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ARTICLE

Informing Management of Henrys Lake, Idaho, using an Integrated Catch-at-Age Model

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Abstract
Henrys Lake, Idaho, supports a popular fishery for Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* and Yellowstone Cutthroat Trout × Rainbow Trout *O. mykiss* hybrids. A majority of the adult population of fish in Henrys Lake are of hatchery origin that were stocked as fingerlings. The fishery is closed to angling during the late winter and spring months, but fisheries managers are considering opening the fishery year-round with catch-and-release-only regulations or with a two-fish bag limit during the extended season. However, there is concern that the proposed management actions may negatively affect the current fishery. Therefore, we developed an integrated catch-at-age model to estimate population parameters for trout in Henrys Lake and used a simulation model to evaluate alternative management actions. Results of this study suggest that catch and release of both Yellowstone Cutthroat Trout and hybrids would increase and that abundance of trout in the spring (i.e., the start of the traditional season) would decrease under both proposed bag limits. Losses in abundance can be mitigated by stocking additional fish as long as no more than approximately 1,520,000 Yellowstone Cutthroat Trout are stocked annually. If catch-and-release-only regulations are implemented during the newly proposed season, total harvest is expected to decrease compared to the current fishery due to additional catch-and-release mortality. Ultimately, managers will need to prioritize harvest or catch-and-release opportunity, both of which provide additional utility to anglers, when choosing how to proceed with bag limit regulations.

Realized outcomes of recreational fisheries management actions at the population level are a result of their effect on population dynamic rates, including recruitment, growth, natural mortality, and fishing mortality (Hilborn and Walters 1992). Each dynamic rate can be affected by biotic or abiotic factors that may or may not be under the

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control of the fisheries manager(s). For instance, managers can directly influence recruitment by stocking fish in some scenarios (Trushenski et al. 2010). Recruitment in other fisheries may be regulated by spawner abundance, environmental conditions, and(or) density-dependent factors associated with habitat quality or quantity (Myers et al. 1999; Munch et al. 2018; McCormick et al. 2021a). Growth and natural mortality are most often influenced by environmental conditions, habitat, or the presence or density of other fish in the population or the assemblage (Pauly 1980; Lorenzen and Enberg 2002; Weisberg et al. 2010). Fishing mortality is the dynamic rate often considered to be most directly influenced by recreational fisheries managers through implementation of fishing regulations, such as bag or length limits, harvest quotas, seasonal or area closures, or gear restrictions (Isermann and Paukert 2010). However, environmental and habitat conditions as well as human influence may also impact fishing mortality by affecting the catchability of fish in the population or influencing angling effort or participation (van Poorten and Post 2005; Kuparinen et al. 2010; Van Leeuwen et al. 2020). The litany of factors that influence fish populations usually do not act independently and are not deterministic; rather, they are frequently a result of complex interactions that often vary through space and time. In addition, dynamic rates and resulting abundance of fish are rarely observed perfectly and are often estimated with a high level of uncertainty (Maunder and Piner 2015). High uncertainty in both the population and observation processes can make understanding the effects of previous management actions difficult and, consequently, can make forecasting the results of alternative management scenarios challenging. Henrys Lake, Idaho, is one such fishery where these challenges are exemplified.

Henrys Lake is one of the most popular fisheries in Idaho, with recent estimates of angling effort exceeding 207,000 h in a single fishing season (Heckel et al. 2020). The sport fishery at Henrys Lake consists of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, sterile Yellowstone Cutthroat Trout × Rainbow Trout *O. mykiss* hybrids (hereafter, hybrids), and sterile Brook Trout *Salvelinus fontinalis*. Recruitment of sport fish in Henrys Lake is almost entirely maintained by annual fingerling stockings. Yellowstone Cutthroat Trout and hybrid fingerlings grow relatively quickly in Henrys Lake; both generally exceed 400 mm on average by age 3, thus providing a fishery for quality-sized fish (Heckel et al. 2020). In an effort to manage fishing mortality, relatively conservative angling regulations are in place at Henrys Lake, where anglers may only harvest two trout per day. The lake was open for fishing from late May through October prior to 2010. However, in 2011 the fishery was extended until January 1 to allow for an ice fishery to occur for an additional month. The majority of fish caught at Henrys Lake are released by anglers, but a smaller percentage of fish are released by anglers during the ice fishery (Heckel et al. 2020).

Management goals for Henrys Lake are to maintain abundant populations of Yellowstone Cutthroat Trout and hybrids to support the robust fishery while maximizing opportunity for anglers to catch fish during both the ice and open-water fishing periods (IDFG 2019). In an effort to increase opportunity, alternative management actions are currently under consideration that include opening the fishery year-round while maintaining the two-fish bag limit or allowing catch-and-release-only fishing during the spring. Both management actions are expected to increase angling opportunity but may have adverse effects on the open-water fishery due to additional harvest or catch-and-release mortality that may occur during the newly created seasons. One option to mitigate this potential effect is to stock more fish. However, it is possible that natural mortality may increase with the addition of more fish through density-dependent mechanisms (Myers et al. 1999; Lorenzen and Enberg 2002), potentially making this option counterproductive.

The high level of participation and varied interest in the Henrys Lake fishery bespeak the importance of effectively managing the fishery to achieve desired management outcomes. To that end, the fishery has been intensively monitored for decades using several methods. For example, relative abundance has been monitored annually using gill nets, angling catch and effort have been monitored periodically using creel surveys, adult spawner abundance data have been collected annually using an adult fish trap, and demographic data have been collected periodically using various methods. Age and length data have also been collected concurrent with many of these surveys. Traditionally, the data sets have been analyzed independently when making inference about the effectiveness of management actions or population status. However, there is potential to leverage multiple data sets in a single analysis to estimate population parameters that were not previously estimable or to increase precision of parameters that are currently estimated (Schaub and Abadi 2011; Kéry and Schaub 2012; Maunder and Punt 2013).

A variety of catch-at-age models has been developed for analyzing multiple types of data in an integrated analysis (Maunder and Punt 2013). Such models have been most frequently applied to marine and larger inland systems. Generally, catch-at-age models combine fishery-dependent estimates of catch or harvest with fishery-independent survey data to estimate population parameters, including recruitment, fishing and natural mortality, and abundance (Fournier and Archibald 1982; Quinn and Deriso 1999; Aeberhard et al. 2018). However, separately estimating fishing and natural mortality is not possible by combining just angler catch data with fishery-independent survey data using the traditional framework, as the parameters are confounded (Quinn and Deriso 1999). Consequently, assumptions are often made about the rate of natural mortality—a commonly recognized shortcoming of fisheries stock assessment models (Maunder and Piner 2015; Mannini et al. 2020). This is problematic when evaluating the proposed alternative management actions at Henrys Lake because opening the fishery for a longer time period could potentially affect fishing mortality, whereas changing stocking rates will likely affect natural mortality. Further, harvest has only been monitored periodically at Henrys Lake. Traditional catch-at-age models have been extended to estimate fishing and natural mortality separately, primarily through the addition of tag-return data (Maunder and Punt 2013), which are not currently available for Henrys Lake. However, other data sets are available at Henrys Lake that can potentially allow for fishing and natural mortality to be separately estimated. The objectives of this study were to develop an integrated catch-at-age model to (1) estimate population parameters for Yellowstone Cutthroat Trout and hybrids in Henrys Lake, (2) estimate the effects of stocking rates on natural mortality, and (3) evaluate potential alternative management actions, including extending the fishery year-round with a two-fish bag limit or catch-and-release-only regulations and stocking additional fish to account for potential increases in fishing mortality.

METHODS

Study area.— Henrys Lake is a 2,630-ha natural lake located in eastern Idaho. Henrys Lake is relatively shallow, with a mean depth of 4 m. The lake is stocked annually, primarily with fingerling Yellowstone Cutthroat Trout and sterile hybrids. Sterile Brook Trout fingerlings are also stocked annually but make up less than 4% of total fish stocked; thus, this study focused only on Yellowstone Cutthroat Trout and hybrids. The fish assemblage at Henrys Lake includes the three species of trout that are stocked as well as nonnative Utah Chub *Gila atraria*. A hatchery with an adult fish ladder and trap is located on Hatchery Creek, a tributary to Henrys Lake, where eggs and milt are collected from spawning Yellowstone Cutthroat Trout returning from the lake annually. Some Yellowstone Cutthroat Trout spawn in the lake proper or in Henrys Lake tributaries other than Hatchery Creek. However, naturally produced Yellowstone Cutthroat Trout are estimated to contribute less than 2% to the adult population and were ignored in this study (Heckel et al. 2020).

Data collection.— Data from five independent sources were used in this study: stocking data, Yellowstone Cutthroat Trout maturity data, annual gill-net survey data, hatchery trap data, and creel survey data. The stocking data were the total number of Yellowstone Cutthroat Trout and hybrid fingerlings stocked on an annual basis from 1999 to 2021. Adult fish are spawned and eggs are hatched in the spring; fingerlings are stocked in the fall (see IDFG 2010 for a more detailed summary of the hatchery practices at Henrys Lake). Age-at-maturity data were based on a study from Irving (1955), where the author determined the maturity status of fish from age 1 to 6 from a random sample of Yellowstone Cutthroat Trout caught in the sport fishery in 1951.

Gill-net survey data were collected annually from 1999 to 2021 (Heckel et al. 2020). Gill-net surveys were conducted shortly after ice-out, which usually occurred in late April or early May. Gill nets generally included paired floating and sinking gill nets. The total number of annual net sets varied from 6 to 100. Gill nets were 46 m long by 2 m deep, with bar mesh sizes of 2.0, 2.5, 3.0, 5.0, and 6.0 cm. Nets were set at dusk and retrieved the following morning; thus, the unit of effort was 1 net-night for each net that was set. Fish captured in gill nets were enumerated and measured to the nearest millimeter (total length), and sagittal otoliths were collected for age and growth analysis. Fish were checked for fin clips, which indicated that they were captured at the hatchery trap, starting in 2021. A sample of 10 fish per 20-mm length-group were aged. In instances where not all fish were aged, an age–length key for all years was used to assign ages to fish by the methods described in Isermann and Knight (2005). A summary of gill-net catch and effort data used in the model can be found in Supplement 1 (available in the online version of this article).

The hatchery at Henrys Lake was established on Hatchery Creek in 1924 as a facility for spawning fish and incubating eggs. A fish ladder and trap are in place on Hatchery Creek, where fish are trapped that ascend the fish ladder in the spring to spawn. The fish ladder was generally open from early to mid-February through late April over the duration of this study. Although some hybrids also ascended the fish ladder, only Yellowstone Cutthroat Trout data from the hatchery trap were used in this study. A random sample of approximately 10% of all fish that ascended the fish ladder were measured for total length. An age–length key (the same age–length key that was used in the gill-net surveys as described above) was then used to assign ages to fish that were measured for total length. The proportion of fish in each age-class was multiplied by the total number of fish that ascended the fish ladder to generate the number of fish in each age-class. All fish that were trapped at the fish ladder were marked with a fin clip annually. Hatchery trap data used in the model can be found in Supplement 1.

Probabilistic on-site creel surveys were conducted in 1999, 2001, 2003, 2005, 2009, 2013, 2016, and 2019 (Heckel et al. 2020). Creel surveys encompassed the entire fishing season where the sampling frame (i.e., days) was stratified by weekdays and weekends in 2-week intervals. Two randomly selected weekdays and weekend days were sampled during each 2-week period during the fishing season. During the open-water period, effort was estimated based on aerial counts, where one count was conducted at a randomly selected time for each day that was selected for sampling. Two on-site counts, selected at random times, were conducted during the ice-fishing season to estimate effort. Catch rates were estimated based on angler interviews that were a combination of access and roving interviews. All fish that were harvested were measured to the nearest millimeter by creel clerks. The number of fish harvested and released was estimated using the multi-day estimator described in McCormick and Meyer (2017). An age–length key (described above) was used to assign ages to all fish that were measured for total length in the creel survey. The proportion of fish in each age-class was multiplied by the estimated total number of fish that were harvested to generate the number of fish harvested in each age-class. The length of fish that were released by anglers could not be measured; therefore, the proportion of each age-class of fish that were caught and released was assumed equal to that observed from the sample of harvested fish. We assumed that the probability of a fish dying as a result of being caught and released was 0.05. Fishery-dependent catch data used in the model can be found in Supplement 1.

Population model.— The population model used in this study was a state-space version of an integrated catch-at-age model. The model included a state-process model that described the true but unknown (i.e., latent) abundance of individuals in each life stage and an observation model that was conditional on the process model. The process model was a stage-structured matrix model (Leslie 1945; Caswell 2001) that linked the demographic rates with population sizes. Demographic stochasticity (process error) was incorporated in the process model using Poisson and normal distributions. The process model was defined as

$$N_{a,t,i} = r_{a,t,i} \text{ for } a = 0,$$

$$N_{a,t,i} \sim Poisson\left[N_{a-1,t-1,i}e^{-(M_{a-1,t-1,i})\times 0.5}\right] \text{ for } a = 1,$$

$$N_{a,t,i} \sim Poisson\left[N_{a-1,t-1,i}e^{-\left(M_{a-1,t-1,i}+F_{a-1,t-1,i}+F'_{a-1,t-1,i}\right)}\right] \text{ for } 1 < a < A,$$

$$N_{a,t,i} \sim Poisson\left[N_{a-1,t-1,i}e^{-\left(M_{a-1,t-1,i}+F_{a-1,t-1,i}+F'_{a-1,t-1,i}\right)} + N_{a,t-1,i}e^{-\left(M_{a,t-1,i}+F_{a,t-1,i}+F'_{a,t-1,i}\right)}\right] \text{ for } a = A,$$

$$F_{a,t,i} \sim normal\left(F_{a,t-1,i}, \sigma_F^2\right),$$

$$F'_{a,t,i} \sim normal\left(F'_{a,t-1,i}, \sigma_{F'}^2\right),$$

$$Z_{a,t,i} = M_{a,t,i} + F_{a,t,i} + F'_{a,t,i},$$

where $N_{a,t,i}$ is the abundance of fish of age-class a in year t of species i (i.e., Yellowstone Cutthroat Trout or hybrids), r is the number of fingerlings stocked, M is instantaneous natural mortality, F is instantaneous harvest mortality, F' is instantaneous catch-and-release mortality, and Z is instantaneous total mortality. The symbol A represents the "plus" age-class, which includes all age-6 and older fish. Both harvest and catch-and-release mortality (collectively, "fishing mortality") were modeled using a random walk process with independent variance σ^2 for both parameters. Note that there was no harvest or catch-and-release mortality for age-0 fish and that "0.5" was included in the exponent for the process that generated age-1 fish because fingerlings are stocked when they are approximately 0.5 years of age.

Observation model.— The observation model included a set of equations that linked the process model described above to the five data sets collected in this study. Catch of Yellowstone Cutthroat Trout and hybrids of age a in year t in the annual gill-net surveys ($I_{a,t,i}$) was conditional on the latent abundance and was modeled as

$$I_{a,t,i} \sim Poisson(N_{a,t,i}E_t s_a q),$$

where E_t is the survey effort in number of net-nights in year t, s_a is the gill-net selectivity of each age-class, and q is the catchability. The gill-net selectivity of each age-class was estimated as part of a separate study (Idaho Department of Fish and Game [IDFG], unpublished data) and was treated as known in the model, whereas catchability (the probability that a fish would be captured in the gill net) was estimated in the model.

The count of Yellowstone Cutthroat Trout of age a in year t ($Y_{a,t}$) captured at the hatchery trap was conditional on the latent abundance of each age-class and was modeled as

$$Y_{a,t} \sim Poisson(N_{a,t,i}m_a p_{hat}),$$

where m_a is the probability that a fish would reach maturity at age a and p_{hat} is the probability that a fish that is mature would spawn at the hatchery. The probability that a fish would reach maturity was modeled using the raw data provided in Irving (1955),

$$y_{mat,a} \sim binomial(m_a, n_{mat,a}),$$

$$logit(m_a) = \beta_0 + \beta_1 a,$$

where $y_{mat,a}$ is the number of mature fish of age-class a, $n_{mat,a}$ is the total sample size of fish of age-class a, and β_0

and β_1 are regression coefficients describing how the probability of maturity changes with age. The probability that a mature fish would spawn at the hatchery was estimated based on recaptures of fish that were marked after being captured at the hatchery trap and returned to the lake and was defined as

$$y_{hat} \sim binomial\left(p_{hat} \times e^{-M_3 \times 0.167}, n_{hat}\right),$$

where y_{hat} is the number of fish captured during the 2021 gill-net sample that were previously captured and marked at the hatchery trap and n_{hat} is the total number of fish captured during the gill-net sampling event. Note that 0.167 (i.e., 2/12) in the exponent for survival was used to account for natural mortality that occurred during the 2 months between the time fish are released at the hatchery and the time they are potentially recaptured during the sampling event. Fishing is closed during this time period; thus, fishing mortality was not included. For simplicity, this part of the model was parameterized using only age-3 natural mortality because the majority of spawning fish are age 3.

Harvest data (collected during the creel surveys) for Yellowstone Cutthroat Trout and hybrids of age a in year t ($C_{a,t,i}$) were conditional on the latent abundance and were modeled using the Baranov catch equation (Baranov 1918) assuming the Poisson distribution:

$$C_{a,t,i} \sim Poisson\left[\frac{F_{a,t,i}}{Z_{a,t,i}}\left(1-e^{-Z_{a,t,i}}\right)N_{a,t,i}\right].$$

The number of fish that were assumed to have died of catch-and-release mortality ($C'_{a,t,i}$) was modeled similarly:

$$C'_{a,t,i} \sim Poisson\left[\frac{F'_{a,t,i}}{Z_{a,t,i}}\left(1-e^{-Z_{a,t,i}}\right)N_{a,t,i}\right].$$

Unlike harvest, the actual number of fish that died due to catch-and-release mortality cannot be observed. Consequently, the probability that a fish would die after being caught and released was assumed to be 0.05 for all years and age-classes. Thus, $C'_{a,t,i}$, which was treated as data in the model, was the estimated number of caught-and-released fish of age-class a in year t of species i times 0.05.

One potential alternative management scenario under consideration for Henrys Lake is to alter the number of fingerling Yellowstone Cutthroat Trout or hybrids to stock. Consequently, we were interested in estimating the effects of this management action on natural mortality. Thus, the following constraint on natural mortality was specified in the model:

$$M_{a,t,i} \sim lognormal\left(\mu_{a,t,i}, \sigma^2_{M,a}\right),$$

$$\mu_{a,t,i} = \beta_{2,a,i} + \beta_{3,a,i} r_t,$$

where μ is the log of the expected natural mortality rate, $\sigma^2_{M,a}$ is the variance on natural mortality, and $\beta_{2,a,i}$ and $\beta_{3,a,i}$ are regression coefficients that describe how natural mortality changes for each age and species as a function of the total number of fingerlings of both species stocked. The number of fish stocked was standardized to a mean of zero and standard deviation of 1 for model fitting.

Evaluating alternative management actions.— The population model described above was used to simulate (i.e., predict) population size and angler catch of both species in the future under alternative management scenarios. The simulation was conducted by extending the time loop for the state processes in the population model for 10 years beyond the current time series. Simulations were conducted for longer time periods (up to 20 years), but point estimates tended to stabilize before 10 years and were similar at longer time periods. The primary management actions under consideration are extending the fishing season, either with the current two-fish bag limit (two-fish scenario) or with catch-and-release-only regulations (C&R scenario). Under the two-fish scenario, both instantaneous harvest mortality (F) and instantaneous catch-and-release mortality (F') are expected to increase compared to current state of the fishery (baseline scenario). However, only instantaneous catch-and-release mortality rate would increase under the C&R scenario. Because the fishery has always been closed during the winter and early spring, the degree to which angling effort and ultimately fishing mortality would increase under each alternative scenario is uncertain. Thus, a range of values for instantaneous harvest and instantaneous catch-and-release mortality rate were simulated during the 10-year projection period. The range of values varied from no change in fishing mortality (i.e., baseline scenario) to double the current estimates of harvest and catch-and-release mortality, respectively. Simulated harvest and catch-and-release mortality were both increased proportionally under the two-fish scenario, whereas only catch-and-release mortality was increased under the C&R scenario.

Catch-and-release angling during the spring, summer, and autumn (i.e., open-water period) accounts for a majority of the fishing activity at Henrys Lake in terms of both effort and catch. The proposed alternative management actions of increasing angling and catch opportunity outside of this time period will likely increase fishing mortality and decrease the number of adult trout available to be caught by catch-and-release anglers during the traditional season. Such a scenario would potentially negatively affect the experience of the largest user group. Stocking additional fish could potentially mitigate this effect given that density-dependent survival does not decrease to levels that make it unsustainable. Therefore, a range of stocking rates was simulated for each level of fishing mortality simulated under the two-fish and C&R management scenarios, respectively. Simulated annual stocking rates varied from 545,367 to 2,181,466 Yellowstone Cutthroat Trout and from 112,412 to 449,648 hybrids, which were 0.5–2.0 times the mean number of fish stocked over the duration of this study. Each stocking level evaluated was held constant over the 10-year projection period. Note that the effect of stocking on natural mortality of each age-class was estimated using the regression model described above, which allowed us to predict how abundance would change as a result of stocking amounts in combination with variable fishing mortality.

The goals of the alternative management scenarios are to increase angling and catch opportunity while maintaining abundant populations of adult (trophy) Yellowstone Cutthroat Trout and hybrids throughout the fishing season. Consequently, abundance, harvest, and the number of Yellowstone Cutthroat Trout and hybrids that were caught and released were the performance metrics that were monitored over the simulated projection period for each management scenario. The results of the simulation are a summary of the posterior distributions of the sum of adult abundance, harvest, and the number of age-3 and older fish that were caught and released at year 10 of the simulations. The data used to estimate instantaneous catch-and-release mortality in the population model were estimates of the number of fish caught and released times 0.05 (i.e., the probability that a fish would die as a result of being caught and released). Thus, the number of fish that would have died due to catch-and-release mortality in the simulation was divided by 0.05 to predict the total number of fish that would have been caught and released.

Model fitting.— It was assumed that each data set used in the model was independent. Thus, the joint likelihood using all of the data was the product of the individual likelihoods for all data sets described above. All models were fit using Bayesian methods. Markov chain–Monte Carlo algorithms were used to estimate posterior distributions for all model parameters. Analyses were performed using the JAGS program (Plummer 2003) implemented in R using the r2jags package (Su and Yajima 2012; R Development Core Team 2015). Posterior distributions were generated using three chains of 1,000,000 iterations that were thinned by six with a burn-in of 500,000. Parameters were checked for convergence based on the Gelman–Rubin statistic (i.e., $\hat{R} < 1.05$; Brooks and Gelman 1998). Estimates of all parameters were summarized as the median of the posterior distributions. Prior distributions used for all model parameters are shown in Supplement 2, and JAGS code can be found in Supplement 3.

RESULTS

Population Model

The mean number of Yellowstone Cutthroat Trout fingerlings stocked annually from 1999 to 2020 was 1,090,733 and varied from 728,886 to 1,633,892. A mean of 224,824 hybrids were stocked annually over the same time period and varied from 38,260 to 978,440. An average of approximately 43,360 (minimum–maximum: 7,650–102,109) Yellowstone Cutthroat Trout and 44,199 (5,166–106,017) hybrids were estimated to be caught during the years in which creel surveys were conducted. Approximately 84% of Yellowstone Cutthroat Trout and 82% of hybrids that were caught by anglers were released. Mean gill-net catch per unit effort of Yellowstone Cutthroat Trout over the duration of the study was 6.9 (1.5–15.4) per net-night, and mean catch per unit effort of hybrids was 3.0 (1.1–5.4) per net-night. The number of Yellowstone Cutthroat Trout captured annually at the hatchery trap varied from 2,298 to 11,879 over the duration of the study and averaged 4,788 fish. Estimated catchability (q) was 0.0000044 (0.000004–0.0000047), and the probability that a fish would spawn at the hatchery was 0.10 (0.09–0.11; Figure 1). Gill-net selectivity and maturity probability are shown in Figure 1. All estimated parameters in the model converged (i.e., $\hat{R}$ was less than 1.05), with the exception of many of the mortality estimates for the plus age-class. Observed versus model-estimated values for gill-net catch per unit effort as well as catch at the trap are shown in Supplement 4.

Estimated abundance of adult (age-3 and older) Yellowstone Cutthroat Trout and hybrids is displayed in Figure 2. Mean estimated abundance of adult Yellowstone Cutthroat Trout was 82,965 (39,506–201,089), and mean estimated abundance of adult hybrids was 46,315 (21,665–81,970). Estimates of natural mortality were variable among years and age-classes for both Yellowstone Cutthroat Trout (Figure 3) and hybrids (Figure 4). Natural mortality was the largest source of mortality for both Yellowstone Cutthroat Trout and hybrids in most years and for most age-classes. Mean annual natural mortality estimates among years and from ages 0 to 5 were 0.57 (0.02–0.98) for Yellowstone Cutthroat Trout and 0.39 (0.01–0.99) for hybrids. Natural, fishing, and catch-and-release mortality estimates for the plus age-class were near 1.0 or zero for both species in every year. Mean estimated annual fishing mortality for ages 3–6 was 0.16 (<0.01–0.73) for Yellowstone Cutthroat Trout and 0.18 (<0.01–0.52) for hybrids. Mean estimated annual catch-and-release mortality for ages 3–6 was 0.05 (<0.01–0.37) for Yellowstone Cutthroat Trout and 0.04 (<0.01–0.19) for hybrids.

Stocking Effect

The estimated effect of stocking on natural mortality of Yellowstone Cutthroat Trout was positive for age-0 fish and negative for all other age-classes (Figure 5). A positive effect suggests that natural mortality increases with increased stocking, whereas a negative effect suggest that natural mortality decreases with increased stocking. The probability of a positive effect of stocking on Yellowstone

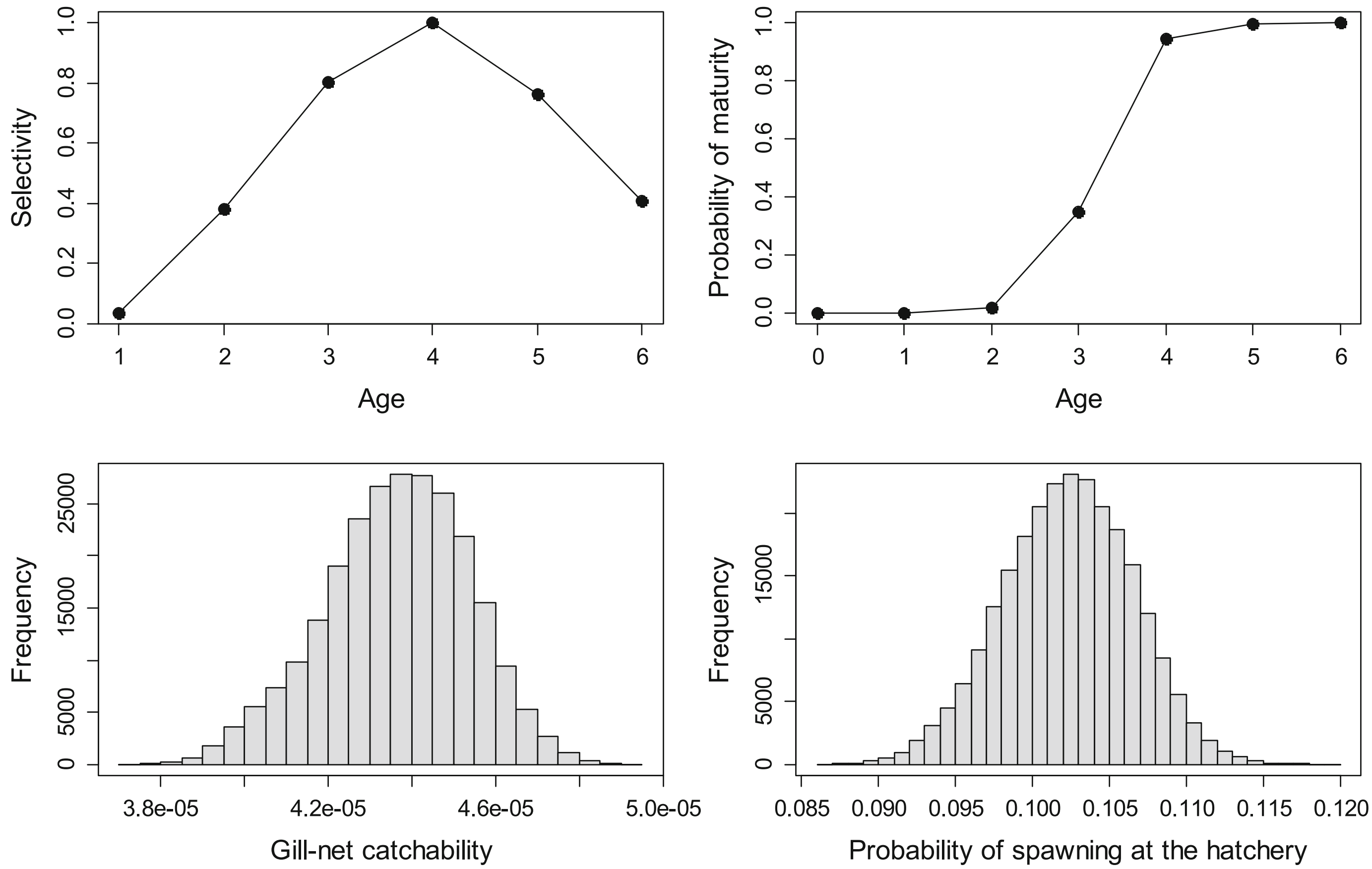

FIGURE 1. Estimated gill-net selectivity of Yellowstone Cutthroat Trout and Yellowstone Cutthroat Trout × Rainbow Trout (hybrids; top left panel), probability of maturity of Yellowstone Cutthroat Trout (top right panel), the posterior distributions for gill-net catchability of Yellowstone Cutthroat Trout and hybrids (bottom left panel), and probability that a Yellowstone Cutthroat Trout would spawn at the hatchery in Henrys Lake, Idaho (bottom right panel).

Cutthroat Trout mortality was 0.93 for age-0 fish; the probability of a negative effect varied from 0.77 to 0.86 for all other age-classes (based on the proportion of the posterior distribution that was greater than zero). The effect of stocking on natural mortality was negative for all age-classes of hybrids with the exception of age-5 fish (Figure 5). The probability of a positive effect was 0.90 for age-5 fish, and the probability of a negative effect varied from 0.46 to 0.87 for all other age-classes.

Evaluating Alternative Management Scenarios

Yellowstone Cutthroat Trout.— Abundance, harvest, and the number of adult Yellowstone Cutthroat Trout caught and released increased among all simulated fishing mortality and bag limit scenarios (i.e., baseline, two-fish, C&R) with increases in stocking until greater than 1,527,026 fish (Figure 5). Abundance and catch decreased when more than 1,527,026 fish were stocked. This result was due to the positive relationship between stocking and natural mortality of age-0 Yellowstone Cutthroat Trout.

Predicted Yellowstone Cutthroat Trout adult abundance at year 10 of the simulation was approximately 262,680 fish under baseline scenario. Abundance decreased to 248,250 and 235,745 when instantaneous harvest and catch-and-release mortality rates were increased to 1.5 and 2.0 times (compared to the baseline rates), respectively, under the two-fish scenario. Note that a range of values for instantaneous harvest and instantaneous catch-and-release mortality was simulated when evaluating alternative management strategies due to uncertainty in how fishing mortality would be affected by opening the fishery year-round. Abundance of Yellowstone Cutthroat Trout decreased as fishing mortality rates increased under all stocking rates under the two-fish scenario compared to the baseline scenario. If stocking was increased from the mean observed over the duration of the study (i.e., 1,090,733) to 1,527,026 fish, abundance was predicted to be 287,219 and 269,700 at 1.5 and 2.0 times the baseline rates of fishing mortality, respectively, compared to 262,680 when mortality was not increased. This suggests that increases in

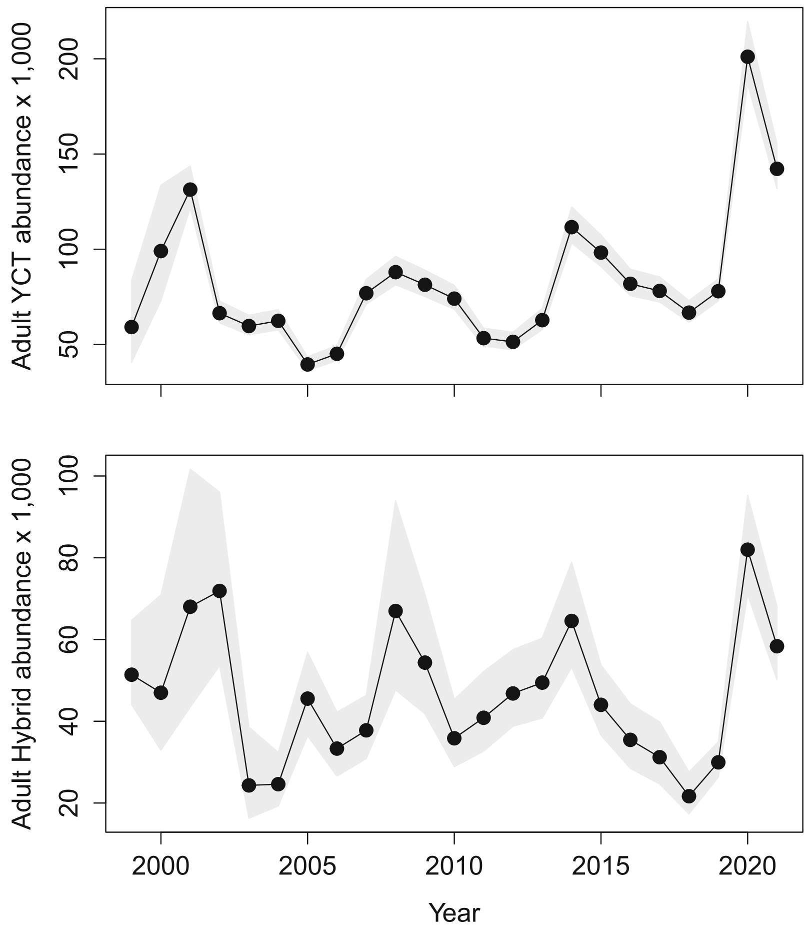

FIGURE 2. Estimated abundance of adult (age-3 and older) Yellowstone Cutthroat Trout (YCT; top panel) and YCT × Rainbow Trout hybrids (bottom panel) in Henrys Lake, Idaho, from 1999 to 2021. Gray shaded area represents 95% credible interval.

stocking can account for additional losses in abundance that may occur by extending the fishing season year-round while managing the fishery with a two-fish bag limit as long as harvest and catch-and-release mortality does not more than double. Increases in the number of fish harvested and caught and released were predicted with increases in overall fishing mortality under the two-fish scenario (Figure 6).

Similar to the two-fish scenario, decreases in abundance of adult Yellowstone Cutthroat Trout were also predicted with increasing simulated catch-and-release mortality rates under the C&R scenario (no changes in instantaneous harvest rates were simulated under this scenario). However, the decreases were much smaller than observed with the two-fish scenario (Figure 5). For instance, when stocking rates were held at the mean and harvest and catch-and-release mortality rates were increased two times relative to the baseline rates, abundance decreased by approximately 10% under the two-fish scenario compared to 2% under the C&R scenario. However, the number of fish harvested slightly decreased under the C&R scenario with increases in catch-and-release mortality, whereas harvest increased under the two-fish scenario (Figure 6). Although abundance and harvest were expected to decrease under C&R scenario compared to the baseline, the number of fish caught and released was expected to increase. The relative increase was greater than that observed under the two-fish scenario. Specifically, the predicted number of fish caught and released increased by 45% compared to the baseline scenario when catch-and-release mortality rates were doubled under the C&R scenario, whereas there was only an expected increase of 29% under the two-fish scenario. Similar to the two-fish scenario, potential losses in abundance due to additional catch-and-release mortality that may be incurred due to extending the fishing season with catch-and-release regulations could be mitigated by stocking additional fish as long as no more than 1,527,026 total fish are stocked.

Hybrids.— Abundance, harvest, and the number of hybrids caught and released all increased with increases in stocking rates in the simulation (Figure 7). The trends in

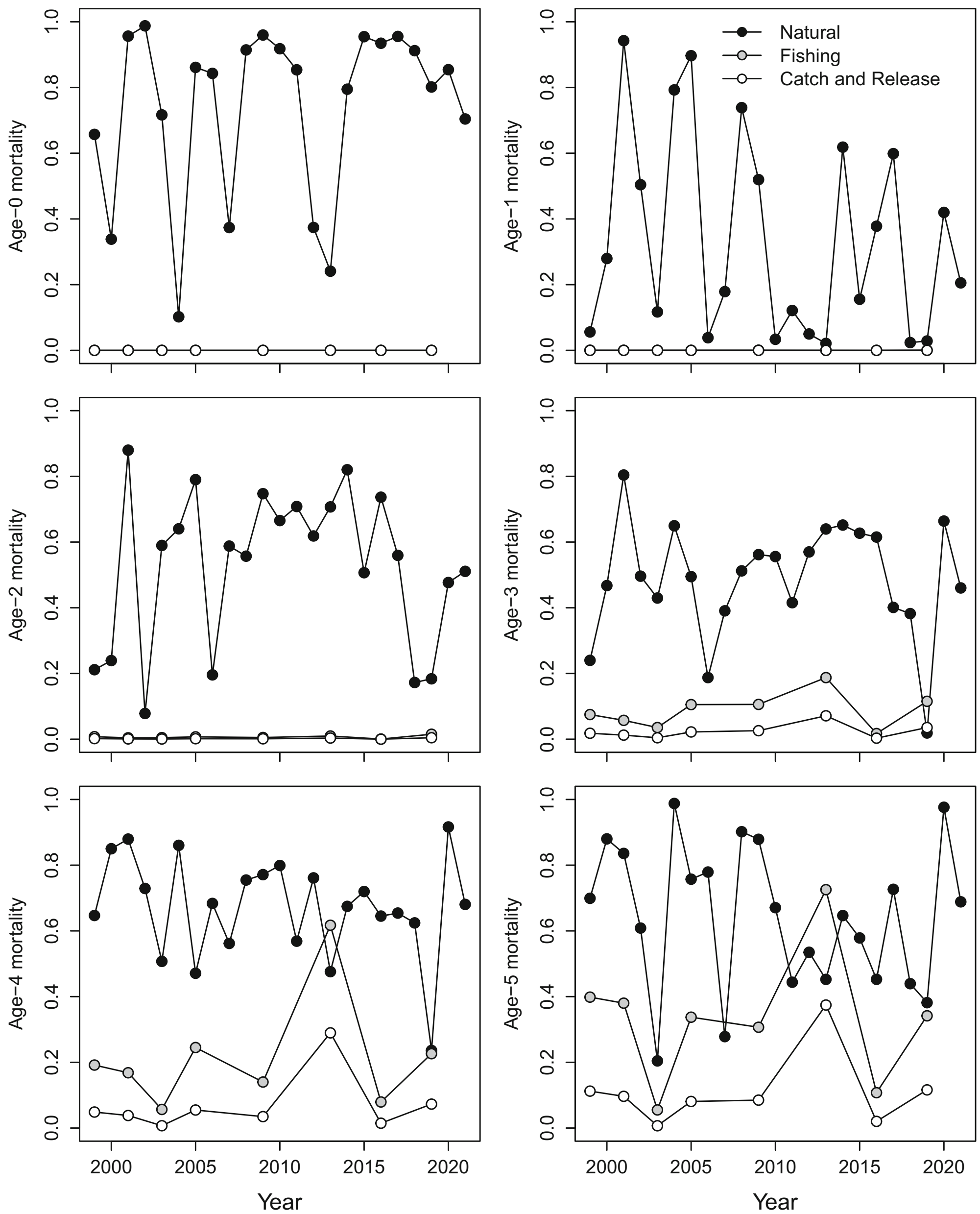

FIGURE 3. Estimated annual natural, harvest, and catch-and-release mortality of age-0 to age-5 Yellowstone Cutthroat Trout in Henrys Lake, Idaho, from 1999 to 2021.

abundance, harvest, and fish caught and released were similar to what was observed for Yellowstone Cutthroat Trout with changes in management scenarios and fishing mortality. For instance, abundance decreased with increases in fishing mortality under the two-fish and C&R scenarios, but the decrease was greater under the two-fish bag limit. Similarly, the number of fish caught and released increased with increases in fishing mortality rates under both scenarios, but more fish are expected to be caught and released under the C&R scenario. Additionally, harvest of hybrids is expected to increase under the two-fish scenario but decrease under the C&R scenario compared to the baseline scenario. The simulation results suggest that losses in abundance of hybrids that may occur due to extending the fishing season with either bag limit could be mitigated by stocking additional fish up to the maximum stocking and mortality levels simulated. Uncertainty in model predictions for Yellowstone Cutthroat Trout can be found in Supplement 5, and uncertainty in predictions for hybrids can be found in Supplement 6.

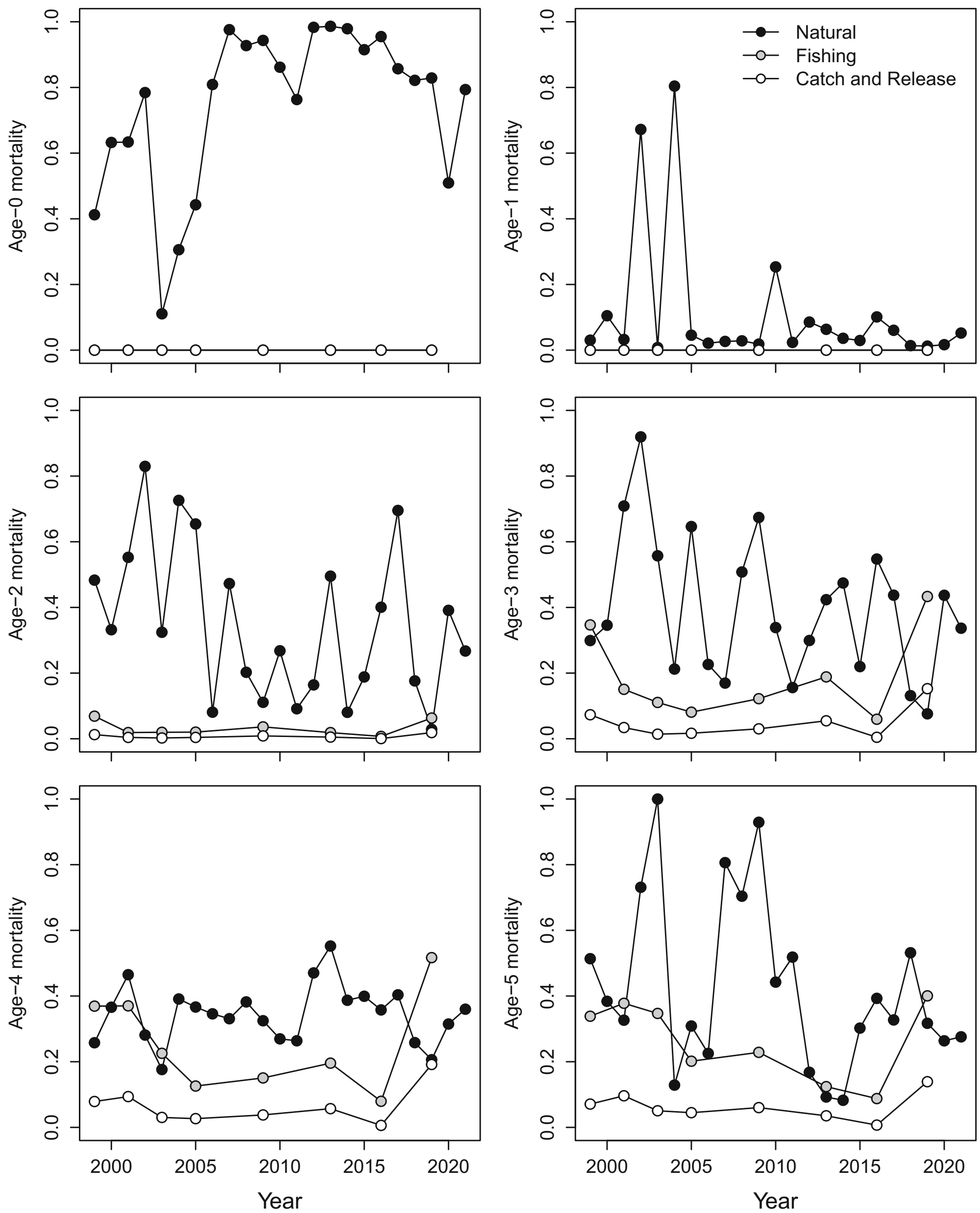

FIGURE 4. Estimated annual natural, harvest, and catch-and-release mortality of age-0 to age-5 Yellowstone Cutthroat Trout × Rainbow Trout hybrids in Henrys Lake, Idaho, from 1999 to 2021.

DISCUSSION

The primary objectives of this study were to evaluate how abundance, harvest, and the number of fish caught and released would be affected by opening the Henrys Lake fishery year-round with a two-fish bag limit or with catch-and-release-only regulations for much of the year. The results of this study suggest that if a two-fish bag limit is implemented, harvest and catch and release of both Yellowstone Cutthroat Trout and hybrids would increase and trout abundance in the spring would decrease. The results also suggest that losses in abundance due to additional harvest and catch-and-release mortality can be mitigated by stocking more fish. However, abundance and catch of Yellowstone Cutthroat Trout are expected to decrease if more than approximately 1,520,000 fish are stocked; such a nonlinear relationship was not apparent for hybrids over the levels evaluated in this study. If catch-and-release regulations are implemented during the extended season, abundance is also expected to decrease compared to the current status but not to the level that would be expected with a

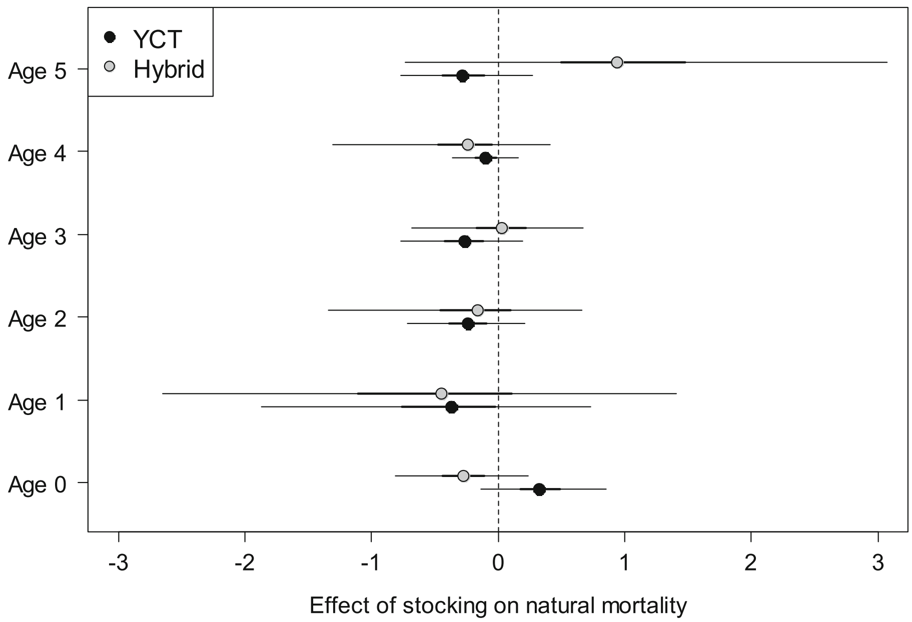

FIGURE 5. Estimated effect size (i.e., coefficient estimates) of stocking rate of Yellowstone Cutthroat Trout (YCT) and YCT × Rainbow Trout hybrids (Hybrid) on natural mortality of age-0 to age-5 YCT and hybrids in Henrys Lake, Idaho. A positive effect suggests that mortality increases with increased stocking, whereas a negative effect suggests that mortality decreases with increased stocking. Thicker horizontal lines represent 50% credible intervals, whereas thinner horizontal lines represent 95% credible intervals.

two-fish bag limit with a year-round fishery. In addition, the number of fish caught and released is expected to increase. Consequently, the number of fish harvested over the duration of the season with catch-and-release regulations is predicted to decrease compared to the baseline scenario due to additional catch-and-release mortality that will likely occur during the extended catch-and-release season. Ultimately, managers will need to prioritize harvest (two-fish scenario) or catch-and-release (C&R scenario) opportunity, both of which provide additional utility to anglers, when choosing how to proceed with bag limit regulations.

The estimated effects of stocking density on natural mortality varied among age-classes and species in this study. Yellowstone Cutthroat Trout appeared to be negatively affected by increases in stocking at age 0 but positively affected at all other age-classes. Density-dependent effects on age-0 survival have also been observed in populations of resident and adfluvial wild Yellowstone Cutthroat Trout populations in the region (McCormick and High 2020; McCormick et al. 2021a). In addition, McCarrick (2021) observed a positive relationship between stocking density and growth of adult Yellowstone Cutthroat Trout in Henrys Lake. The age-specific stocking-survival dynamics observed with Yellowstone Cutthroat Trout in Henrys Lake resulted in a nonlinear relationship between stocking density and preferred management outcomes. Previous studies of Henrys Lake have also documented this nonlinear relationship, which motivated IDFG to prescribe a stocking target of 1.3 million fingerling Yellowstone Cutthroat Trout annually (IDFG 2019). The optimal stocking rate identified in the current study of approximately 1.5 million Yellowstone Cutthroat Trout fingerlings is similar to that recommended in the current IDFG management plan. Conversely, the results of this study suggest that more total fingerlings could be stocked without negatively affecting survival of hybrids. However, the analysis was based on stocking fingerlings of both species, which suggests that additional stocking of both species collectively could negatively affect Yellowstone Cutthroat Trout survival. One potential option to mitigate this is to stock a higher proportion of hybrids, which had higher survival than Yellowstone Cutthroat Trout on average. Hybrids also had a greater contribution to angler catch relative to their stocking rate compared to Yellowstone Cutthroat Trout. However, there is potential that stocking additional fish may negatively affect growth—something that may be worthwhile to monitor in the future if changes in stocking rate are implemented (Lorenzen and Enberg 2002).

A range of values was simulated for the instantaneous fishing mortality rates in this study rather than a single value due to uncertainty in how these parameters would change under implementation of the alternative management scenarios. It was assumed that catch would increase with additional fishing opportunity regardless of the bag limit. However, this may not be the case in practice,

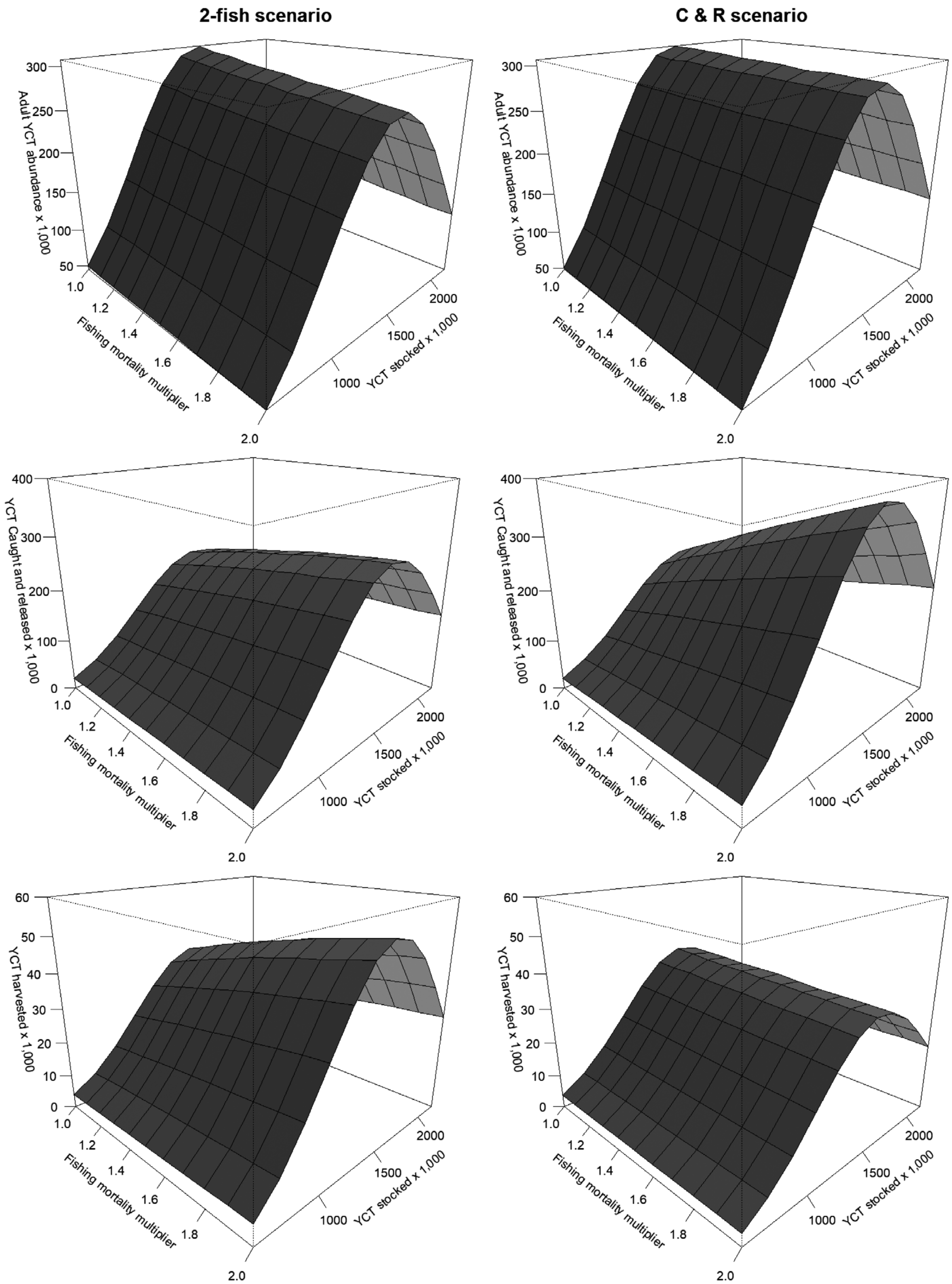

FIGURE 6. Predicted Yellowstone Cutthroat Trout (YCT) adult abundance (top panels), number caught and released (middle panels), and number harvested (bottom panels) at Henrys Lake, Idaho, given the number of fish stocked and the fishing mortality given a two-fish bag limit (left panels) and catch-and-release (C&R) regulations (right panels). The fishing mortality multiplier is the simulated increase compared to the current estimated fishing mortality. The surfaces are represented by the median of the predicted parameters.

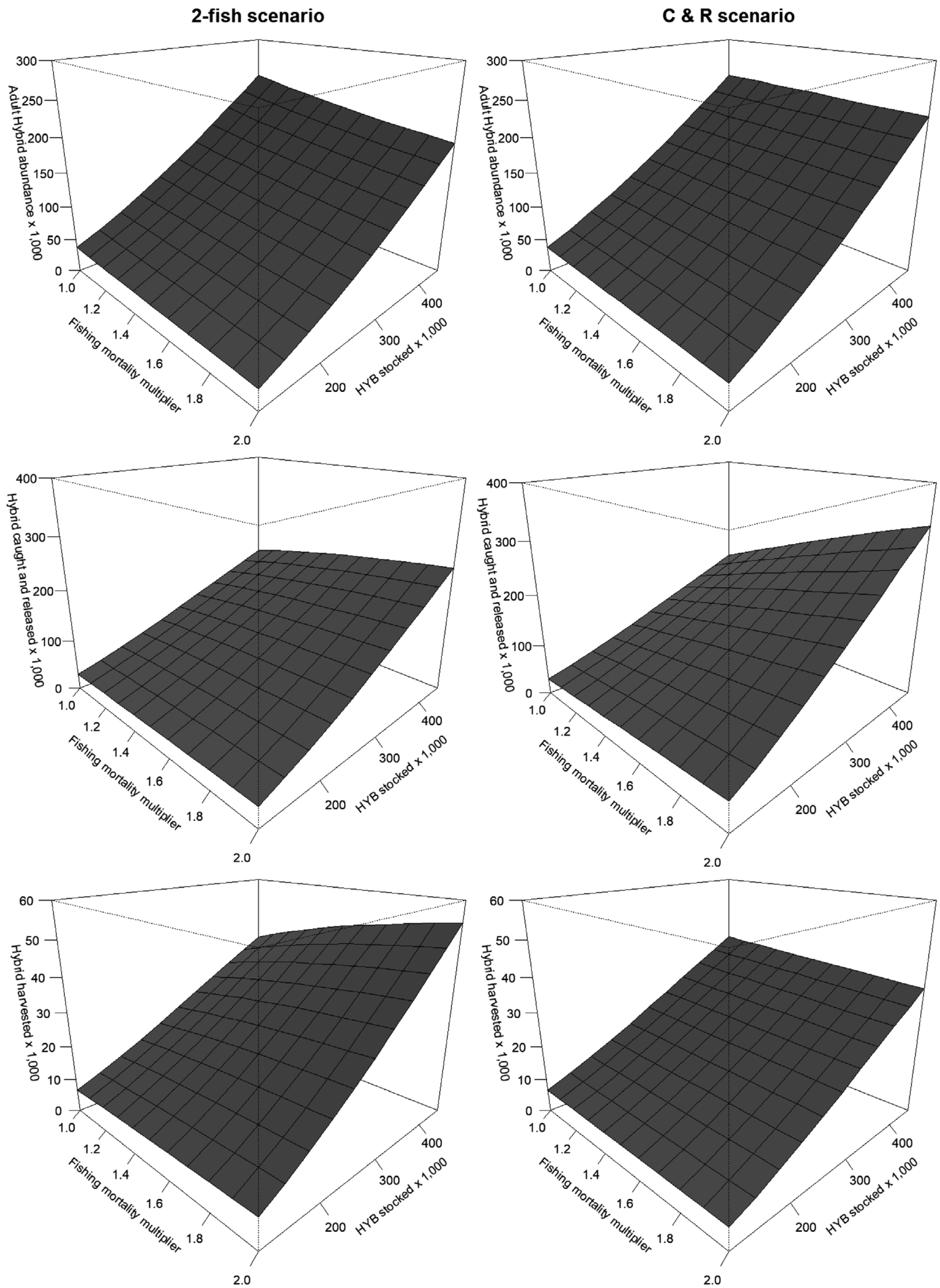

FIGURE 7. Predicted Yellowstone Cutthroat Trout × Rainbow Trout hybrid (HYB) adult abundance (top panels), number caught and released (middle panels), and number harvested (bottom panels) at Henrys Lake, Idaho, given the number of fish stocked and the fishing mortality given a two-fish bag limit (left panels) and catch-and-release (C&R) regulations (right panels). The fishing mortality multiplier is the simulated increase compared to the current estimated fishing mortality. The surfaces are represented by the median of the predicted parameters.

particularly for the C&R scenario. For instance, van Poorten and Post (2005) found that catchability of a previously unexploited Rainbow Trout population quickly declined with the introduction of catch-and-release angling. The authors suggested that behavioral changes may have been responsible for the temporal decrease in catchability but also noted decreases in catchability in already exploited populations due to seasonal changes. Askey et al. (2006) also concluded that a decline in catchability of Rainbow Trout was due to learned behavior from catch-and-release angling. Catch rates of Yellowstone Cutthroat Trout and hybrids at Henrys Lake are often highest near the opening of the spring fishing season following the winter and spring closure (Heckel et al. 2020). Catch rates may decrease during this time period with the implementation of a year-round fishing season, resulting in no net change in catch. However, catch rates at Henrys Lake also tend to increase again during the initial ice-fishing period and then decline as the ice fishery progresses, which suggests that changes in catchability may be due to seasonal changes rather than behavioral changes that may occur during the time period when the fishery is closed. Additionally, Askey et al. (2006) and van Poorten and Post (2005) focused on Rainbow Trout, which generally were not caught and released multiple times. Schill et al. (1986) estimated that Yellowstone Cutthroat Trout in the Yellowstone River were caught 9.7 times on average throughout the fishing season, suggesting that they may not have the same propensity as Rainbow Trout to learned behavioral changes due to catch-and-release angling.

Combining the data sets collected at Henrys Lake into a single model allowed for estimation of parameters, such as abundance and age-specific fishing and natural mortality, which were not estimable when analyzed separately. However, several assumptions were still required to allow for parameters to be uniquely estimated. For instance, it was assumed that mean gill-net catchability did not vary through time and was equal for Yellowstone Cutthroat Trout and hybrids. Several studies have suggested that catchability may not be constant (Hilborn and Walters 1992; Harley et al. 2001; DuFour et al. 2019). In addition, only 1 year of fin-clipping and maturity data were available to estimate the probability that a Yellowstone Cutthroat Trout would be captured at the hatchery trap. We also assumed that growth did not change throughout the sampling period, which could have resulted in inaccurate ages assigned to the fishery-dependent data. These assumptions can be evaluated in the future with little additional effort beyond what is currently being expended while monitoring the fishery. Furthermore, it was assumed that (1) the age distribution of fish that were caught and released was similar to the age distribution of fish that were harvested and (2) the probability that a fish would die as a result of being caught and released was 0.05. Some studies have suggested that size structure of harvested and released fish may differ (Lennox et al. 2016), and probability of postrelease mortality has varied among studies (Schill et al. 1986; Taylor and White 1992; Schill 1996). However, catch-and-release mortality accounted for a relatively small proportion of total mortality in this study.

Building population models, estimating model parameters, and projecting outcomes of alternative management strategies and their uncertainties are recognized as a powerful tool for informing management decisions, particularly when competing management objectives (e.g., concurrent harvest and catch-and-release fisheries) are desired (Maunder et al. 2006; Butterworth 2007; Punt et al. 2016). Although many of the parameters were estimated relatively precisely in this study, predictions about the future state of abundance and catch contained a considerable amount of uncertainty. It is likely that variability about future predictions was a result of the complex processes that generate abundance of trout in Henrys Lake rather than insufficient data. For instance, there was high annual variability in fishing and natural mortality for most age-classes in this study; such uncertainties are likely irreducible in practice (Mangel 2000). Integrated models are acknowledged as providing more accurate propagation of uncertainty in the future state of nature (Aeberhard et al. 2018) compared to deterministic models (which contain no uncertainty) or two-stage simulation models, where parameters and stochasticity are supplied externally (e.g., Leslie matrix projection models) to the model (Maunder and Punt 2013). Consequently, integrated models can result in larger prediction uncertainty (e.g., McCormick et al. 2021a, 2021b) than more traditional methods that may ignore or fail to fully account for uncertainty—particularly process uncertainty (Maunder and Punt 2013). Underestimation of prediction uncertainty can result in misleading low quantification of risk of alternative management or harvest scenarios (Butterworth et al. 2010). Nonetheless, decisions about management of Henrys Lake are required in spite of the relatively large amount of uncertainty in predictions. Generally, precautionary approaches (i.e., more risk averse) are applied when making management decisions in the presence of uncertainty (Richards and Maguire 1998) due to potential negative long-term consequences of harvest for naturally reproducing fish populations. However, in the case of Henrys Lake, long-term consequences of overharvest are not necessarily a concern because recruitment is mostly dependent on fingerling stocking and any overharvest risk would be short term and short lived. Additionally, evaluations of management strategies, such as those conducted in this study, are generally concerned with the relative performance of alternative management scenarios rather than absolute performance of any single alternative (Butterworth et al. 2010). However, uncertainty in predictions about the future state of abundance and catch in this study elucidates the need for continued monitoring at Henrys Lake and recognition that population modeling is an iterative process to be continued in the future rather than a completed task.

Integrated catch-at-age models are rarely published for relatively small inland recreational fisheries such as Henrys Lake (Feltz and Catalano 2017). Moreover, we are unaware of any published integrated assessments for fisheries that are maintained or supplemented through juvenile fish stocking. However, collecting a time series of catch-at-age data from such fisheries is not uncommon (e.g., Parsons and Pereira 2001; Felts et al. 2020; McDougall et al. 2020; Budy et al. 2021). Estimating recruitment using catch-at-age models for populations with natural recruitment can add considerable uncertainty to estimated parameters and predictions (Fournier and Archibald 1982; Maunder and Deriso 2003; Maunder and Piner 2015). However, recruitment is often known with a relatively high level of certainty in fisheries that are primarily supported by supplemental stocking, which can allow for estimation (or more precise estimation) of parameters using relatively simple integrated models that may not be estimable in fisheries with only natural recruitment. For example, Porch et al. (2006) and Feltz and Catalano (2017) showed how a statistical catch-free model could be used to estimate mortality and an index of recruitment as parameters in the model. Integrating stocking data when applicable in such a model could allow for estimation of additional parameters, such as abundance and age-specific mortality, in a single model. The state-space formulation of the model used in this study allows for intuitive integration of additional data by conveniently separating observation and population dynamics models while accounting for multiple sources of uncertainty (Newman et al. 2014). In the case of Henrys Lake, the proposed management alternatives would affect both fishing and natural mortality; thus, it was critical to estimate each parameter separately in the model. Integrating the available data sets in a single analysis allowed us to forecast the state of the fishery while accounting for potential changes to fishing and natural mortality under each scenario. Henrys Lake is not unique in that certain management actions may affect fishing mortality while others may affect natural mortality. However, rarely do models allow for estimating the effects of management actions on each parameter separately. Integrated catch-at-age models provide one potential method to achieve this objective using a variety of data types (Maunder and Punt 2013). Developing hypotheses about which dynamic rates will be affected by alternative management actions and designing monitoring programs that allow for estimation of such parameters using integrated models can help inform management evaluations prior to implementation.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.