 17. Predicted relationship between egg and age-0 fry survival post-emergence until reaching Upper Red Rock Lake (*R*) and Red Rock Creek discharge days above bankfull (*cbf*).

The third instream conditions model tests the hypothesis that grayling egg and age-0 in-stream survival is most influenced by cumulative degree days. The relationship between survival and cumulative degree days was hypothesized to be linear across the range of values expected to be experienced, where

$$R = a \cdot cdd + b. \tag{18}$$

The stream temperature time series available for fitting the *cdd* model was limited to seven years, most of which did not coincide with available estimates of grayling abundance (Figure 18). This precluded fitting this model to existing data at this time. Additional legacy temperature data may be available and if located may allow model fitting with the existing time series of grayling abundances.

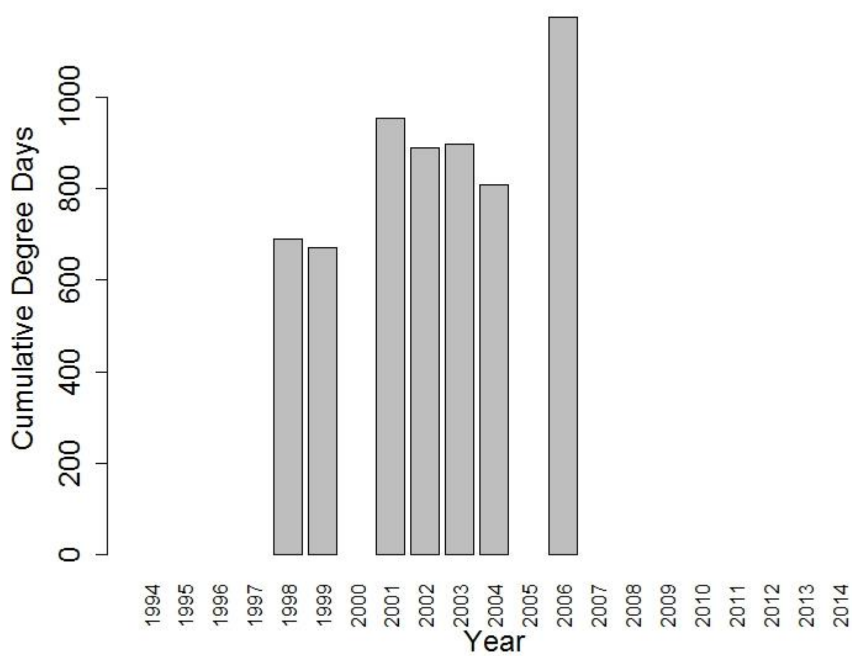

Figure 18. Cumulative degree days for Red Rock Creek 15 May – 31 July, 1994–2014.

The final instream conditions model incorporates a synthetic variable that combines stream discharge and temperature. This allows us to test the hypothesis that grayling cohort strength is maximal during warm, dry springs when grayling development rates are high and the likelihood of egg sedimentation or fry stranding events low. We combined mean daily water temperature, mean daily discharge, and whether mean daily discharge exceeded 67% of bankfull (i.e., 0 or 1). The latter two variables are highly correlated ($\rho = 0.806$). Similar to the mean daily discharge model, we chose the Ricker function (Ricker 1954, Bolker 2008) to relate survival to the synthetic variable, where

$$R = a \cdot (pca + 1) \cdot e^{-b \cdot (pca+1)}. \tag{19}$$

The location parameter was set at the 15th percentile value representing cold, high flow springs based on 1994–2014 data, which results in $R = 0$ at $pca = -1$.

Null Population Model—A discrete-time logistic growth equation was included as a 'null' model for grayling for the purpose of comparison to more highly parameterized hypothesis-specific models. If the null model is able to best predict grayling abundance it indicates fundamental flaws in either the structure or underlying hypotheses of the other candidate models. The null model was based on abundance estimates beginning with 1994, where

$$N_{t+1} = N_t + rN_t\left(1 - \frac{N_t}{K}\right). \tag{20}$$

In this equation, N_t is the population at time *t*, *r* is the intrinsic rate of population growth, and *K* is carrying capacity. The model is deterministic, i.e., no stochastic variation is included. There are two primary sources of variation that can be considered, process error and observation error. Process error is the result of uncertainty in how a population varies in space and time due to birth and death processes. Importantly, process error propagates through time in time-series data, with gaps in that data (i.e., missing years) significantly increasing the difficulty in estimating process error (Hilborn and Mangel 1997). Observation error is variation due to imperfect enumeration of the population of interest, i.e., our inability to accurately estimate abundance. Observation error does not propagate through time. If we assume observation error is log-normally distributed (commonly done for the logistic equation), observation error is

$$N_{obs,t} = N_t V, \tag{21}$$

$$V = exp\left(Z\sigma_v - \frac{\sigma_v^2}{2}\right), \tag{22}$$

where *Z* is normally distributed with a mean of zero and a standard deviation of 1, and the standard deviation of the observation uncertainty is σ_V (Hilborn and Mangel 1997). To calculate maximum-likelihood estimates of *r* and *K* assuming observation error only, we first calculate the deviation between the observed and true (predicted from the deterministic logistic growth equation) values of population size. This is accomplished by substituting equation 3 into equation 2 and solving for *Z* ($\sigma_v = 1$). The deviation in year *t*, $D_{t,}$ is the annual realization of the random variable *Z*, so substituting D_t for *Z* after solving for Z gives us

$$D_t = \log(N_{obs,t}) - \log(N_t) + \frac{\sigma_{V^2}}{2}. \tag{23}$$

We then find the most likely set of parameter values, *r* and *K*, given our data, as the set of values that maximize the summed log-likelihoods of D_t.

The logistic growth model was fit using grayling count data from 1994–2013 corrected for imperfect detection (Paterson 2013). Initial starting value, N_0, was set equal to the 1994 estimate (i.e., 407 grayling). Estimated grayling population growth rate, *r*, and carrying capacity, *K*, during 1994–2013 was 0.20 and 1366, respectively (Figure 19).

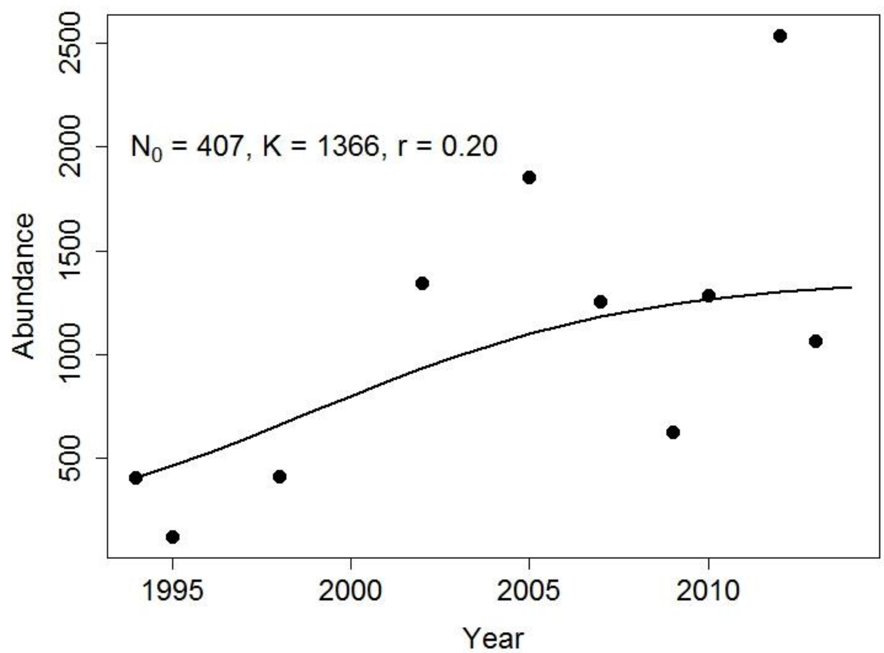

Figure 19. Discrete-time logistic population growth for Arctic grayling, 1994–2013. Data are from the Red Rock Creek fish weir operated near the Elk Lake Road crossing. Data are bias corrected abundance estimates (Paterson 2013). Starting values for *r* and *K* were 0.3 and 700, respectively.

Model comparison—Model selection uncertainty is quantified using model weights, which are normalized (i.e., sum to 1) relative model likelihoods given the data. Model weights will be calculated annually 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, $p_{i,t+1}$, 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 ($\sum_{j=1}^{n} p_t(model_j)P(response_{t+1}|model_j)$),

$$p_{i,t+1} = (model_i|response_{t+1}) = \frac{p_t(model_i)P(response_{t+1}|model_i)}{\sum_{j=1}^{n} p_t(model_j)P(response_{t+1}|model_j)} \quad (24)$$

AMP ITERATIVE PHASE

The iterative phase of the AMP guides annual selection of management actions in response to predicted grayling abundance relative to population objectives. To make our adaptive decision making proactive rather than reactive, predicted grayling abundance (rather than contemporarily observed abundance) will be used as the trigger to initiate management action(s). Taking this approach will allow us to forecast when grayling abundances are likely to decline below management objectives and intervene with actions most likely to prevent that occurrence. Following completion of the management by experiment phase (i.e., once the scenarios described in Table 3 have been satisfied) we will select whether to implement a management action in a given year based on predicted abundance of spawning grayling. A model-weighted prediction of grayling abundance will be made each January after the first survey of winter habitat using the spawning habitat, non-native fish, and winter habitat model weights (ω) and predicted abundances ($\widehat{N}$)(eqn. 25).

$$\sum_{i=1}^{j} \omega_j \widehat{N}_j - \begin{cases} \geq 1000 - No\ action \\ < 1000 - Management\ action \end{cases}. \qquad (25)$$

If predicted abundance is lower than the objective of 1000 grayling in the spawning population, a management action(s) would be triggered. Management action(s) will be selected that either 1) prevent the population from declining below our trigger threshold (e.g., mitigate winter habitat), or 2) most quickly restore the population to above the threshold (e.g., reduce trout abundance or increase availability of spawning habitat). For example, if model weights were 0.5, 0.25, and 0.25, and model predictions were 1000, 500, and 100 fish, the model-weighted population estimate would be $0.5 \times 1000 + 0.25 \times 500 + 0.25 \times 100 = 650$ grayling. Because this value is below objective, a management action would be triggered. The recommended action would be based on model-weighted predicted grayling response to a finite set of management alternatives, including trout reduction and increased availability of suitable spawning habitat. No management action has been identified for mitigating winter habitat.

A simple decision table will be used to evaluate the consequences of each potential management action (Table 5). Alternative hypotheses (H_j) are provided in the first row, with model weights (ω_j) (i.e., relative support for the hypothesis conditional on the data and model set) in the second row. Alternative management actions (A_i) are provided in the first column, model-weighted population predictions are in the last column. Consequences of an alternative action A_i assuming hypothesis H_j is true are given in the (*i, j*) cells in terms of grayling population. For example, the first row of consequences predicts grayling population if 25 ha of winter habitat were maintained in Upper Lake when winter habitat availability is low (10 ha) and no actions were taken to influence non-native trout abundance or spawning habitat. This is carried through for the other actions, i.e., substituting a hypothesis-specific management action for current conditions, until each action has a model-weighted grayling abundance projection. Model-weighted population projections are all made over a three-year period to allow comparison of management actions that have different temporal scales of grayling response. For example, if a January survey of winter conditions in Upper Lake indicate winter habitat may be limiting, an immediate mitigating action (e.g., aeration) would be predicted to increase grayling abundance in the subsequent spawning run. Reducing trout abundance or increasing spawning habitat would be predicted to increase the number of recruits to the population three years after the action (e.g., reducing trout in 2017 would be predicted to increase the number of recruits in 2020). All predictions assume winter habitat during intervening years is not limiting.

In the example decision table below (Table 5), the projected population is below objective, triggering a management action. The most effective management action is that which increases predicted grayling abundance the most. The scenario provided in Table 5 uses 2014–2016 fish abundance and spawning habitat data, and the first survey of winter habitat conditions for the winter of 2017. The extent of suitable winter habitat in January 2017 was ≈10 ha, and the predicted population response indicated mitigating winter conditions (i.e., ensuring >25 ha of suitable winter habitat) would have been more beneficial at that time then either reducing trout or increasing spawning habitat during the subsequent spring/summer. No management action would be triggered if all of the predictions are above objective.

How the 1000 fish objective relates to initiation of management intervention can be illustrated by reviewing historical population estimates (Figure 20). For example, the ≈400 adult grayling in 1994 would have triggered implementation of management action(s) predicted to recover the population to >1000 fish. Once abundance increased to >1000 fish in 2002, management intervention would have ceased until 2016 when abundances declined to ≈200 fish and management intervention would have been triggered.

Table 5. A simple decision table to evaluate consequences of management actions for achieving the upper Centennial Valley Arctic grayling population objective of 1000 spawning fish. Predicted abundance ($\widehat{N}$) from each combination of management action and model is used to estimate a model-weighted grayling abundance to determine the best management action given the current state of knowledge. Model weights from the CVAGMP 2017 Spring Update are provided parenthetically. Data used to create the table are described above.

	Hypotheses (H_j)			
Action (A_i)	Winter Habitat (0.582)	Spawning Habitat (0.302)	Non-native Fish (0.112)	$\sum_{i=1}^{j} \omega_j \widehat{N}_j$
Maintain 25 ha winter habitat	163	500	906	350
Increase spawning habitat 25%	115	536	906	292
Reduce trout 25%	115	500	1006	300

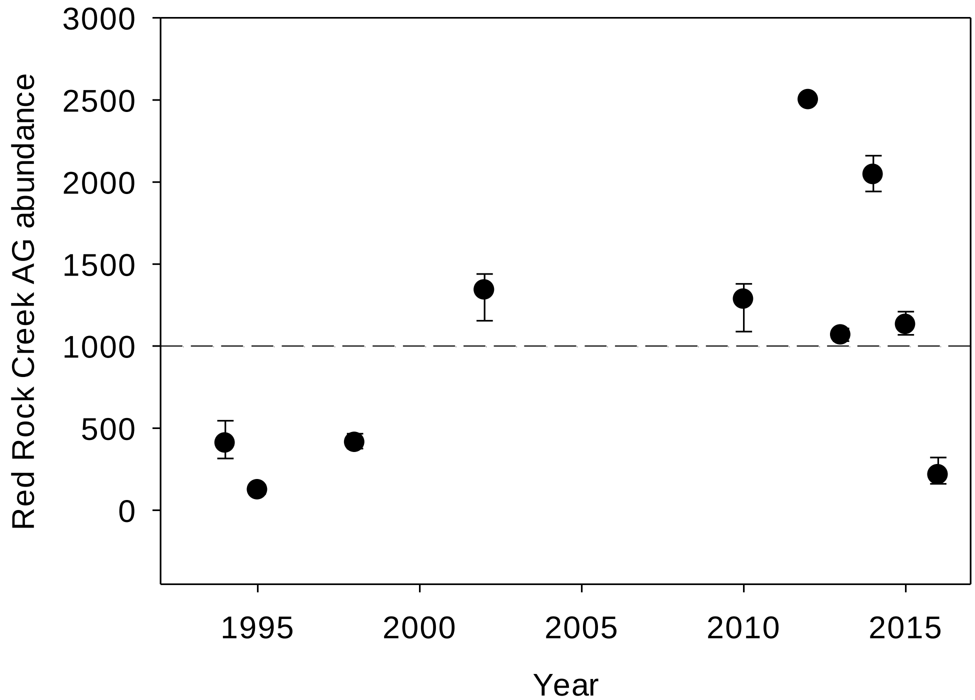

Figure 20. Abundance of spawning Arctic grayling in Red Rock Creek.

Data needed to make predictions from the spawning habitat and non-native fish models will be collected by the prior September. Winter habitat conditions in Upper Lake tend to stabilize by late December, and surveying in late December or early January will enable prediction of grayling abundance with the winter model for the following spring (Davis 2016).

LITERATURE CITED

Achord, S., R. Zabel, and B. Sanford. 2007. Migration timing, growth, and estimated parr-to-smolt survival rates of wild Snake River spring-summer chinook salmon from the Salmon River Basin, Idaho, to the lower Snake River. Transactions of the American Fisheries Society 136:142-154.

Al-Chokhachy, R. and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722.

Allen, C. R., J. J. Fontaine, K. L. Pope, and A. S. Garmestani. 2011. Adaptive management for a turbulent future. Journal of Environmental Management 92:1339-1345.

Barica, J., and J. A. Mathias. 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. Journal of the Fisheries Research Board of Canada 39:980-986.

Bishop, F. G. 1971. Observations on spawning habits and fecundity of the Arctic grayling. Progressive Fish-Culturist 33:12-19.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey.

Boltz. G. 2000. Fisheries investigations on the Red Rock Lakes National Wildlife Refuge, Montana. U.S. Fish and Wildlife Service, Bozeman, Montana.

Bowerman, T. and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for bull trout. North American Journal of Fisheries Management 32:1123-1136.

Boyd, J. 2014. Arctic grayling SSA expert elicitation workshop. U.S. Fish and Wildlife Service, Helena, Montana.

Brower, J. V. 1896. The Missouri River. Pioneer Press, St. Paul, Minnesota.

Centennial Valley Historical Society. 2006. Centennial Valley: a journey through time 1820–1930. Vol. 1. Artcraft Printers, Butte, Montana.

Clark, R. A. 1992. Influence of stream flows and stock size on recruitment of Arctic grayling (*Thymallus arcticus*) in the Chena River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 49:1027-1034.

Clary, W. P., and B. F. Webster. 1989. Managing grazing of riparian areas in the Intermountain Region. U.S. Department of Agriculture, Forest Service. General Technical Report INT-263.

Crecco, V.A., and T.F. Savoy. 1984. Effect in fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 41:1216-1223.

Cutting, K. A., W. F. Cross, M. L. Anderson, and E. G. Reese. 2016. Seasonal change in trophic niche of ddfluvial Arctic grayling (*Thymallus arcticus*) and coexisting fishes in a high-elevation lake system. PLOS ONE 11:e0156187.

Davis, M. N. 2016. Winter survival and habitat as limiting factors for Arctic grayling at Red Rock Lakes National Wildlife Refuge. Thesis, Montana State University, Bozeman, Montana.

Deeds, J. F. and W. N. White. 1926. Water power and irrigation in the Jefferson River basin, Montana. U.S. Geologic Survey water-supply paper No. 580:41-116.

Deegan, L.A., H. E. Golden, C. J. Harvey, and B. J. Peterson. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. Transactions of the American Fisheries Society 128:1163-1175.

Dieterman, D.J. and R.J.H. Hoxmeier. 2011. Demography of juvenile and adult brown trout in streams of southeastern Minnesota. Transactions of the American Fisheries Society 140:1642-1656.

Dunne, T., and L. B. Leopold. 1978. Water in environmental Planning. W. H. Freeman and Co., San Francisco, California.

Fang, X., and H. G. Stefan. 1997. Simulated climate change effects on dissolved oxygen characteristics in ice-covered lakes. Ecological Modelling 103:209-229.

Fang, X., H. G. Stefan, J. G. Eaton, J. H. McCormick, and S. R. Alam. 2004. Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios: Part 1. Cool-water fish in the contiguous US. Ecological Modelling 172:13-37.

Feldmeth, C. R., and C. H. Eriksen. 1978. A hypothesis to explain the distribution of native trout in a drainage of Montana's Big Hole River. Verhandlungen Internationale Vereinigung fur Theoretische und Ungewandte Limnologie 20.

Fischman, R. L., and J. B. Ruhl. 2016. Judging adaptive management practices of U.S. agencies. Conservation Biology 30:268-275.

Gangloff, M. M. 1996. Winter habitat and distribution of Arctic grayling in Upper Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana. Thesis, Montana State University, Bozeman, Montana.

Gillin, G. 2001. Literature Review of Fisheries Information for the Centennial Valley, Montana. Unpublished report, U.S. Fish and Wildlife Service, Dillon, Montana.

Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecological Monographs 15:343-392.

Haugen, T. O., and L. A. Vøllestad. 2001. A century of life-history evolution in grayling. Genetica 112:475-491.

Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Monographs in Population Biology 28. Princeton University Press, Princeton, New Jersey.

Hubert, W. A., R. S. Helzner, L. A. Lee, and P. C. Nelson. 1985. Habitat suitability index models and instream flow suitability curves: Arctic grayling riverine populations. Biological Report 82, Division of Biological Services, U.S. Fish and Wildlife Service, Washington D.C.

Kaeding, L. R., and G. D. Boltz. 1999. A study of Arctic grayling and their stream habitat in support of reserved water right applications, Red Rock Lakes National Wildlife Refuge, Montana. Unpublished Report, U.S. Fish and Wildlife Service, Bozeman, Montana.

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

Katzman, L. M. 1998. Effects of predation on status of Arctic grayling at Red Rock Lakes National Wildlife Refuge, Montana. Thesis, Montana State University, Bozeman, Montana.

Kendall, W. L. 2001. Using models to facilitate complex decisions. Pages 147-170 *in* Modeling in natural resource management: development, interpretation, and application. *eds.*T. M. Shenk and A. B. Franklin. Island Press, Washington D.C.

Kusnierz, P., A. Welch, and D. Kron. 2013. The Montana Department of Environmental Quality sediment assessment method: considerations, physical and biological parameters, and decision making. Helena, Montana: Montana Dept. of Environmental Quality.

Lawlor, S. M. 2004. Determination of channel-morphology characteristics, bankfull discharge, and various design-peak discharges in western Montana. Scientific Investigations Report 2004-5264, U.S. Geological Survey, Reston, Virginia.

Lund, J. A. 1974. The reproduction of salmonids in the inlets of Elk Lake, Montana. Thesis, Montana State University, Bozeman, Montana.

MAGWG (Montana Arctic Grayling Working Group). In Press. Montana Arctic grayling conservation plan. Bozeman, Montana.

Macnab, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin 11:397-401.

Mathias, J. A., and J. Barica. 1980. Factors Controlling Oxygen Depletion in Ice-Covered Lakes. Canadian Journal of Fisheries and Aquatic Sciences 37:185-194.

Metcalfe, R.A., R.W. Mackereth, B. Grantham N. Jones, R.S. Pyrce, T. Haxton, J.J. Luce, and R. Stainton. 2013. Aquatic Ecosystem Assessments for Rivers. Science and Research Branch, Ministry of Natural Resources, Peterborough, Ontario. 210 pp.

MCA (Montana Code Annotated) 2000. United States Fish and Wildlife Service Red Rock Lakes-Montana Compact ratified. 85-20-801, Helena, Montana.

Mills, C. A. and Mann, R. H. K. 1985. Environmentally-induced fluctuations in year-class strength and their implications for management. Journal of Fish Biology 27:209-226.

Mogen, J. T. 1996. Status and biology of the spawning population of Red Rock Lakes Arctic grayling. Thesis, Montana State University, Bozeman, Montana.

MTFWP (Montana Fish, Wildlife & Parks). 1989. Application for reservations of water in the Missouri River basin above Fort Peck Dam, Volume 2, Reservation requests for waters above Canyon Ferry Dam. Unpublished Report, Montana Fish, Wildlife and Parks, Helena, Montana.

Mueller, E.R., J. Pitlick, and J.M. Nelson. 2005. Variation in the reference shields stress for bed load transport in gravel-bed streams and river. Water Resources Research, 41, W04006, doi:10.1029/2004WR003692.

Mumma, S. A. 2010. A 20,000-yr-old record of vegetation and climate from Lower Red Rock Lake, Centennial Valley, southwestern Montana. Thesis. Montana State University, Bozeman, Montana.

Murphy, D. D., and P. S. Weiland. 2011. The route to best science in implementation of the Endangered Species Act's consultation mandate: the benefits of structured effects analysis. Environmental Management 47:161-172.

Myers, L. 1977. Interagency fisheries habitat inventory for the Centennial Valley. Unpublished report. Bureau of Land Management, Dillon, Montana.

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

Nunn, A. D., Cowx, I. G. , Frear, P. A. and Harvey, J. P. 2003. Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? Freshwater Biology 48:579-588.

Oswald, R. A., S. Hochhalter, L. Rosenthal. 2008. Southwest Montana native fish research and conservation April 1, 2007–December 31, 2007. Montana Fish, Wildlife & Parks State Wildlife Grant Project Performance Report T-26-3, Helena, Montana.

Paterson, T. 2013. Estimation of the abundance and apparent survival of spawning Arctic grayling in Red Rock Creek; Red Rock Lakes National Wildlife Refuge. Thesis, Montana State University, Bozeman, Montana.

Peterson, N. P. and C. J. Cederholm. 1984. A comparison of the removal and mark-recapture methods of population estimation for juvenile coho salmon in a small stream. North American Journal of Fish Management 4:99-102.

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

Randall, L. C. 1978. Red Rock Lakes National Wildlife Refuge: an aquatic history 1899–1977. Unpublished report. U.S. Fish and Wildlife Service, Kalispell, Montana.

Ricker, W. E. 1954. Stock and Recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.

Shepard, B. B., and R. A. Oswald. 1989. Timing, location, and population characteristics of spawning Montana Arctic grayling (*Thymallus arcticus montanus* [Milner]) in the Big Hole River drainage, 1988. Unpublished report. Montana Fish, Wildlife and Parks, Dillon, Montana.

Skates, R. C. 1985. Red Rock Lakes National Wildlife Refuge Fishery Management Report. U.S. Fish and Wildlife Service, Kalispell, MT.

Sonderegger, J. L. 1981. Geology and geothermal resources of the eastern Centennial Valley. Montana Geological Society, Field and Conference Symposium Guidebook to Southwest Montana.

Unthank, A. 1989. Historical Overview of Red Rock Lakes National Wildlife Refuge Grayling Fisheries. U.S Fish and Wildlife Service, Lima, MT.

USFWS (U.S. Fish and Wildlife Service). 2009. Comprehensive Conservation Plan Red Rock Lakes National Wildlife Refuge. Lima, MT.

USFWS (U.S. Fish and Wildlife Service). 2014. Endangered and threatened wildlife and plants; revised 12-month finding on a petition to list the upper Missouri River distinct population segment of Arctic grayling as an endangered or threatened species; proposed rule. Federal Register, Vol. 79, No 161, 49384-49422.

Vincent, R. E. 1962. Biogeographical and ecological factors contributing to the decline of the Arctic grayling, *Thymallus arcticus* Pallus, in Michigan and Montana. Dissertation, University of Michigan, Ann Arbor, MI.

Vincent, R. 1971. River electrofishing and fish population estimates. The Progressive Fish-Culturist 33:163-169.

Walters, C. 1986. Adaptive management of renewable resources. Blackburn Press, Caldwell, New Jersey.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060-2068.

Warren, D. R., A. G. Ernst, and B. P. Baldigo. 2009. Influence of spring floods on year-class strength of fall- and spring-spawning salmonids in Catskill Mountain Streams. Transactions of the American Fisheries Society 138:200-210.

Warren, J. M., M. Jaeger, A. Gilham, K. Cutting, L. Bateman, T. Paterson, and M. Duncan. 2017. Centennial Valley Arctic Grayling Adaptive Management Project Annual Report, 2016. U.S. Fish and Wildlife Service and Montana Fish Wildlife and Parks, Lima, MT.

West, R. L., M. W. Smith, W. E. Barber, J. B. Reynolds, and H. Hop. 1992. Autumn migration and overwintering of Arctic grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. Transactions of the American Fisheries Society 121:709-715.

Williams, B. K. 2011. Passive and active adaptive management: approaches and an example. Journal of Environmental Management 92:1371-1378.

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2009. Adaptive Management: The U.S. Department of the Interior Technical Guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.

APPENDIX I

DATA STRUCTURE

Fish Population Data—Data beginning with 1962 fish weir counts are imported as dataframe 'fish.all.years'. The early data are only used for graphically displaying counts through time. Data are subset based on year starting with 1994 as dataframe 'grayling'. These are the data used in fitting models for the AMP using the following variables:

<u>Grayling abundance (grayling$grayling)</u>. Grayling data after 1993 are corrected for detection probability. Estimates for 2005, 2007, 2009 were calculated as the number of grayling captured during electrofishing divided by the mean efficiency rate (0.075).

<u>Cutthroat trout abundance (grayling$cutt)</u>. Cutthroat data are a combination of the number of fish 1) harvested by anglers, 2) removed at the fish weir, and 3) remaining in the system.

<u>Grayling apparent survival (ϕ, grayling$phi)</u>. Estimated annual adult survival from a Bayesian random effects model fitted to 2010–current-year data. Estimates prior to that (i.e., 1994–1996) are from Paterson (2013). Survival interval is from trap session prior year to trap session current year (i.e., survival for May 2010 to May 2011 is in the 2011 record). We will estimate phi annually within the workflow process once full implementation is achieved.

<u>Age-3 grayling (grayling$p3YO)</u>. Percent of Arctic grayling captured electrofishing that are age-3 fish (i.e., new recruits). Age-3 fish were those between 12.9" (329 mm) and 14.9" (379 mm) based on Mogen (1996). Additional age-length data are being collected through scale-reading efforts currently underway. This information will be added to the existing workflow process once it is finalized.

<u>Mean grayling female length (grayling$mn.fl)</u>. Mean annual female length (cm) based on individuals captured on the MFWP's Red Rock Creek electrofishing trend section and/or captured at the fish weir.

<u>Cutthroat trout removed (grayling$cutt.rm)</u>. Estimate of cutthroat trout removed via the fish weir and angler harvest.

Variables calculated and appended to the grayling dataframe include:

<u>Time (grayling$time)</u>. Time variable (in years) with 1994 as year 1.

<u>Grayling recruits (grayling$est3YO)</u>. Estimated number of recruits for a given year calculated by multiplying proportion age-3 grayling observed during electrofishing on the Red Rock Creek trend section by estimated abundance corrected for detection probability.

<u>Grayling females *t* -3 (grayling$ft3)</u>. Estimated number of females three years prior for a given year calculated as half of the estimated abundance corrected for detection probability.

<u>Mean grayling female length *t* -3 (grayling$mn.flt3)</u>. Mean female length three years prior for a given year.

Abiotic and Habitat Data—Variables describing spawning habitat, winter habitat, and spring hydrology are calculated in the workflow process and added to the grayling dataframe. These include:

<u>Mean daily stream discharge (grayling$mdd).</u> Annual critical period mean daily stream discharge for Red Rock Creek estimated based on USGS gaging station (06006000) daily discharge data, 1997 to current. Estimates from 1994–1996 were from manual flow readings available in Refuge files.

Days above bankfull (grayling$cbf). Annual critical period count of days with mean daily stream discharge ≥ bankfull (142.7 cfs).

Days above 67% bankfull (grayling$c67bf). Annual critical period count of days with mean daily stream discharge ≥ 67% bankfull (95.6 cfs).

Discharge data to calculate the above variables need to be downloaded annually for 1 April – 1 September from http://nwis.waterdata.usgs.gov/nwis/dv?cb_00060=on&format=html&site_no=06006000&referred_module=sw&period=&begin_date=2013-05-15&end_date=2013-07-31. Annual updates need to be appended to 'Red_Rock_Cr_discharge_data.csv' located in the project's AnnualReport folder.

Cumulative degree days (grayling$cdd). Annual cumulative degree days from peak grayling emergence to 5 weeks post-emergence. Red Rock Creek temperature data were collected by the USFWS Management Assistance Office via Onset HOBO dataloggers starting in 1998 (excluding part of 2001, and 2006, 2007, 2009, and 2014). Data from other CV streams are variously available. These data are housed in a database maintained by M. Jaeger, J. Warren, and J. Dullum.

Synthetic spring hydrology variable (grayling$pca). Synthetic variable combining *mdd*, *c67bf*, and *cdd* using principal components analysis to create a variable that describes cold, high flow springs to warm, low flow springs along a single axis.

Per capita suitable spawning habitat (grayling$Ats). Per capita suitable spawning habitat within Red Rock Creek based on binary suitability (i.e., suitable or not suitable).

Per capita suitable spawning habitat (grayling$Atw). Per capita suitable spawning habitat within Red Rock Creek based on weighted habitat suitability.

Per capita suitable winter habitat (grayling$Wt). Per capita suitable winter habitat within Upper Red Rock Lake.

APPENDIX II

SPAWNING HABITAT SAMPLING REACHES

Pebble count sample reaches and number of sites within each reach used to quantify suitability and area of spawning habitat.

Stream	Reach	# Sites	Total riffles	Comments
Red Rock Cr.	Hellroaring Cr.	1	4	TNC Section
Red Rock Cr.	Huntsman	2	8	1 upper and 1 lower site
Red Rock Cr.	U.S. Corral Cr.	2	8	State land above Corral Cr; 1 upper and 1 lower site
Red Rock Cr.	D.S. Corral Cr.	2	8	State land below Corral Cr; 1 upper and 1 lower site
Red Rock Cr.	Antelope Beaver Dams	2	8	1 site starting below beaver dams and 1 site above or in between dams in backwater
Red Rock Cr.	U.S. Elk Lake Rd.	2	8	Refuge land above Elk Lake Rd.; 1 upper and 1 lower site
Red Rock Cr.	D.S. Elk Lake Rd. & U.S. Battle Cr.	2	8	Refuge land below Elk Lake Rd.; 1 upper and 1 lower site
Red Rock Cr.	D.S. Battle Cr.	1	4	Refuge land below Elk Lake Rd.; 1 upper and 1 lower site
Elk Springs Cr.	Picnic Cr.	1	4	Picnic Cr. Between Widgeon and Culver ponds
Elk Springs Cr.	U.S. McDonald	1	4	Upstream of McDonald Pond
Elk Springs Cr.	McDonald	1	4	In bed of McDonald Pond
Elk Springs Cr.	D.S. McDonald	1	4	Between McDonald Pond and Elk Lake Rd.
Elk Springs Cr.	Below Road and beaver pond	1	4	Below Elk Lake Rd.
O'dell Cr.	Upper	1	4	Above South Valley Rd.
O'dell Cr.	Middle	1	4	Between S. Valley and "Sparrow Slough" roads (sec 24)
O'dell Cr.	Lower	1	4	Below "Sparrow Sl. Rd" (Sec 14)

APPENDIX III.

Annual estimates of angler harvest of hybrid Yellowstone cutthroat trout (YCT) in Red Rock Creek are required by models developed in the Centennial Valley Arctic Grayling Adaptive Management Plan. The goals of this survey were to provide annual estimates of:

1. The number of YCT harvested by anglers
2. Angler catch per effort of YCT
3. Distribution of angler effort up and down stream of the Elk Lake Road

A complemented survey over the duration of the spring angling season using 1) catch cards and 2) an access point survey was used to minimize bias and maximize accuracy of the aforementioned estimates. This survey was prepared using information referenced from Angler Survey Methods (Pollock et al. 1994) and Recreational Angler Survey Methods (Jones and Pollock 2012) *in* Fisheries Techniques (Zale et al. 2012).

Catch Cards: Catch cards are generally considered to be an off-site sampling method because they contain angler reported data and survey agents do not have to be present at a fishery to distribute or recover them. The advantages of these types of surveys are that they are inexpensive, simple to administer relative to all other methods, and continuously sample the fishery (i.e., catch cards are available to anglers at all hours of all days of the fishing season). The disadvantages of these types of surveys are that there are typically large biases associated with nonreporting, untruthful reports of catch, misunderstanding of questions, and misrepresentation of the angling population because of different likelihoods of responding contingent on the relative avidity of anglers.

Catch cards were used as part of this survey because of the simplicity of the fishery (one stream with a single primary access point where angling occurs over a short duration) and the information we require (number of YCT harvested). We anticipate that the primary source of bias will be nonreporting. Nonreporting rate will be independently and directly estimated by an access point survey as described below and will allow for correction of catch and harvest estimates reported on catch cards. In years when nonreporting rate was not adequately estimated, reported catch and harvest rates will be corrected using averaged nonreporting rate estimates from other years.

One of the primary sources of bias in all types of angler surveys is related to poor question structure and diction. This is especially true of open-ended questions, which we were included on our catch cards. The questions on the catch cards were simple, direct, and only pertained to information we required. Our catch cards contained the following questions:

1. **Date: ______ (month) / _______ (day) / 2014**
2. **Total number of cutthroat trout caught:_____________**
3. **Number of cutthroat trout harvested:_____________**

4. **Number of hours you were angling: ______________**

5. **Were you primarily fishing (circle one) DOWNSTREAM or UPSTREAM of the Elk Lake Road Bridge?**

The catch card portion of the survey occurred as follows:

- Catch cards were made available for the duration of the angling season at the Elk Lake Road bridge over Red Rock Creek and likely secondary access sites (i.e., the old bridge site on the road to Culver Pond).

- Pencils or pens were provided for anglers to complete catch cards.

- Clearly visible signage was strategically placed at the selected access site(s) that stated: "**Every angler must complete a survey card immediately following fishing each day**."

- An "iron warden" or some other type of deposit box was provided at each selected access site for anglers to submit completed surveys.

- Catch cards were retrieved daily and put in an envelope or file with the date written on it.

- Access sites were checked daily to ensure that signage was present and an adequate number of catch cards and pencils were available.

Access Point Survey: Access point surveys and other types of on-site methods have more accuracy and less bias than other approaches because harvest is directly observed by trained clerks. The primary disadvantage of these types of surveys is the expense associated with conducting them. Because of the narrow temporal and spatial scope of the Red Rock Creek cutthroat trout fishery a single access point can be surveyed without introducing meaningful bias.

The access point survey was conducted to estimate under or nonreporting rates of catch cards by providing an independent estimate of angler effort, total catch, and number of YCT harvested by sub-sampling during the angling season. The sampling design was structured to survey the highest proportion of total angling effort possible while taking into account likely variation among types of days. A stratified random sampling design was used to select days to conduct the access point survey. The strata were weekdays and weekends. At minimum, one weekday and one weekend day was randomly selected each week of the angling season for the access point survey. If additional sampling was possible it occurred in a manner that coincided with the highest amount of angler effort (i.e., selection of a weekend day rather than a weekday). Similarly, additional randomly selected days or effort was added to coincide with observed increases in angling effort during the season.

The access point survey occurred at the junction of the South Valley and Elk Lake roads and away from the primary parking and catch card distribution area. Because nonreporting rate of catch cards was estimated as part of the access point survey the access point survey was physically and psychologically separated from the catch card survey; anglers were not lead to believe that the access point survey in any way replaced their obligation to complete catch cards. A creel clerk was stationed at this location for the entire angling day during each day that was selected for sampling. Because it was unlikely that any anglers completed angling early in the morning surveys began around 9 am but continued until sunset. The creel clerk placed signs visible by vehicles approaching this intersection from all directions that indicated "**All anglers must stop**." The creel clerk recorded the same information as that requested by the catch cards for each angler:

1. **Date: ______ (month) / _______ (day) / 2014**
2. **Total number of cutthroat trout caught:_____________**
3. **Number of cutthroat trout harvested:_____________**
4. **Number of hours you were angling: ______________**
5. **Were you primarily fishing (circle one) DOWNSTREAM or UPSTREAM of the Elk Lake Road Bridge?**

Duration of surveys: The entire angling season was surveyed as described above during most years (access surveys were not conducted during some years). The start of the angling season varied among years based on snow and road conditions and usually began sometime after April 1st. The end of the angling season coincided with the FWP closure beginning on May 15th. As such, the maximum duration of the complemented survey was about 6 weeks (April 1 to May 15) and included a minimum of 13 days (7 week days and 6 weekend days) of access point surveys each year. The catch cards were deployed every day throughout the angling season.

Analysis of data: Total effort, catch, and harvest of YCT will be calculated from catch cards by adding those values submitted for all catch cards over the entire angling season (equations 19.4 and 19.5 in Jones and Pollock 2012) and dividing by their respective reporting rates (1-nonreporting rate). Daily reporting rate of total effort, catch, and harvest was determined by dividing the effort, catch, and harvest reported on catch cards by that observed and reported during the access point surveys on days where both types of surveys occur. Mean reporting rates were determined by averaging all daily rates. Data were analyzed to determine if there are statistically significant differences in reporting rates among strata (weekdays versus weekends) and the results were applied accordingly. Angler harvest of YCT in 2013 and 2014 were adjusted by using the nonreporting rates calculated in subsequent years.

Total effort, catch, and harvest of YCT were independently estimated using the access point survey data and applying equations 19.6 and 19.7 in Jones and Pollock (2012).

The final annual estimate of effort, catch, and harvest of YCT were determined by averaging the estimates of these parameters provided by each of the survey types. Mean annual catch per effort was determined by dividing each angler's catch by their effort and averaging those over the angling season for each survey type. Data pertaining to fishing location (above or below Elk Lake Road) was analyzed to determine whether it is meaningful to spatially segregate description of catch per effort.

1) Removal of non-native fish at the Red Rock Creek fish trap
   i) Number and removals
   ii) Estimate of the number of cutthroats that made it past the weir
      (1) Estimating the number of cutthroats that made it past the trap will allow us to estimate 1) the total number of cutthroats in the spawning population, 2) proportion removed (i.e. capture efficiency, $E = c/N$, where *c* is the number of captured fish and *N* is the total spawning population size), 3) and the number that spawned upstream of the trap. We can most easily estimate this using a two-sample Lincoln-Peterson estimator, with the first sample being fish caught, marked, and released upstream of the weir (n_1) and the second sample being fish caught during electrofishing (n_2). The number of fish recaptured during the second period is m_2. A bias-corrected Lincoln-Peterson estimator for population size is

$$\widehat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1,$$

      with an approximately unbiased variance estimate

$$\widehat{var} = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

      from Seber (1970).

      (2) Due to violations of assumptions with the approach above, we'll also use the 1) number of cutthroats captured in the downstream trap up to the point when electrofishing begins and 2) the number of cutthroats enumerated during electrofishing to estimate the number of cutthroats that spawned above the trap.