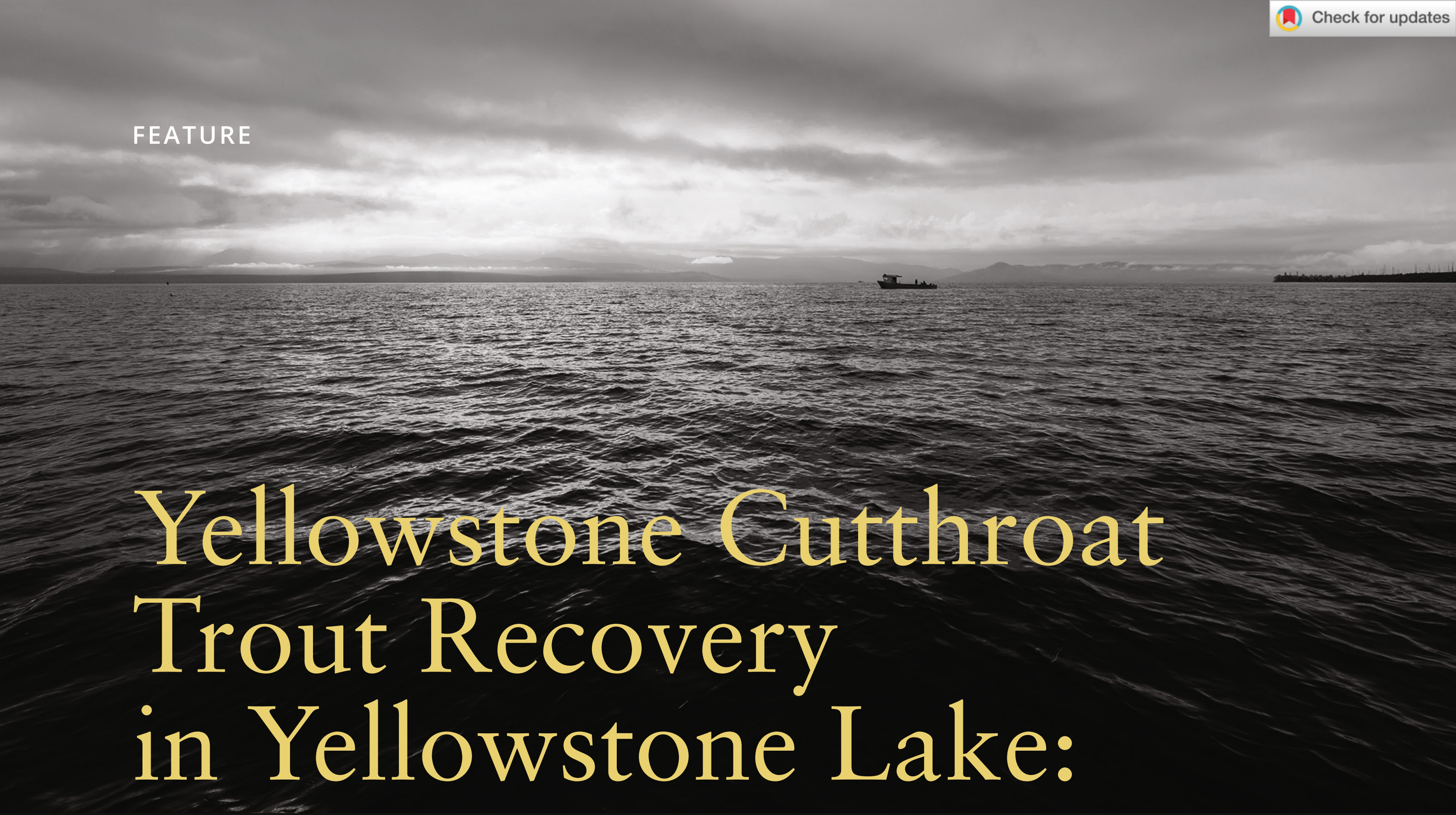

FEATURE

# Yellowstone Cutthroat Trout Recovery in Yellowstone Lake: Complex Interactions Among Invasive Species Suppression, Disease, and Climate Change

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Gill netting boat on Yellowstone Lake, Yellowstone National Park. Photo credit: Christopher Guy, U.S. Geological Survey


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In Yellowstone Lake, Wyoming, the largest inland population of nonhybridized Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, hereafter Cutthroat Trout, declined throughout the 2000s because of predation from invasive Lake Trout *Salvelinus namaycush*, drought, and whirling disease *Myxobolus cerebralis*. To maintain ecosystem function and conserve Cutthroat Trout, a Lake Trout gill netting suppression program was established in 1995, decreasing Lake Trout abundance and biomass. Yet, the response of Cutthroat Trout to varying Lake Trout suppression levels, collectively with the influence of disease and climate, is unknown. We developed an ecosystem model (calibrated to historical data) to forecast (2020–2050) whether Cutthroat Trout would achieve recovery benchmarks given disease, varying suppression effort, and climate change. Lake Trout suppression influenced Cutthroat Trout recovery; current suppression effort levels resulted in Cutthroat Trout recovering from historical lows in the early 2000s. However, Cutthroat Trout did not achieve conservation benchmarks when incorporating the influence of disease and climate. Therefore, the National Park Service intends to incorporate age-specific abundance, spawner biomass, or both in conservation benchmarks to provide better indication of how management actions and environmental conditions influence Cutthroat Trout. Our results illustrate how complex interactions within an ecosystem must be simultaneously considered to establish and achieve realistic benchmarks for species of conservation concern.

## INTRODUCTION

Disturbances occurring during the Anthropocene have altered conservation baselines to the extent where even protected ecosystems, such as U.S. national parks, and the species they support, are threatened (Palomo et al. 2014). Fishes, as one of the most at-risk vertebrate groups in the world, can be especially sensitive to anthropogenic disturbances (Darwall and Freyhof 2015). Salmonids are particularly susceptible to anthropogenic disturbances due to synergistic effects resulting from climate change-driven warming temperatures and nonnative species introductions that lead to competition, predation, or hybridization between native and nonnative fishes (Muhlfeld et al. 2019; Sinnatamby et al. 2020).

In North America, the negative effects of climate change and invasive species have profoundly affected Cutthroat Trout *Oncorhynchus clarkii* to the extent that all subspecies are protected at some level (Budy et al. 2019). For example, extirpation or introgression occurs in 71% of the historical distribution of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* (Budy et al. 2019), a species with high social (Quist and Hubert 2004), economic (Gresswell and Liss 1995), and ecological value (Koel et al. 2005). Yellowstone Cutthroat Trout are considered a keystone species as a prey resource for many terrestrial species, thus providing an important aquatic–terrestrial linkage (Koel et al. 2019).

In Yellowstone National Park, the largest population of nonhybridized Yellowstone Cutthroat Trout, hereafter Cutthroat Trout, occurs in Yellowstone Lake, making the population of utmost conservation importance. Throughout the late 1990s and 2000s, abundance of Cutthroat Trout declined because of increasing abundance of Lake Trout *Salvelinus namaycush*, outbreaks of whirling disease *Myxobolus cerebralis*, and climate change (Koel et al. 2006, 2020a; Kaeding 2020). Lake Trout, an invasive species in the western United States first discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996), caused the decline of the Cutthroat Trout population through predation (Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023). The decline of Cutthroat Trout in Yellowstone Lake caused a trophic cascade (Tronstad et al. 2010) that affected terrestrial and aquatic food webs throughout the Greater Yellowstone Ecosystem (Koel et al. 2019), threatening the integrity of one of the largest, mostly intact, temperate zone ecosystems in the world (National Park Service 2020). To maintain ecosystem function and conserve the Cutthroat Trout population, a Lake Trout gill netting suppression program was initiated in 1995 by the National Park Service (NPS) with the objective of decreasing Lake Trout abundance (Syslo et al. 2016; Koel et al. 2020a).

The Lake Trout gill netting suppression program has continued into the 2020s, and available evidence suggests gill netting has reduced biomass of adult Lake Trout, which have the largest predatory effect on Cutthroat Trout, by >79%, despite recruitment of immature Lake Trout remaining high (Syslo et al. 2011, 2020; Koel et al. 2020a). Single-species statistical catch-at-age modeling is used to annually estimate Lake Trout population dynamics and demographics, which in turn are used to forecast the response of the Lake Trout population to suppression-induced fishing mortality levels (Syslo et al. 2011, 2020). This approach has been useful to estimate the amount of gill netting effort needed to suppress Lake Trout (Syslo et al. 2020), with a suppression program cost of US$2.85 million in 2019 (Koel et al. 2020a). Ways to reduce suppression cost, including reducing gill netting effort and using alternative suppression methods, such as embryo suppression via carcass analog pellets (Koel et al. 2020b, 2023a), have been suggested. Carcass analog pellets deposited on Lake Trout spawning sites have proven to increase mortality in Lake Trout embryos at spawning locations (Koel et al. 2020b, 2023a). Pellet application is unlikely to have long-term effects on nontarget organisms, such as benthic invertebrates and periphyton (Briggs et al. 2020; Lujan et al. 2022), making pellets a promising alternative suppression method in Yellowstone Lake. However, the response of the focal conservation species, Cutthroat Trout, to various Lake Trout suppression strategies is unknown.

Abiotic factors and complex predator–prey dynamics within the Yellowstone Lake ecosystem have also been identified as contributing to changes in Cutthroat Trout abundance (Kaeding 2020). Whirling disease prevalence and severity has been intermittently quantified for Cutthroat Trout in Yellowstone Lake and may have contributed to the population decline during the early 2000s (Koel et al. 2005, 2006). Moreover, climate change can affect fish habitat (Gaeta et al. 2014; Glassic and Gaeta 2019, 2020) and may influence year-class strength in Yellowstone Lake by inhibiting outmigration of Cutthroat Trout from tributaries to the lake during drought (Koel et al. 2005; Kaeding 2020). Lake Trout exhibit diet plasticity in Yellowstone Lake—as Lake Trout density increases, consumption of Cutthroat Trout decreases, whereas consumption of amphipods increases (Glassic et al. 2023). Cutthroat Trout have not recovered as expected in comparison with the reduction of predatory Lake Trout due to Lake Trout diet plasticity (Glassic et al. 2023). Although recovery benchmarks for Cutthroat Trout exist (Koel et al. 2010; Koel et al. 2020a), understanding how Cutthroat Trout respond to Lake Trout suppression simultaneously with disease prevalence, diet plasticity of Lake Trout, and climate change has not been evaluated.

Combining knowledge about species of conservation concern, invasive species, and environmental factors is crucial given cascading effects of invasive species (Zavaleta et al. 2001; Tronstad et al. 2010; Chagaris et al. 2017; Koel et al. 2019) and the complexities that environmental conditions can introduce to conservation or suppression goals (Healy et al. 2020). Though single-species management strategies can result in desired management outcomes, community interactions and environmental factors can influence the efficacy of different strategies (NOAA 2020). Ecosystem-based models incorporate biotic and abiotic factors that may influence management outcomes and have proven to be useful in the management of invasive species, predator–prey systems, and commercial fisheries, particularly in marine ecosystems (e.g., Colléter et al. 2015; Chagaris et al. 2017, 2020). Despite a push to apply ecosystem-based models to freshwater fisheries, much of the application to date has been limited to the Great Lakes (e.g., Rutherford et al. 2021). A unique opportunity existed to apply an ecosystem-based approach to a highly valued species and ecosystem given the synergistic threats faced by Cutthroat Trout in Yellowstone Lake, the trophic cascade that resulted from Lake Tout invasion, food web dynamics, and complex predator–prey dynamics between Cutthroat Trout and Lake Trout.

We estimated whether the Cutthroat Trout population would reach established recovery benchmarks outlined by Koel et al. (2010; Table 1), given available suppression strategies, need for reduction in suppression program cost, disease, climate change, and predator–prey dynamics. Specific questions related to Lake Trout suppression management actions and the subsequent response by Cutthroat Trout that we addressed were: How often would the Cutthroat Trout and Lake Trout populations achieve benchmarks in the future if (1) Lake Trout gill net suppression effort was maintained or reduced from current levels, (2) Lake Trout gill net suppression effort was reduced and carcass analog pellets are applied to spawning reefs, and (3) Lake Trout gill net suppression effort was reduced during a forecasted climate change regime? Answers to these questions will improve the efficacy of the Lake Trout suppression program, aid in understanding whether benchmarks established in 2010 remain realistic, and help secure the long-term persistence of Cutthroat Trout in the Yellowstone Lake ecosystem.

## METHODS

### Study Site

Yellowstone Lake is a large, oligo-mesotrophic lake (Theriot et al. 1997) located in Yellowstone National Park, Wyoming (Figure 1). The lake is the largest lake above 2,000 m in elevation in North America with a surface area of 34,020 ha, a mean depth of 48 m, and a maximum depth of 133 m (Kaplinski 1991). The lake is typically ice covered from mid-December until late May or early June. Water temperatures fluctuate between 9°C and 18°C in the summer and a thermocline develops during stratification from July through September at about 15 m (Koel et al. 2019).

The climate of the Greater Yellowstone Area has changed compared to 1950 and is projected to continue to change (Hostetler et al. 2021). Observations of air temperature have increased by 1.3°C since 1950 and a 25% loss in snowfall has been recorded (Hostetler et al. 2021). Compared to the 30-year period between 1986 and 2005, a 40% loss in snowpack and a 35% decrease in summer runoff is expected in the next century (Hostetler et al. 2021). Within Yellowstone Lake, surface water temperatures increased by approximately 1.9°C from 1976 to 2018 (Koel et al. 2019).

### Ecopath with Ecosim

#### *The Yellowstone Lake EwE Model*

Broadly, Ecopath with Ecosim (EwE) is a modeling software developed to analyze ecosystem trophic mass balance (biomass and flow) with a dynamic component to explore the past and future influence of fishing and environmental disturbances (Christensen and Walters 2004). Ecopath with Ecosim is open source (https://ecopath.org/), and details of the software and how Ecopath uses data inputs and species interactions can be found on the developer website (https://bit.ly/3PzMSll). The Ecopath component of EwE is a static, mass-balance model of the ecosystem, which provides initial conditions for dynamic simulations in the Ecosim module. Ecopath requires inputs of biomass, consumption rates, mortality rates, diet compositions, and fisheries removals. Ecosim simulates biomass dynamics on a monthly time step as a series of differential equations, where a biomass change for each group is predicted as consumption minus losses to predation, fishing, migration, and other unexplained natural mortality (Walters et al. 1997).

In Ecosim, consumption by predators is modeled using vulnerability parameters, which are based on foraging arena theory (Ahrens et al. 2012), where predation rates are limited by prey biomass "moving" from invulnerable states (resting, hiding) into the foraging arena and becoming

TABLE 1. Primary and secondary benchmarks for Yellowstone Cutthroat Trout and Lake Trout in Yellowstone Lake used for comparisons for the forecasted Ecosim models. Individual age-class benchmarks for Yellowstone Cutthroat Trout calculated as the mean CPUE from 1980 to 1989 for the primary benchmark and the mean CPUE from 1990 to 1999 for the secondary benchmark; 95% confidence intervals (CI) calculated from CPUE from 1980 to 1989 for the primary benchmark and from 1990 to 1999 for the secondary benchmark. Primary benchmark for Lake Trout from Koel et al. (2010).

| Species and age-class | Primary benchmark (CI) | Secondary benchmark (CI) |
|---|---|---|
| Yellowstone Cutthroat Trout age 2 CPUE | 14.5 (10.9–18.1) | 8.3 (6.2–10.3) |
| Yellowstone Cutthroat Trout age 3 CPUE | 11.7 (7.9–15.6) | 6.7 (5.1–8.5) |
| Yellowstone Cutthroat Trout age 4 | 9.9 (6.3–13.4) | 6.6 (5.6–7.6) |
| Yellowstone Cutthroat Trout ≥ age 5 CPUE | 9.6 (6.8–12.4) | 9.5 (8.8–10.1) |
| All Yellowstone Cutthroat Trout (≥ age 2) CPUE | 41.9 (30.6–53.4) | 26.3 (22.1–30.5) |
| All gill-netted Lake Trout (≥ age 2) abundance | 100,000 | No benchmark |

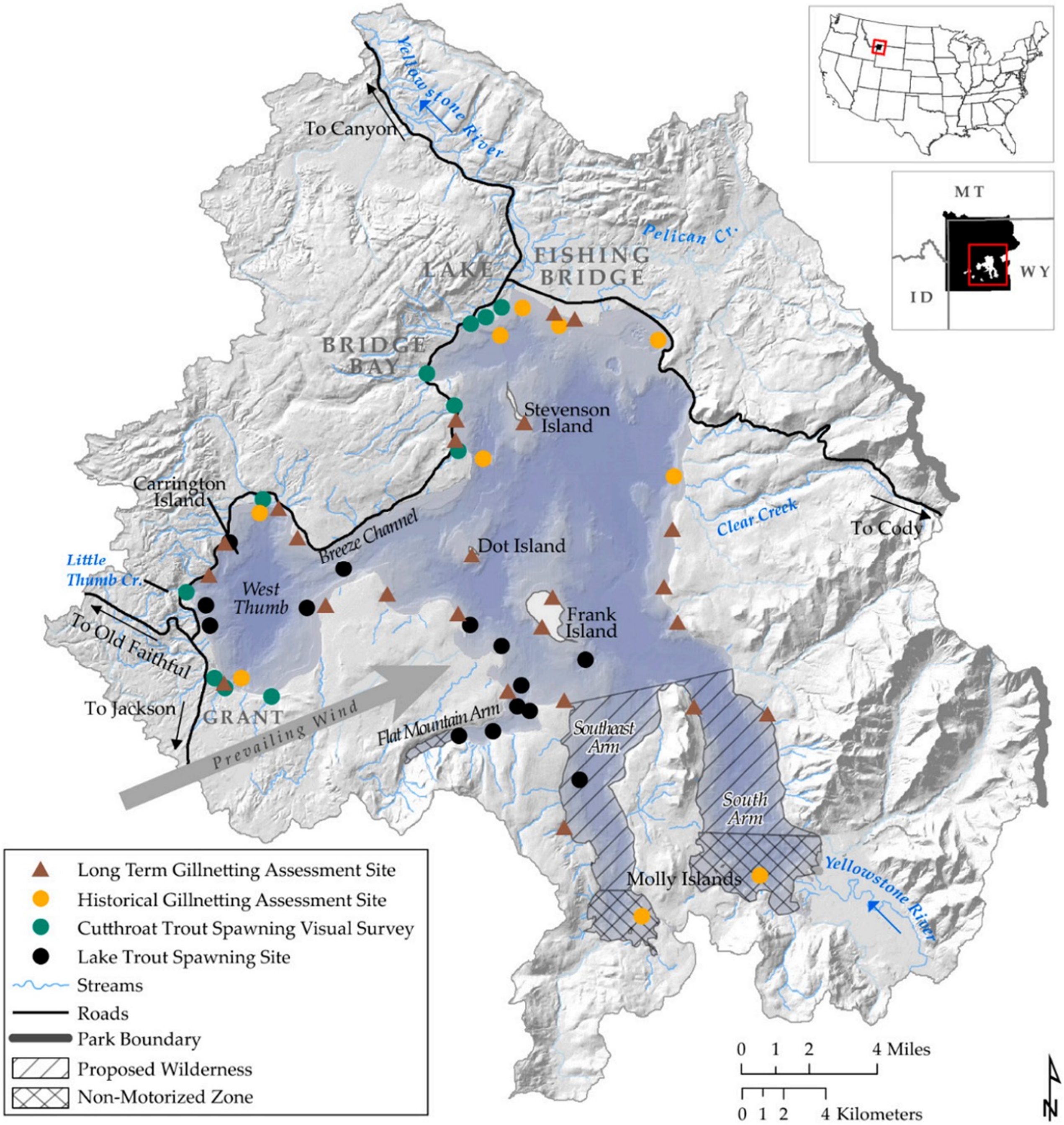


FIGURE 1. Yellowstone Lake within Yellowstone National Park in northwestern Wyoming, USA, indicating locations of long-term gill netting assessment sites for annual lakewide monitoring of Yellowstone Cutthroat Trout and Lake Trout (gill netting data used for historical model fitting), historical gill netting assessment sites that were sampled for Yellowstone Cutthroat Trout (prior to 2010; gill netting data used for historical model fitting), tributaries visually surveyed for spawning Yellowstone Cutthroat Trout each spring (potentially affected by future climate change), and verified Lake Trout spawning sites (where carcass analog pellets would be applied for Lake Trout embryo suppression; Koel et al. 2023a). Map provided by coauthors from the National Park Service.

vulnerable to predation. At high vulnerability values (>10), prey become vulnerable to predation at faster rates, which implies strong top–down control, leading to greater predator biomass increases and a reciprocal decline in prey. At low vulnerability values (<2), predation mortality rates remain relatively constant when predator abundance changes (Chagaris et al. 2015). Vulnerability parameters are influential in Ecosim models and are estimated by fitting models to time series of observed abundance and fishing landings (i.e., harvest). The application of Ecopath for evaluating Lake Trout suppression in Yellowstone Lake relied on mass-balance modeling of 1980 conditions and Ecosim time dynamic simulations calibrated to observed data to create projections (2020–2050).

The Ecopath model that we developed emphasized dynamics between Lake Trout and Cutthroat Trout in Yellowstone Lake (Table 2). Lake Trout were represented in the model by five age-classes (≤6 months, 7 months to 1 year, 2 years, 3–4 years, ≥5 years) to capture application of suppression strategies (Koel et al. 2020a; Syslo et al. 2020) and ontogenetic diet shifts (Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023). Cutthroat Trout were represented by five age-classes (≤23 months, 2 years, 3 years, 4 years, ≥5 years) to capture ontogenetic diet shifts (Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023), vulnerability to Lake Trout predation (≤23 months, 2 years, 3 years; Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023), vulnerability to tributary disconnection or reduction in discharge (≤23 months; Kaeding 2020), and susceptibility to disease (≤23 months, 2 years; Koel et al. 2006, 2019). Other organisms included in the model were aggregated or listed as a single species to reflect the categories from diet studies of Lake Trout and Cutthroat Trout (Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023) and were necessary for a complete food web. One fisheries fleet was included in the model to represent the Lake Trout gill net suppression effort in Yellowstone Lake (Koel et al. 2020a). Initial balancing of the Yellowstone Lake Ecopath model included parameters relating to biomass, diets, and the suppression fishery (Tables S1–S6). The resulting model consisted of 18 biomass pools, 12 fish groups, 3 invertebrate groups, 2 primary producers, and 1 detritus group (Table 2; Figure 2). The balancing of the Ecopath model was necessary for historical fitting and future projections. The Ecopath model was successfully balanced (most adjustments were made to Lake Trout landings and initial Lake Trout biomass) to simulate invasion of Lake Trout (Table S7) so that further analysis could be conducted on the community of Yellowstone Lake.

### Assumptions

The Ecopath model assumes the food web is balanced for the first modeling year. We selected 1980 as the Ecopath base year due to data availability and because the Lake Trout population was not yet established or detected. By choosing 1980 as the first modeling year, we assumed that the ecosystem was in a natural, balanced state before Lake Trout invasion. We modeled the invasion of Lake Trout by including low initial Lake Trout biomass and creating an artificial fishery to suppress their biomass until the estimated year of invasion, similar to Chagaris et al. (2017). Throughout our simulations, we assumed that gear selectivity was constant.

We included Yellowstone Lake water level as a proxy for climate change in Ecosim model calibration and forecasting scenarios. Water levels from 1980 through 2019 (Table S9) were applied as a forcing function on the search rate of the consumer group for Cutthroat Trout ≤23 months for model calibration. Forcing functions represent physical or other environmental parameters that may influence trophic interactions. For example, at the base water level, the production/

TABLE 2. Inputs for groups included in the 1980 balance year for the Yellowstone Lake, Yellowstone National Park, Wyoming, USA, Ecopath model.

| Group name | Biomass (*t*/km²) | Instantaneous total mortality (per year) | Production/ biomass (per year) | Consumption/ biomass (per year) |
|---|---|---|---|---|
| Lake Trout ≤6 months | Ecopath estimated | 3.97[g] | – | Ecopath estimated |
| Lake Trout 7 months to 1 year | Ecopath estimated | 1.72[g] | – | Ecopath estimated |
| Lake Trout age 2 | Ecopath estimated | 1.02[g] | – | Ecopath estimated |
| Lake Trout age 3–4 | Ecopath estimated | 0.77[g] | – | Ecopath estimated |
| Lake Trout ≥ age 5 | 0.02* | 0.32[g] | – | 1.22[h] |
| Yellowstone Cutthroat Trout ≤23 months | Ecopath estimated | 1.33[a] | – | Ecopath estimated |
| Yellowstone Cutthroat Trout age 2 | Ecopath estimated | 0.48[a] | – | Ecopath estimated |
| Yellowstone Cutthroat Trout age 3 | Ecopath estimated | 0.41[a] | – | Ecopath estimated |
| Yellowstone Cutthroat Trout age 4 | Ecopath estimated | 0.46[a] | – | Ecopath estimated |
| Yellowstone Cutthroat Trout ≥ age 5 | 3.77[a] | 0.33[a] | – | 2.95[i] |
| Longnose Sucker | 0.89[b] | – | 1.63 | 8.29[j] |
| Leucisids | 0.01[c] | – | 0.74 | 14.49[k] |
| Invertebrates | 1.28[d] | – | 8.92 | 17.16** |
| Amphipods | 1.00[d] | – | 4.97 | 13.50** |
| Zooplankton | 6.33[e] | – | 10.01 | 24.64** |
| Periphyton | 0.13[f] | – | 122.41 | 0 |
| Phytoplankton | 0.83[e] | – | Ecopath estimated | 0 |
| Detritus | 5.00 | – | – | – |

*Calculated using Monte Carlo simulation tool in Ecosim with 1,000 simulations and CV of 0.2.
**Value selected to balance model while keeping other parameters similar to published estimates.
[a]Derived from Walsworth and Gaeta, unpublished.
[b]Derived from Vinson et al. (2019).
[c]Derived from Stables and Perrin (2016).
[d]Derived from Wilmot et al. (2016).
[e]Derived from Tronstad et al. (2010).
[f]Derived from Lujan (2020).
[g]Derived from Syslo et al. (2020).
[h]Derived from FishBase Ecopath parameters life history tool for *Salvelinus namaycush*.
[i]Derived from FishBase Ecopath parameters life history tool for *Oncorhynchus clarkii*.
[j]Derived from FishBase Ecopath parameters life history tool for *Catostomus catostomus*.
[k]Derived from FishBase Ecopath parameters life history tool for *Richardsonius balteatus*.

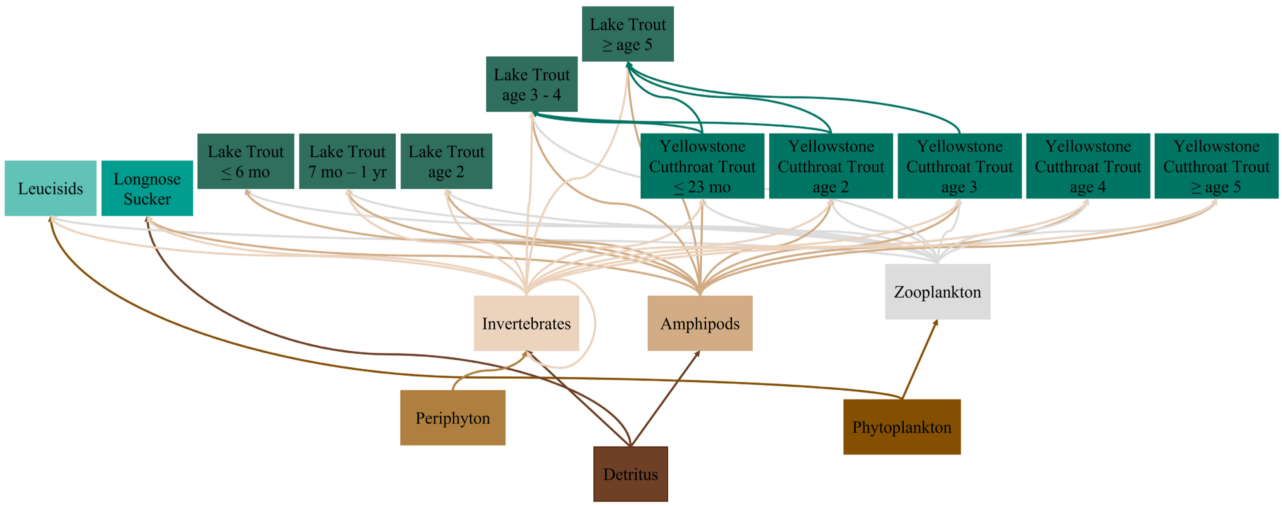


FIGURE 2. Yellowstone Lake, Wyoming, USA, food web diagram post Lake Trout introduction. Lines represent flow of biomass from prey to predator. Colors represent different groups included in the food web within the Ecopath with Ecosim modeling framework. Proportions of diet items contributing to Yellowstone Cutthroat Trout and Lake Trout diets change based on the biomass of other groups in Yellowstone Lake. Therefore, we did not include the magnitude of biomass flows or diet proportions in this conceptual diagram.

biomass of Cutthroat Trout ≤23 months is equal to the base Ecopath production/biomass. Any changes in relation to base water level (increase or decrease) force the production/biomass of Cutthroat Trout ≤23 months to change. In non-climate change forecasting scenarios, "normal" water levels for 2020–2050 were randomly sampled with replacement from the natural variation of water levels that occurred from 1980 through 2019 (Table S9) and were applied as a forcing function on the search rate of the consumer group Cutthroat Trout ≤23 months. We did not include any influence of water level on Lake Trout or other organisms included in the model due to lack of evidence showing a relationship between our measure of climate change (water level) and the non-trout groups.

Whirling disease, caused by an exotic parasite, was first documented in Cutthroat Trout in Yellowstone Lake in 1998 (Koel et al. 2006). Cutthroat Trout fry are most susceptible to infection in spawning tributaries immediately post hatch (Murcia et al. 2006). Although *M. cerebralis* was not detected in most spawning tributaries, some, including Pelican Creek and the Yellowstone River below the lake outlet, had 100% prevalence with high disease severity (Koel et al. 2006). Juvenile and adult Cutthroat Trout that survived *M. cerebralis* occurred within the lake with a prevalence of 10–20% over the past two decades (Koel et al. 2023b). As such, Cutthroat Trout from ≤23 months and 2 years in age were assumed susceptible to whirling disease for the fitting process and projection scenarios. We assumed a percentage of the population would contract whirling disease affecting survival, though prevalence may not be equivalent to the same percent decrease in survival. A challenge of including whirling disease in the model was that no prevalence data existed for the Ecopath base year (1980). Therefore, we assumed some baseline prevalence of whirling disease for years that did not have recorded prevalence data (Table S10). The baseline prevalence was calculated for use in the forecasting scenarios by scaling the forcing function assuming a maximum instantaneous mortality ($Z$) of 1.5. In each scenario, whirling disease was applied as an environmental response on mortality for Cutthroat Trout ≤23 months and 2 years, and assumed to follow the same pattern as 1980–2019 for any forecasting scenarios (Table S10).

Carcass analog pellets have been found to increase mortality in Lake Trout embryos at spawning reefs (Koel et al. 2020b, 2023a) and are believed to be a promising complimentary suppression method for Yellowstone Lake in addition to gill nets. Pellet application is unlikely to have long-term effects on nontarget organisms (Briggs et al. 2020; Lujan et al. 2022), did not deter future spawning by adults, or result in other unintended consequences (Koel et al. 2023a). We did not have specific information regarding the production of Lake Trout at different spawning sites and making assumptions about the effect of pellets at the different sites without those data could be misleading. Therefore, we assumed carcass analog pellets had equal application and equal mortality at all spawning sites to represent an ideal pellet application scenario. Some spawning sites are concentrated in distant locations or at depths that are too great for uniform pellet application from the lake surface (Koel et al. 2020b, 2023a). We acknowledge that application of carcass analog pellets to all spawning sites is currently infeasible due to the logistics that would be involved to make, transport, and apply the carcass analog pellets.

### Model Calibration

After food web linkages and fisheries were defined and balanced in Ecopath, we used Ecosim to fit our model to historical data. Historical data calibration was necessary to confirm that the model reflected observed dynamics as closely as possible so that future projections were realistic. To fit the model to historical data, we included inputs for biomass (Table S8), fishing effort (Table S8), fishing landings (Table S8), water level (Table S9), whirling disease (Table S10) time series, predator behavior parameters such as Lake Trout diet plasticity (Table S11), and vulnerability parameters. We incorporated Lake Trout diet plasticity into the model by adding a "switching power parameter" to Lake Trout 3–4 years and ≥5 years (Table S11). Water level affected Cutthroat Trout classes ≤23 months. Whirling disease affected Cutthroat Trout

≤23 months and 2 years. The vulnerability search ("Fit to time series" plugin) was iteratively fit until the sum of squares was minimized compared to the previous search to identify the best fit model (Chagaris et al. 2015).

#### *Incorporation of Uncertainty*

We incorporated uncertainty into the simulations by using Ecosampler (Steenbeek et al. 2018) to generate alternative mass balanced Ecopath models and then recalibrated each one to time series data. Ecosampler uses a Monte Carlo approach to randomly select Ecopath input values from a uniform distribution, where the mean was the Ecopath base value representing the first modeling year (1980) and the upper and lower limits were based on uncertainty in the source data (Table S12). If the selected parameters resulted in an unbalanced Ecopath model, they were discarded, and another draw was made. This continued until we obtained 30 mass balanced Ecopath models representing the 1980 condition of Yellowstone Lake. Because the Ecosim vulnerability parameters are conditioned on the Ecopath starting values, each of the 30 models was refit to our time series data using the same procedure outlined in the "Model Calibration" section of this paper. An Ecosampler record was not selected if the fitting procedure resulted in unstable predator–prey dynamics (i.e., either Cutthroat Trout or Lake Trout biomass crashed or exponentially increased within the first 10 years of the simulation, creating completely unrealistic biomass values) or if the sum of square deviations between observed and estimated exceeded 90.

#### *Forecasting Scenarios*

We used the Yellowstone Lake EwE model to forecast biomass for Lake Trout and Cutthroat Trout from 2020 to 2050 to address our research questions. Though biomass is used as the unit of comparison in EwE, we reported estimates in abundance for Lake Trout and CPUE for Cutthroat Trout because these units are most consistent with historical data and established benchmarks (refer to the supplementary materials regarding conversion of biomass to CPUE or abundance). Koel et al. (2010) established an initial benchmark for all Cutthroat Trout (i.e., all ages combined). However, we created benchmarks by age-classes to better understand the effects of management actions, disease, and climate for the ontogeny of Cutthroat Trout (Table 1). All Ecosim scenario output was compared to primary and secondary benchmarks for Cutthroat Trout and primary benchmarks for Lake Trout (Table 1).

### Suppression Effort Scenarios

Our first four scenarios evaluated whether the Cutthroat Trout CPUE would reach the recovery benchmarks (Table 1) given varying levels of Lake Trout suppression gill netting effort (1 unit effort = 100 m of net set for one night), whirling disease, and a forecasted non-climate change regime. The four suppression effort scenarios were a percentage of 97,397 units of suppression effort, which was the level of effort expended in 2018 (100% = 97,397 units; 75% = 73,048 units, 50% = 48,699 units, 25% = 24,349 units). The amount of effort in each scenario was held constant from 2020 to 2050.

### Carcass Analog Pellet Scenarios

We evaluated whether the Cutthroat Trout population would reach recovery benchmarks given use of carcass analog pellets, reduced effort of Lake Trout suppression gill netting at 25% and 50% of 97,397 units, whirling disease, and a forecasted non-climate change regime. We did not create scenarios including carcass analog pellets with 75% or 100% suppression gill netting effort because carcass analog pellets would ideally be used to increase suppression efficacy at low gill netting effort, while still reducing cost for the suppression program (addition of carcass analog pellets at high gill netting effort would increase program cost). For these scenarios, we reduced gill netting effort and added embryo mortality to Lake Trout assumed to be inflicted by carcass analog pellets. Carcass analog pellet application was simulated by applying a fishing mortality forcing function (instantaneous fishing mortality = 3.91; estimated from 98% mortality from Koel et al. 2020b) to Lake Trout ≤6 months from 2020 to 2050.

### Climate Change Scenarios

We evaluated whether the Cutthroat Trout population would reach recovery benchmarks given a forecasted climate change regime (i.e., a long-term [decadal] decrease in lake water level via a decrease in precipitation), reduced Lake Trout suppression gill netting effort at 50% and 75% of 97,397 units, and whirling disease. For the climate change scenarios, we wanted to simulate a potential decrease in lake level reflecting climate projections for the Greater Yellowstone Area. To simulate climate change, we created a distribution of Yellowstone Lake level from 1986 through 2005 (the same years as the comparison in Hostetler et al. 2021). We then created another distribution for the climate change scenario ($n = 100$), where the mean was 35% less than the distribution from 1986 through 2005, reflecting the reduction in summer runoff expected as estimated by Hostetler et al. (2021), and the standard deviation was the same value as in 1986–2005. The values for the climate change scenario from 2020 to 2050 were randomly selected with replacement from the climate change scenario distribution (Table S13).

## RESULTS

### Historical Fitting and Uncertainty

The Ecosim model reproduced historical time series in Cutthroat Trout CPUE, Lake Trout abundance, and catch for the period 1980–2019, with a total sum of squares of 59.28 (Figure 3). Inclusion of Lake Trout diet plasticity, whirling disease, and water level were necessary to fit Cutthroat Trout to the historical CPUE time series. Vulnerabilities were estimated to be high (≥60) for Lake Trout on their prey, especially Cutthroat Trout, and for Cutthroat Trout on zooplankton and amphipods (Table S14). The model fit best to Lake Trout time series and Cutthroat Trout time series; historical trends were not as closely reproduced for other organisms as the trout groups (Figure S1). The model underpredicted relative biomass of age 2 and ≥age 5 Cutthroat Trout for some years (Figure 3). Of the 30 randomly selected Ecosampler runs, 18 were selected to simulate error around model fit and scenario projections because they produced reasonable biomass projections and had a sum of squares <90. All historical fitting figures and tables, as well as Ecosampler error model fits and scenario projections, are available in the supplemental material (Figures S1–S6).

### Forecasting Scenarios

#### *Suppression Effort Scenarios*

Cutthroat Trout CPUE and Lake Trout abundance were compared to recovery benchmarks based on past CPUE or

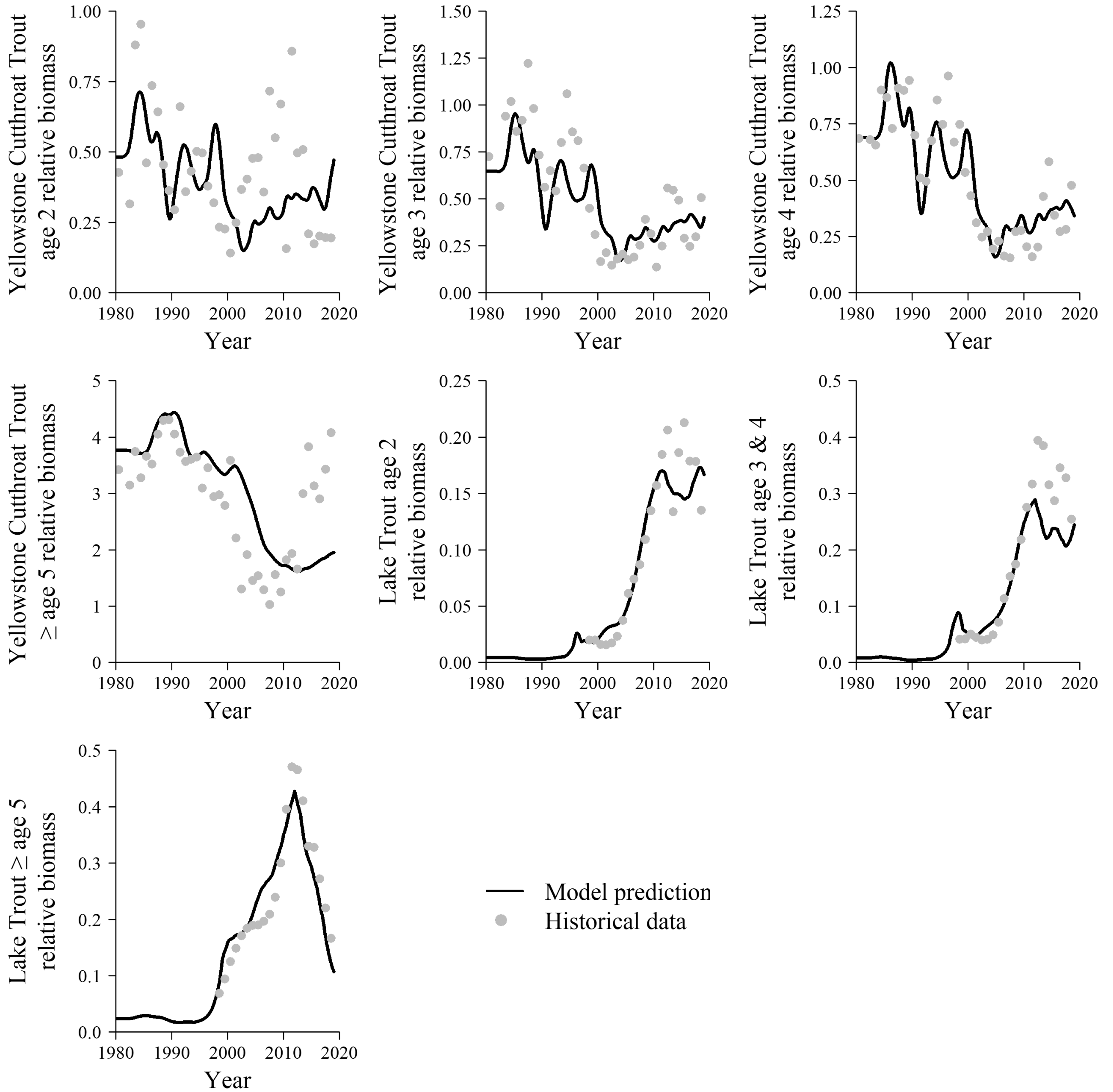


FIGURE 3. Ecosim model calibration to historical data for Yellowstone Cutthroat Trout and Lake Trout in Yellowstone Lake, Yellowstone National Park, Wyoming, USA, from 1980 to 2019. Model prediction is a black, solid line and historical data are gray points. Output is shown in relative biomass because historical data inputs were CPUE for Yellowstone Cutthroat Trout and biomass for Lake Trout. Points do not account for error in historical data.

abundances for suppression effort scenarios (100%, 75%, 50%, 25% of 97,397 units) with whirling disease under a forecasted (2020–2050) non-climate change regime. Cutthroat Trout recovered to the highest CPUE with 100% of the Lake Trout suppression effort and had potential to become extirpated at 25% effort (Figures 4–6). For the 100% effort scenario, all Cutthroat Trout ≥age 2 achieved secondary benchmarks in 100% of forecasted years (Figures 4–6; Table 3). When reducing suppression effort to 75%, percentage of years achieving the secondary benchmark was the same as the 100% effort scenario for all age-classes except age 4 Cutthroat Trout, which was reduced by 15 percentage points (Figures 4 and 5; Table 3). The percentage of years achieving the secondary benchmark was reduced for all ages for the 50% effort scenario (Figures 4 and 5; Table 3). When reducing effort to 25%, Cutthroat Trout ages 2–4 achieved secondary benchmarks 7–23% of forecasted years, age 5+ achieved secondary benchmarks 0% of forecasted years, and all Cutthroat Trout ≥age 2 achieved secondary benchmarks 26% of forecasted years (Figures 4 and 5; Table 3). More variation in the alternative ecosystem fits (i.e., proxy for error) was associated with Cutthroat Trout achieving benchmarks when Lake Trout suppression effort decreased from 100% (Figure 4).

Not surprisingly, Cutthroat Trout achieved primary benchmarks fewer times than secondary benchmarks, even

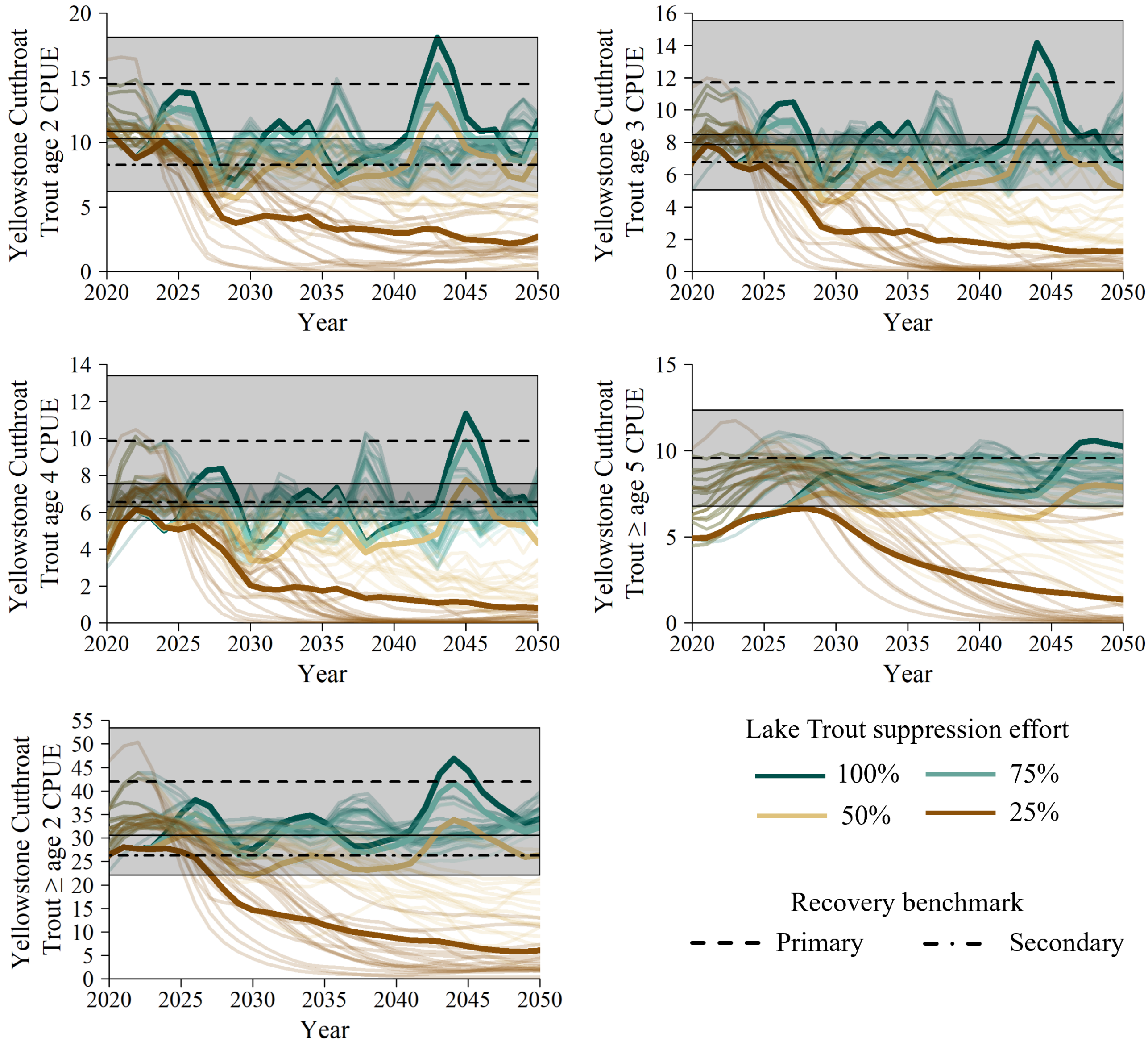


FIGURE 4. Yellowstone Cutthroat Trout simulations in Yellowstone Lake from 2020 to 2050 at varying Lake Trout suppression effort scenarios (percentage of 97,397 units of effort). Best model fit is represented by solid bold lines. Alternative ecosystem fits, a proxy for error, is represented by transparent lines. Recovery benchmarks were derived for each age-class from Koel et al. (2010); individual age-class benchmarks were the mean CPUE from 1980 to 1989 for the primary benchmark and the mean CPUE from 1990 to 1999 for the secondary benchmark. Primary and secondary benchmarks for Yellowstone Cutthroat Trout ≥ age 5 were nearly identical, so only a primary benchmark is shown. Gray shaded polygons are 95% confidence intervals around the mean CPUE from 1980 to 1989 for the primary benchmark and from 1990 to 1999 for the secondary benchmark.

under high suppression effort scenarios. Cutthroat Trout ages 2–4 achieved primary benchmarks in more than 42% of forecasted years under the 100% effort scenario, in 77% of forecasted years for age 5+, and in 61% of forecasted years for ≥age 2 (Figure 4; Table 3). For the 75% effort scenario, the percentage of forecasted years that ages 2–4 Cutthroat Trout achieved primary benchmarks declined compared to the 100% effort scenario, but the percentage of forecasted years that Cutthroat Trout ≥age 2 achieved primary benchmarks was similar to that of the 100% effort scenario (Figures 4 and 6; Table 3). For the 50% effort scenario, Cutthroat Trout ages 2–4 achieved primary benchmarks 10–19% of forecasted years, whereas age 5+ and age 2+ achieved primary benchmarks in 32% and 16% of forecasted years, respectively (Figures 4 and 6; Table 3). For the 25% effort scenario, primary benchmarks were achieved in 3% of years for age 2 Cutthroat Trout and were never achieved for other age-classes (Figures 4 and 6; Table 3).

Total Lake Trout abundance declined most rapidly under 100% effort, although abundance also declined at 75% and 50% effort (Figure 5). For the 25% suppression effort, total lake trout abundance increased over time (Figure 5). For the 100% effort scenarios, Lake Trout age 2+ were reduced to the benchmark in 77% of the forecasted years (Table 3). The 25% effort scenario resulted in the Lake Trout age 2+ benchmark never being met (Table 3).

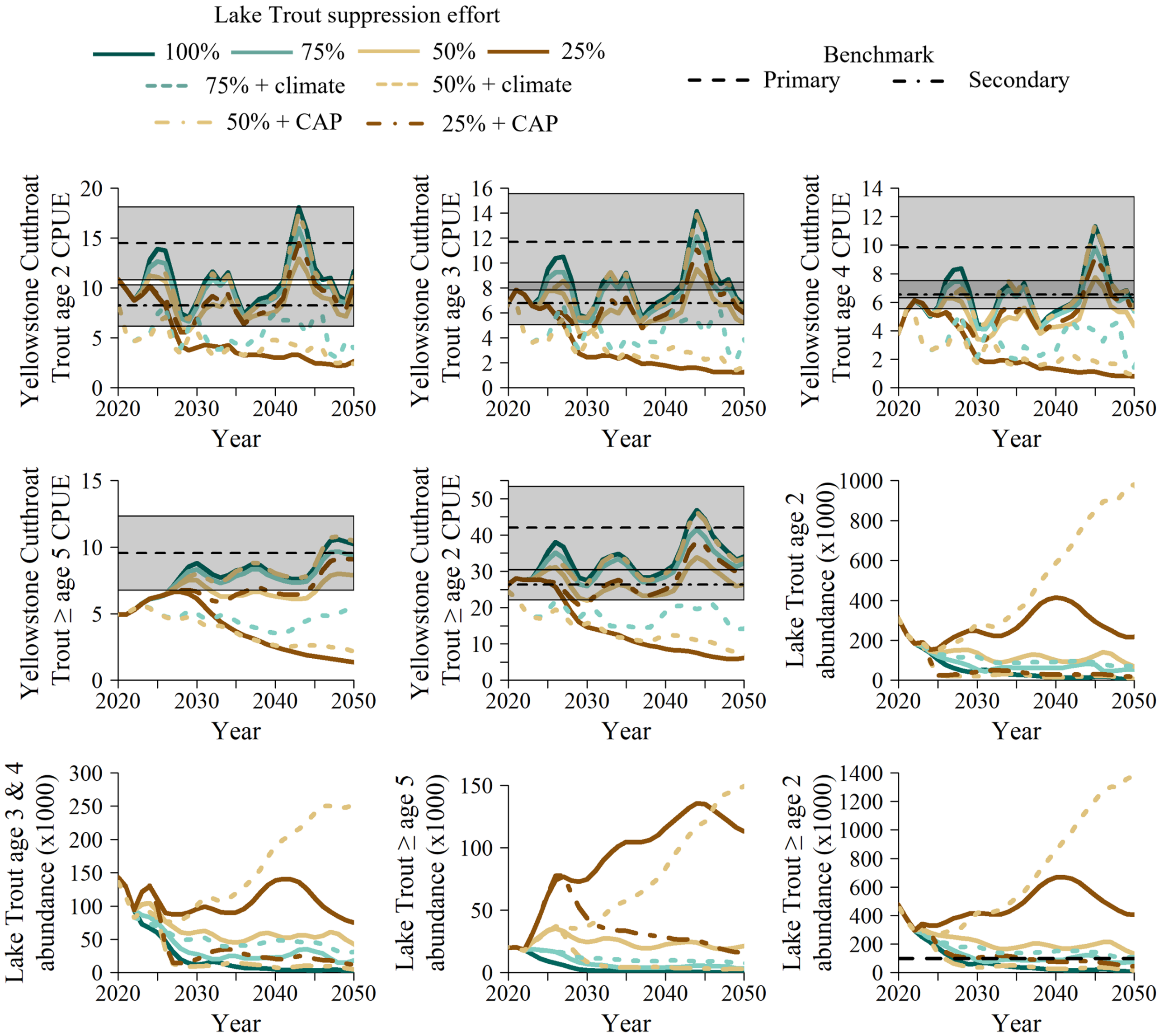


FIGURE 5. Yellowstone Cutthroat Trout and Lake Trout simulations in Yellowstone Lake from 2020 to 2050 at varying Lake Trout suppression effort scenarios (percentage of 97,397 units of effort), scenarios with climate change (climate), and scenarios with carcass analog pellets (CAP). Recovery benchmarks were derived for each age-class from Koel et al. (2010); individual age-class benchmarks were the mean CPUE from 1980 to 1989 for the primary benchmark and means CPUE from 1990 to 1999 for the secondary benchmark. Primary and secondary benchmarks for Yellowstone Cutthroat Trout ≥ age 5 were nearly identical, so only a primary benchmark is shown. Gray shaded polygons are 95% confidence intervals around the mean CPUE from 1980 to 1989 for the primary benchmark and from 1990 to 1999 for the secondary benchmark.

### *Carcass analog pellet scenarios*

Cutthroat Trout CPUE was compared to primary and secondary benchmark ranges and Lake Trout abundance was compared to a primary benchmark for suppression effort scenarios (50%, 25%) with carcass analog pellets and whirling disease under a forecasted (2020–2050) nonclimate change regime. Carcass analog pellets improved the likelihood of the recovery of Cutthroat Trout when added to 50% and 25% effort scenarios compared to 50% and 25% effort scenarios without carcass analog pellets (Figures 4–6; Table 3). The 50% effort scenario with carcass analog pellets resulted in the secondary benchmark being achieved on average in 13% more of forecasted years across age-classes and in 26% more of forecasted years for the primary benchmark compared to the scenario without carcass analog pellets (Table 3); overall achievement of the benchmarks was attained in less than 50% of forecasted years for multiple age-classes. The 25% effort scenario with carcass analog pellets resulted in the secondary benchmark being achieved on average in 51% more of forecasted years and in 17% more of forecasted years for the primary benchmark across all age-classes compared to the scenario without carcass analog pellets (Table 3); overall achievement of the benchmarks was attained in less than 30% of forecasted years for multiple age-classes.

Carcass analog pellets contributed to Lake Trout (all ≥age 2) achieving benchmarks when added to 50% and 25% effort scenarios compared to the scenarios without carcass analog pellets (Figure 5; Table 3). The scenarios with carcass analog pellets resulted in the Lake Trout age 2+ benchmark being achieved in 80% of forecasted years in combination with 50%

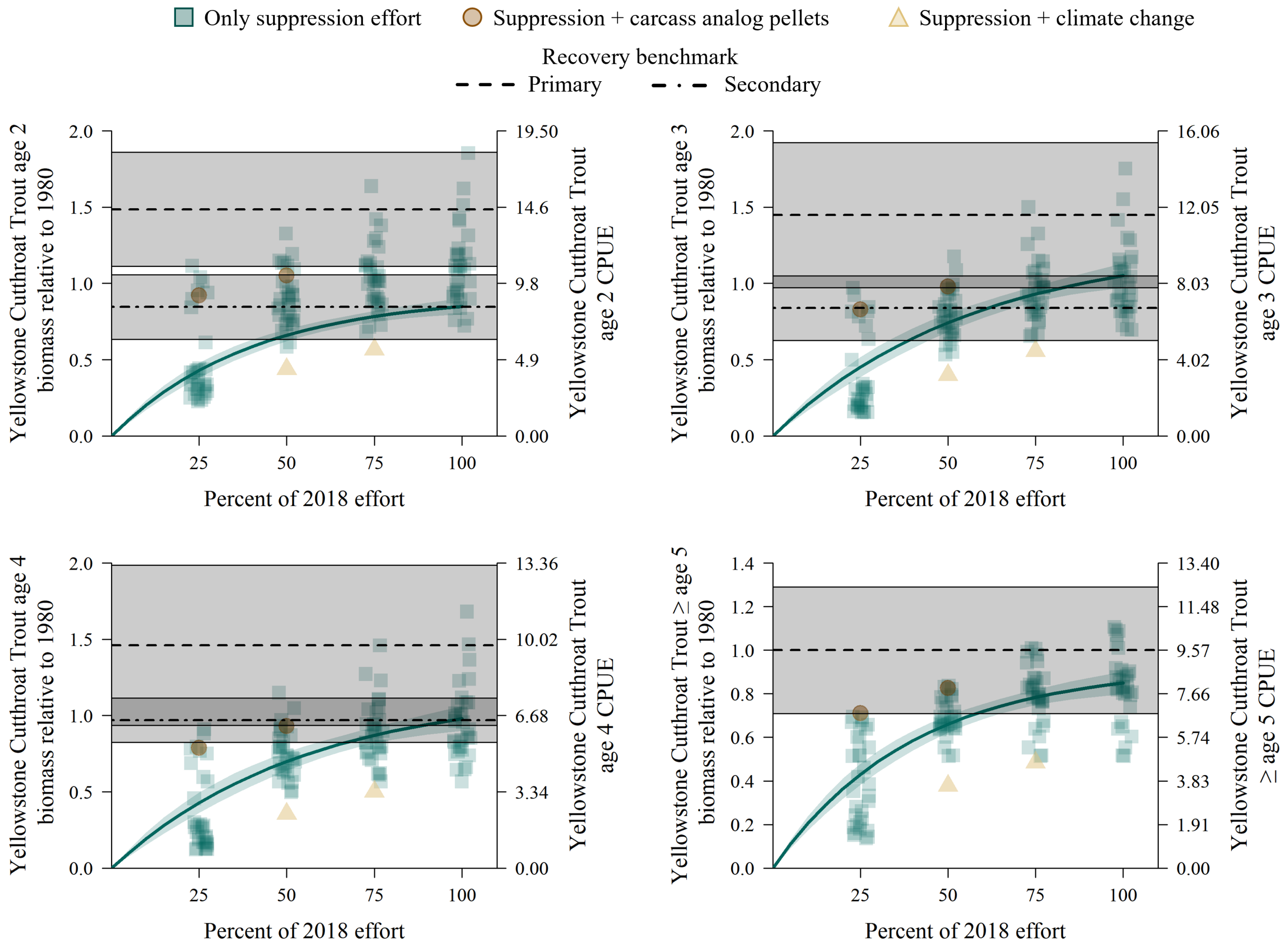


FIGURE 6. Summary results of Lake Trout suppression effort scenarios for Yellowstone Cutthroat Trout in Yellowstone Lake. Teal squares represent yearly biomass estimates for the best fit model. Teal line represents mean relationship between effort and biomass for best fit model. Shaded area represents 95% confidence intervals. Tan triangles represent mean biomass estimates for climate change scenarios. Brown circles represent mean biomass estimates for carcass analog pellet (CAP) scenarios. Recovery benchmarks were derived for each age-class from Koel et al. (2010); individual age-class benchmarks were the mean CPUE from 1980 to 1989 for the primary benchmark and the mean CPUE from 1990 to 1999 for the secondary benchmark. Primary and secondary benchmarks for Yellowstone Cutthroat Trout ≥ age 5 were nearly identical, so only a primary benchmark is shown. Gray shaded polygons are 95% confidence intervals around the mean CPUE from 1980 to 1989 for the primary benchmark and from 1990 to 1999 for the secondary benchmark.

suppression effort and in 48% of forecasted years in combination with 25% effort (Table 3).

### *Climate Change Scenarios*

Climate change scenarios resulted in a reduction in Cutthroat Trout CPUE by 50% or more compared to scenarios without climate effects for most years (Figures 4 and 5). The 75% effort scenario with climate change resulted in the secondary benchmark being achieved 35% of forecasted years for age 2 and 39% for age 3 Cutthroat Trout, 0% of years for ages 4 and 5+, and 7% of years for Cutthroat Trout ≥age 2 (Table 3). The 50% effort scenario with climate change resulted in the secondary benchmark being achieved 10% of forecasted years for age 2 and 3 Cutthroat Trout, 0% of years for ages 4 and 5+, and 7% of years for age 2 and older (Table 3). At 75% and 50% effort during climate change, CPUE of Cutthroat Trout never reached primary benchmarks (Figures 4–6; Table 3).

Age 2 and older Lake Trout increased in abundance more rapidly during climate change than a normal water regime with equivalent suppression effort. Lake Trout age 2+ abundance during climate change rapidly increased for the 50% effort scenario (Figure 5). However, Lake Trout age 2+ abundance with climate change for the 75% effort scenario still resulted in a reduction in abundance, especially for the 5+ age-class (Figure 5). The Lake Trout benchmark for ≥age 2 was never achieved during the 75 and 50% effort scenarios with climate change (Table 3).

## DISCUSSION

We showed that Cutthroat Trout recovery in Yellowstone Lake will likely depend on several factors in addition to Lake Trout suppression. Although Lake Trout predation is credited as a major factor decreasing Cutthroat Trout biomass in the lake, we could not fit the Ecopath model to historical data without also incorporating the effect of whirling disease and lake levels (sporadic historical drought), suggesting that all three factors in concert may affect the Cutthroat Trout population. Nevertheless, the gill netting suppression program enacted by the NPS over the past 30 years has likely prevented the collapse of the Cutthroat Trout population in

TABLE 3. Percentage of times a species by age met or exceeded the benchmark lower confidence interval for different Ecosim scenarios forecasted from 2020 to 2050 for Yellowstone Lake, Yellowstone National Park, Wyoming, USA. Effort is the percentage of Lake Trout suppression gill netting effort (97,397 units; 1 unit effort = 100 m of net/night). Values ≥50% are in bold. A secondary Lake Trout benchmark does not exist. CAP = carcass analog pellets.

| Scenario | Species and age | Percentage of times meets or exceeds primary benchmark 2020–2050 | Percentage of times meets or exceeds secondary benchmark 2020–2050 |
|---|---|---|---|
| 100% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 42% | **100%** |
| | Yellowstone Cutthroat Trout age 3 | 48% | **100%** |
| | Yellowstone Cutthroat Trout age 4 | 48% | **70%** |
| | Yellowstone Cutthroat Trout ≥ age 5 | **77%** | **77%** |
| | All Yellowstone Cutthroat Trout (≥ age 2) | **61%** | **100%** |
| | All gill-netted Lake Trout (≥ age 2) | **77%** | |
| 75% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 32% | **100%** |
| | Yellowstone Cutthroat Trout age 3 | 39% | **100%** |
| | Yellowstone Cutthroat Trout age 4 | 39% | **55%** |
| | Yellowstone Cutthroat Trout ≥ age 5 | **77%** | **77%** |
| | All Yellowstone Cutthroat Trout (≥ age 2) | **52%** | **100%** |
| | All gill-netted Lake Trout (≥ age 2) | **54%** | |
| 50% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 19% | **94%** |
| | Yellowstone Cutthroat Trout age 3 | 10% | **87%** |
| | Yellowstone Cutthroat Trout age 4 | 10% | 32% |
| | Yellowstone Cutthroat Trout ≥ age 5 | 32% | 32% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | 16% | **97%** |
| | All gill-netted Lake Trout (≥ age 2) | 0% | |
| 25% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 3% | 23% |
| | Yellowstone Cutthroat Trout age 3 | 0% | 26% |
| | Yellowstone Cutthroat Trout age 4 | 0% | 7% |
| | Yellowstone Cutthroat Trout ≥ age 5 | 0% | 0% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | 0% | 26% |
| | All gill-netted Lake Trout (≥ age 2) | 0% | |
| CAP + 50% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 35% | **100%** |
| | Yellowstone Cutthroat Trout age 3 | 41% | **100%** |
| | Yellowstone Cutthroat Trout age 4 | 42% | **61%** |
| | Yellowstone Cutthroat Trout ≥ age 5 | 44% | 44% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | **54%** | **100%** |
| | All gill-netted Lake Trout (≥ age 2) | **80%** | |
| CAP + 25% effort + whirling disease + no climate change | Yellowstone Cutthroat Trout age 2 | 13% | **93%** |
| | Yellowstone Cutthroat Trout age 3 | 13% | **90%** |
| | Yellowstone Cutthroat Trout age 4 | 13% | 32% |
| | Yellowstone Cutthroat Trout ≥ age 5 | 29% | 29% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | 19% | **93%** |
| | All gill-netted Lake Trout (≥ age 2) | 48% | |
| 75% effort + whirling disease + climate change | Yellowstone Cutthroat Trout age 2 | 0% | 35% |
| | Yellowstone Cutthroat Trout age 3 | 0% | 39% |
| | Yellowstone Cutthroat Trout age 4 | 0% | 0% |
| | Yellowstone Cutthroat Trout ≥ age 5 | 0% | 0% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | 0% | 7% |
| | All gill-netted Lake Trout (≥ age 2) | 0% | |
| 50% effort + whirling disease + climate change | Yellowstone Cutthroat Trout age 2 | 0% | 10% |
| | Yellowstone Cutthroat Trout age 3 | 0% | 10% |
| | Yellowstone Cutthroat Trout age 4 | 0% | 0% |
| | Yellowstone Cutthroat Trout ≥ age 5 | 0% | 0% |
| | All Yellowstone Cutthroat Trout (≥ age 2) | 0% | 7% |
| | All gill-netted Lake Trout (≥ age 2) | 0% | |

Yellowstone Lake (Koel et al. 2020a). Based on our results, Lake Trout predation greatly influenced Cutthroat Trout abundance. A suppression effort of at least 73,048 units of 100-m net nights was necessary for Cutthroat Trout to have the greatest probability of reaching recovery benchmarks without the incorporation of future climate change. In addition, carcass analog pellets could provide additional recovery benefit to Cutthroat Trout at lower gill netting effort levels. However, reduction in lake level driven by extreme climate change in the Greater Yellowstone Ecosystem may inhibit the Cutthroat Trout population from reaching desired recovery benchmarks established by Koel et al. (2010) if Lake Trout suppression effort is reduced relative to recent levels of suppression effort (97,397 units 100 m of net/night).

Extreme reduction in runoff, and assumed reduction in lake level, predicted by climate change models (Hostetler et al. 2021) influenced predator–prey dynamics between Lake Trout and Cutthroat Trout, which may inhibit Cutthroat Trout recovery in the presence of Lake Trout. Lake Trout were forecasted to expand during climate change under the 50% effort scenario, potentially due to release from competition with Cutthroat Trout for a shared prey item, amphipods (Ruzycki et al. 2003; Syslo et al. 2016; Glassic et al. 2023). This climate change scenario resulted in a 10-fold increase in Lake Trout predation mortality of amphipods compared to all other scenarios. Cutthroat Trout are known to control abundance of amphipods (Wilmot et al. 2016). Cutthroat Trout decline during the 50% effort scenario with extreme climate change may have been large enough to allow Lake Trout to exhibit diet plasticity (Glassic et al. 2023) and increase consumption of amphipods. Though the conclusion that Cutthroat Trout may never reach primary benchmarks during extreme climate change may be discouraging, similar conclusions have been made for other lake ecosystems balancing hydrological changes and native fish conservation (Wang et al. 2016).

Understanding the relative importance of top–down versus bottom–up regulation of food webs has implications for fisheries management (Carpenter et al. 1985; Quiròs and Boveri 1999), especially for suppression programs. The model parameters that controlled the predation rate limits (i.e., vulnerability parameters) supported top–down control of the ecosystem; Lake Trout consume and control dynamics of Cutthroat Trout, and Cutthroat Trout consume and control dynamics of amphipods and zooplankton. This model structure is supported by the observed trophic cascade after Lake Trout invasion (Tronstad et al. 2010; Koel et al. 2019). Lake Trout are often a top predator in the ecosystems they inhabit (Martinez et al. 2009; Ellis et al. 2011), so the top–down dynamics in Yellowstone Lake are unsurprising. The vulnerabilities of Lake Trout and Cutthroat Trout could not be changed without loss of model fit, emphasizing the importance of the top–down relationship, driven by piscivorous Lake Trout, in the ecosystem.

Without explicit representation of age-classes and trophic interactions, recognizing counterintuitive management actions can be challenging (Walters et al. 2008). We showed that Lake Trout may not need to be suppressed as intensively to achieve age-class-based Cutthroat Trout recovery benchmarks in the absence of changes in lake levels due to climate change. This conclusion agrees with other modeling approaches; achievement of Lake Trout management objectives was estimated to occur at as low as 75,000 units of effort using single-species statistical catch-at-age models (Syslo et al. 2020). Predatory Lake Trout abundance is low at efforts ≥75,000 units and may be sufficient to allow Cutthroat Trout recovery. However, this amount of effort is conditional on the current Lake Trout recruitment levels. Given historical model fit underpredicted relative biomass for age 2 and ≥ age 5 Cutthroat Trout, a likelihood exists that the forecasted output may underestimate the response of Cutthroat Trout to higher Lake Trout suppression efforts. Therefore, our estimation of the reduction to suppression effort is likely conservative, which is encouraging given the importance of Cutthroat Trout to the ecosystem. By incorporating uncertainty with each age-class, we also showed that with lower suppression effort, predictions for the alternative model fits (i.e., our proxy for error) became more chaotic—the likelihood of achieving a benchmark had greater variability over the forecasted period, suggesting that suppression is a stabilizing force within the ecosystem.

Establishing well-defined benchmarks for suppression programs are essential to provide explicit, measurable goals regarding what should be achieved (Klein et al. 2023). The NPS clearly defined suppression program benchmarks for Yellowstone Lake in 2010, nearly 20 years after Lake Trout invasion and initial suppression began. Establishment of the benchmarks undoubtedly contributed to the achievement of the secondary benchmark for Cutthroat Trout shown in annual monitoring efforts. However, the benchmarks are for the entire population of Cutthroat Trout or Lake Trout and appear to oversimplify predator–prey dynamics or susceptibility to disease (Ruzycki et al. 2003; Koel et al. 2006; Syslo et al. 2016; Glassic et al. 2023). Collecting data during the "preliminary" years of suppression can be used to develop more realistic or biologically meaningful objectives as suppression advances (Parkes and Panetta 2009; Dux et al. 2019). The almost 30 years of research on the Yellowstone Lake ecosystem since the invasion of Lake Trout can better inform conservation and suppression benchmarks. Benchmarks for each age-class, or benchmarks that include spawning potential ratio and spawning stock biomass that include inherent variability related to past data could provide better indication of how management actions and environmental conditions influence suppression and conservation targets. Achieving conservation benchmarks through comparison to some past baseline can be difficult given that baselines often change (Alagona et al. 2012; McNellie et al. 2020). This research adds to a growing body of literature that emphasizes the need to have benchmarks that acknowledge past baselines but are further contextualized given environmentally driven oscillations in productivity that cannot be managed by biologists (Mackenzie et al. 2007; Cunningham et al. 2015; Gardner and Bullock 2021).

The EwE approach used here is well established and allowed us to include food web dynamics, disease, climate change, invasive species influences, and uncertainty in both initial conditions and time dynamic simulations. Though some EwE models may incorporate the influence of invasive species or trade-offs between prioritizing different fisheries, few include environmental influences (Colléter et al. 2015; e.g., Wang et al. 2016). However, the Great Lakes have many models, including the influence of invasive species on native fish (e.g., Rutherford et al. 2021), but do not directly measure the effect of invasive suppression outcomes on the ecosystem.

Considering multiple stressors and the variation associated with those stressors will be valuable to set realistic expectations and benchmarks for native species recovery.

Understanding functional interactions in ecosystems may be challenging (Geist 2011), but single species strategies to conservation may not be enough, given interactions between species and abiotic factors. We demonstrated the importance of incorporating community dynamics, environmental variation, disease, and age-specific responses into evaluation of management strategies. Native species recovery benchmarks are unlikely to be realistic if multiple threats are not simultaneously evaluated and addressed. By using ecosystem models, the cascading effects of invasive species (Zavaleta et al. 2001; Chagaris et al. 2017; Koel et al. 2019) and the complexities that changing environmental conditions can introduce to achieving conservation or suppression goals (Healy et al. 2020) can be fully integrated, promoting realistic recovery benchmarks and identifying strategies most likely to promote recovery.

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## SUPPORTING INFORMATION

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

**Figure S1.**
**Figure S2.**
**Figure S3.**
**Figure S4.**
**Figure S5.**
**Figure S6.**
**Data S1.** AFS