



# New climate regime started and further shaped the historic Yellowstone Lake cutthroat trout population decline commonly attributed entirely to nonnative lake trout predation

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**Abstract** The storied Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*; YCT) population of Yellowstone Lake, Yellowstone National Park, Wyoming, USA, has shown a profound and mostly continuous decline since the 1970s despite pristine habitat and vanishing angler harvests. An age-structured Leslie model that had a broad climate index as its only driver (regulating age-0 YCT survival) was Bayesian-fitted to data for a key YCT spawning stock from 1977 to 1992, arguably before predation from an introduced lake trout (*Salvelinus namaycush*) population (1994 discovery) measurably affected YCT population dynamics. The middle 50% of model fits encompassed 12 of 14 observed spawning populations and nominally excluded the others. Forecasting to 2007 (the final empirical data year) showed the new climate regime largely explained declining YCT numbers, but a growing predation effect became evident soon after lake trout discovery and quickly became the major YCT population driver. The climate effect may have involved the fatal blockage of out-emigrating YCT fry by natural alluvial deposits at spawning tributary mouths in warm, dry years. The previously reported Yellowstone Lake ecosystem shift suggested by the YCT population decline actually

began with the 1977 North Pacific Basin climate shift and was only later enhanced by lake trout predation. This study showed identifying and accounting for the overarching population drivers is important to structuring statistical models intended to detect and assess the effects of new and emerging population impacts across historic data sets. Management actions intended to protect these YCT must consider climate effects and probable future climates.

**Keywords** Climate change · Salmonid · Reproduction · Recruitment · Regime shift

## Introduction

The storied Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*; YCT) population of Yellowstone Lake, Yellowstone National Park, Wyoming, USA, has shown a profound and nearly continuous decline since the 1970s despite pristine habitat and vanishing angler harvests (Koel et al. 2005; Kaeding 2010, 2013a). An iteroparous fish and obligate stream spawner, adult YCT from the lake historically spawned in most lake tributaries (Gresswell and Varley 1988). In one tributary, Clear Creek, spawning run size was estimated over much of several decades (Kaeding and Koel 2011) and its temporal trend closely paralleled that of the lake's adult YCT population (Kaeding 2013a). The observed run size—

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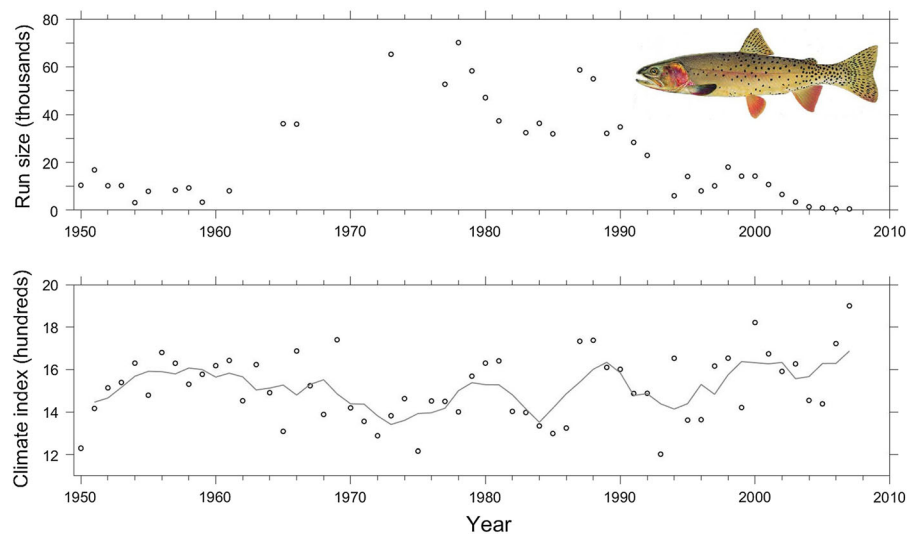
widely considered the key indicator of the YCT population's well-being—peaked at  $\sim 70,000$  fish in the 1970s (Fig. 1).

Koel et al. (2005) speculated the YCT population decline had resulted from one or more of three factors: (1) predation from a reproducing population of lake trout (*Salvelinus namaycush*), a nonnative species discovered in the lake in 1994 (Kaeding et al. 1996); (2) the debilitating effects on infected fish of “whirling” disease, found in the lake's YCT in 1998 (Koel et al. 2006); and (3) a regional drought that those authors believed had begun in 1998 and harmed YCT reproduction. Subsequent studies have indicated the relative importance of each factor to the decline.

Munro et al. (2005) used otolith chemistry to show lake trout had reproduced in Yellowstone Lake since at least the mid-1980s. But when lake trout occurred there is undocumented and could have preceded the 1980s. Ruzycki et al. (2003) estimated 8300 age 3–5 and 3000 age 6–23 lake trout in the lake in 1996—before developing control actions became effective—and the 1998 YCT population as 1.74 million fish  $> 100$  mm total length (TL). Syslo et al. (2011) estimated the lake trout's finite increase rate ( $\lambda$ ), absent control mortality, as 1.29 [the geometric mean; 95% confidence interval (CI) 1.14, 1.39]. If Ruzycki et al.'s (2003) 1996 lake trout population had grown at that rate (or its CI), its respective sizes would have

been 4081 fish (6691 fish, 3027 fish) in 1992 and 90 fish (937 fish, 22 fish) in 1977. It is implausible that the piscivory of so few lake trout reversed the upward growth trajectory of the large YCT population evident in the 1970s (Fig. 1) and thus started the population's decline, although that growing predation effect subsequently impacted the population. Specifically, Ruzycki et al. (2003) estimated lake trout consumed 10% of the vulnerable (i.e., on the basis of prey size and habitat use) YCT population in 1996.

Whirling disease is caused by the nonnative myxosporean parasite *Myxobolus cerebralis*, which consumes the developing cartilage of young fish. Its intermediate host, the aquatic oligochaete worm *Tubifex tubifex*, prefers organic sediments and low water velocities (Kerans and Zale 2002). Thus, YCT fry are most susceptible to the nonmotile parasite during the few days or weeks between their emergence from stream gravels and emigration to the lake. Koel et al. (2006) found YCT fry held in cages in the lake outlet and near the mouths of 12 spatially disparate Yellowstone Lake tributaries that were spawning streams for YCT from the lake became infected with the parasite at only three locations, all in the northeast lake region: Pelican Creek (75–100% infection incidence of fry among annual exposure periods and study years) and—to a much lesser extent—Clear Creek (0–2%) and the lake outlet (0–20%). A 2012 study



**Fig. 1** Number of Yellowstone cutthroat trout in the annual spawning run in Clear Creek, Yellowstone National Park, during 41 years between 1950 and 2007 (upper panel), and the climate

indexes reported by Kaeding (2013b; lower panel). The solid line is the five-point moving average for the indexes; it shows the general upward trend since the 1970s

repeated that of Koel et al. (2006) and had similar results (Koel et al. 2015). Thus, whirling disease was unlikely to have negatively affected Clear Creek's lacustrine–adfluvial YCT spawning population, i.e., the life-history form that has fish mostly living in a lake but spawning in a lake tributary (Varley and Gresswell 1988). Furthermore, because the Pelican Creek drainage constituted only 7.9% of the entire drainage upstream from Yellowstone Lake (Koel et al. 2006) potentially accessible to lacustrine–adfluvial YCT, it was improbable that whirling disease measurably impacted the lake's YCT population.

Kaeding (2010, 2013b) showed a broad climate index, calculated as total annual mean-daily air temperatures  $> 0\text{ }^{\circ}\text{C}$  on Yellowstone Lake's north shore, generally increased since the 1970s (Fig. 1) and strongly correlated with Clear Creek discharge (negative association) and temperature (positive association) during the mid-May–mid-July YCT spawning season. Increasing indexes thus indicated warmer, drier climatic conditions. Kaeding (2010) used that climate index as a predictor in nested matrix population models fitted to Clear Creek's YCT spawning run size and the mean TL of run fish during 1977–2007. The models included a growing effect of lake trout predation. The climate, predation, and full models explained 73%, 47%, and 87% of variation in observed run size, respectively, and strongly suggested climate was a key driver of first-year (i.e., age-0) YCT recruitment to subsequent spawning runs. Elsewhere, age-0 survival was the main determinant of recruitment to the adult stocks of numerous salmonids (e.g., Milner et al. 2003).

But Kaeding's (2010) models had 12 of their up to 18 parameters set as constants and were fitted to data using simulated annealing, which estimated only one “not-constant” parameter at a time. Moreover, he reported that evidence of a predation effect for the full model emerged only near the end of the run's data time series. That could have been due to statistical confounding of the climate and predation effects. A solution would be to separate the pre-predation period of the time series from the subsequent, possibly predation-affected period; fit a suitable population model to the pre-predation data; and then use that model to project the population forward through the possible predation period. Divergence of the observed and predicted populations during that projected

“forecast” period could indicate the predation effect's onset and provide a measure of its subsequent magnitude.

This study's main objective was to determine the role of climate in the historic, three-decade decline of Clear Creek's lacustrine–adfluvial YCT spawning population. Its results will also be important to assessments of the efficacy of ongoing management actions intended to protect YCT by controlling the lake trout population (Ruzycki et al. 2003; Koel et al. 2005; Syslo et al. 2011). I use a population model that had the climate index as its only driver and Bayesian methods to examine Clear Creek YCT data collected before the lake trout were discovered. I then compare and interpret the predicted and observed population trajectories across the subsequent forecast period. Because both climate variation and lake trout predation could have equally reduced YCT survival and thus had statistically inseparable population effects—at least across the recent years—contemporary model selection techniques (e.g., Hilborn and Mangel 1997) were not useful.

## Methods

### Study area and data collection

The Yellowstone Lake and Clear Creek study area, as well as the lake's fishes, were detailed by Koel et al. (2006) and Kaeding and Koel (2011). Likewise, Kaeding and Koel (2011) detailed both the operation of the Clear Creek trap and the data taken from its captured YCT between 1977 and 2007 (28 data years), when data collection was most comprehensive. In spring 2008, high creek discharge destroyed the trap and its weir, which have not been replaced.

### Population model

The model for Clear Creek's lacustrine–adfluvial YCT population (Eq. 1) was of the time-variant, nonlinear, Leslie form (Caswell 2001) and consisted of the transition matrix  $\mathbf{A}_n$  and population state vector  $\mathbf{n}$

$$\mathbf{n}(t+1) = \mathbf{A}_n(t) \cdot \mathbf{n}(t), \quad (1)$$

where  $t$  is the time. Because maximum longevity for these YCT was  $\sim 10$  years (Kaeding and Koel 2011), the transition matrix was  $10 \times 10$ . These YCT

represented an “ideal” birth-pulse population (Caswell 2001) for simulation using Leslie matrices because spawning and subsequent embryo incubation were limited to a short period ( $\sim 3$  months), thus the fish effectively reproduced on their birthday. The model’s time step was 1 year.

### Model parameters

The model had 13 parameters, 10 of which were obtained from previous studies of these YCT or from analyses of them performed here (Table 1). The remaining three parameters were estimated.

The first row of the transition matrix **A** (Eq. 1)—the age-specific fertilities ( $F_x$ ; i.e., the per-capita, age- $x$  contribution of young to age 1)—was the products of a female proportion of the Clear Creek spawning run, an age-specific fecundity, an age-specific maturity proportion, and an effect of climate on age-0 survival (Eq. 2). The female proportion ( $p_f$ ) was reported by Kaeding and Koel (2011).

$$F_x = p_f \cdot f_x \cdot \mathbf{p}_x \cdot f_T \quad (2)$$

The age-specific fecundities ( $f_x$ ) were based on Kaeding and Koel’s (2011) linear regression fit of the combined YCT fecundity–TL data for Clear Creek and Arnica Creek (another Yellowstone Lake tributary), which was made age specific in the model by

using the modification of the von Bertalanffy growth model (von Bertalanffy 1938) proposed by Gallucci and Quinn (1979; Eq. 3)

$$L_x = L_\infty \cdot [1 - \exp(-(\omega/L_\infty) \cdot x)] + \varepsilon, \quad (3)$$

where  $L_x$  is the TL (mm) at age  $x$  (years),  $L_\infty$  and  $\omega$

are the parameters reported by Kaeding and Koel (2011), and  $\varepsilon$  is the additive, normal error for the model’s fit to the data for gill-net-caught Yellowstone Lake YCT provided by their scale “analyst 8,” whom they showed provided the most accurate age estimates. (Across the 28 data years, nine scale analysts had sequentially determined the YCT ages.) The model did not include an effect of population density on YCT somatic growth (and thus fecundity) because that effect did not become evident until the mid- to late 1990s—after the “pre-predation” fitting period—when the YCT population was much smaller (Kaeding 2013a).

Kaeding and Koel (2011) reported maturity proportion–TL relations for the gill-net Yellowstone Lake YCT. For this study, the “analyst 8” age-specific maturity proportions were estimated for those YCT. Results showed only a trivial proportion ( $\sim 3\%$ ) of age-3 YCT ( $n = 1680$  fish) were mature, whereas about 29% of age-4 YCT ( $n = 1472$  fish), 75% of age-5 YCT ( $n = 2275$  fish), and effectively all older YCT ( $n = 2707$  fish) were mature. Thus, the vector

estimates and standard deviations (SD) for their normal probability distributions

**Table 1** Parameters considered normal random variables in the model for the lacustrine–adfluvial Yellowstone cutthroat trout population of Clear Creek, their symbols, data sources, and

Parameter description	Symbol <sup>†</sup>	Source <sup>‡</sup>	Estimate <sup>§</sup>	SD
Female proportion of run	$p_f$	1	0.610	0.013
Slope of linear fecundity–TL relationship		1	3.599	0.569
Intercept of linear fecundity–TL relationship		1	– 160.3	210.1
$L_\infty$ of Eq. 2, somatic growth	$L_\infty$	1	600.90	5.85
$\omega$ of Eq. 2, somatic growth	$\omega$	1	120.00	0.78
Mature proportion age 4	$\mathbf{p}_4$	3	0.285	0.012
Mature proportion age 5	$\mathbf{p}_5$	3	0.750	0.009
Immature (< age 5) survival probability	$S_{1-4}$	2	0.369	0.032
Mature ( $\geq$ age 5) survival probability	$S_{5-9}$	2	0.480	0.023
Prespawner proportion	$p_p$	1	0.658	0.015

<sup>†</sup>Provided only for parameters that appear in numbered equations

<sup>‡</sup>1 = Kaeding and Koel (2011); 2 = Stapp and Hayward (2002); 3 = present study

<sup>§</sup>Calculated as arithmetic proportions or means

$\mathbf{p}$  (Eq. 2) of age-specific maturity proportions had its first three elements as zero, elements 4 and 5 as the respective parameters  $\mathbf{p}_4$  and  $\mathbf{p}_5$  (Table 1), and its remaining elements as unity. Immature YCT were set as fish  $<$  age 5 and mature YCT as  $\geq$  age 5.

Kaeding (2010) showed poor age-0 YCT survival occurred in years when the climate index was high. Although there were no estimates of age-0 YCT survival when climate was least restrictive, Stapp and Hayward (2002) reported mean age-0 survival for Yellowstone Lake YCT as 0.0265 (0.0024 SD). Accordingly, in the present study, the upper bound of the parameter space searched for that unknown age-0 survival probability in “suitable” climate years was arbitrarily set as 0.075 (i.e.,  $\sim 3 \times 0.0265$ ), whereas its lower bound was arbitrarily set as 0.001 because none of the total gill-net catches between 1969 and 2007 indicated YCT reproduction failure (see annual TL–frequency histograms in Kaeding 2010). Age-0 survival in “adverse” climates—the second estimated model parameter—was arbitrarily given an upper bound of 0.0125 (i.e.,  $\sim 0.5 \times 0.0265$ ) along with the 0.001 lower bound. The third and final estimated parameter was the climate index that separated the suitable and adverse climates. The climate index (i.e., its Fig. 1 data) showed a roughly bimodal distribution and a trough near 1550 (Fig. 2). Thus, the lower and upper bounds for the separation parameter’s search space were arbitrarily set as the index’s 10th and 90th percentiles (i.e., 1313 and 1712), respectively. Consequently, whether the suitable or adverse age-0 survival parameter ( $f_T$ ; Eq. 2) was considered during model fitting was dependent upon the climate index at year  $t$  and its relation to the separation parameter.

The elements in the immediate sub-diagonal of matrix  $\mathbf{A}$  (Eq. 1)—the age-specific survival

probabilities ( $S_x$ ; i.e., the proportion of age- $x$  individuals that survive to age  $x + 1$ )—were those reported by Stapp and Hayward (2002) for immature ( $S_{1-4}$ ) and mature ( $S_{5-9}$ ) YCT (Table 1). Remaining matrix  $\mathbf{A}$  elements were set as zero.

### Initial conditions

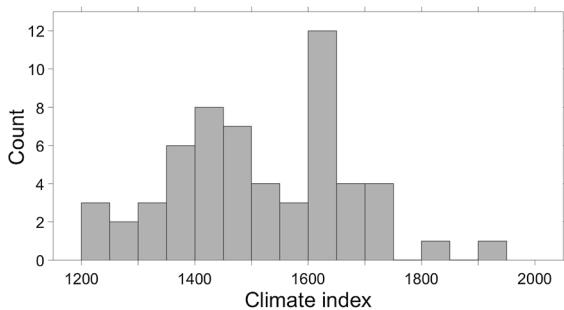
The start year (i.e., time step  $t = 1$ ) for population simulations was 1973, when the Clear Creek spawning run had totaled 65,215 YCT. That year was chosen because its spawning run was markedly larger than those of the preceding decades (Fig. 1), which suggested the effects of the factors that may have formerly suppressed the YCT population had been substantially reduced by 1973. Those factors consisted of harmful angler harvests, the stocking of hatchery-produced YCT (almost exclusively as fry) into the lake and some of its tributaries, and the effects of hatchery-based spawn-taking operations on Clear Creek and several other lake tributaries (Kaeding 2010). Thus, those factors’ possible effects on YCT population dynamics would no longer have been evident in 1973.

For the starting population, the 65,215 YCT were divided equally among age classes 4–6 of the state vector  $\mathbf{n}(1)$  (Eq. 1)—the ages that constituted  $\sim 73\%$  of the actual spawning run (Kaeding and Koel 2011). Because  $\sim 66\%$  of mature female Yellowstone Lake YCT were “prespawners,” i.e., fish whose excised ovaries in fall indicated the fish would have spawned the next spring (Kaeding and Koel 2011), the age classes 4–6 were divided by that prespawner proportion ( $p_p$ ; Table 1) and thus made representative of all simulated fish in those age classes. For objective representation of age classes 1–3 in  $\mathbf{n}(1)$ , the immature survival probability ( $S_{1-4}$ ) was used to back-project the age-class 4 YCT to each of age classes 1–3.

### Distinguishing the simulated spawning run

Separation of the predicted spawning run  $N_{pt}$  from the total simulated population at each model time step was accomplished by vector multiplication of the population state  $\mathbf{n}(t)$ , the age-specific maturity  $\mathbf{p}$ , and the prespawner proportion  $p_p$  (Eq. 4).

$$N_{pt} = \mathbf{n}(t) \cdot \mathbf{p} \cdot p_p. \tag{4}$$



**Fig. 2** Histogram of climate indexes for 1950–2007 (Fig. 1;  $n = 58$ )

## Model fitting

Bayesian data analysis (Gelman et al. 2003) was used to simultaneously consider all model uncertainties and fit the model to the data, i.e., the annual spawning run sizes. Accordingly, a Gaussian likelihood function was used to relate the predicted to observed run size, with an estimated variance parameter sigma. The objective function minimized by model fitting (Eq. 5) was the total sum of squared differences (*SST*) between the observed run size ( $N_o$ ) and the run size predicted ( $N_p$ ; both variables ln-transformed and then collectively calculated as *z*-scores) across the years  $j$  (1977–1992), i.e., before the lake trout were discovered and presumably had a measurable effect on YCT population dynamics.

$$SST = \sum_{j=1977}^{1992} (N_{pj} - N_{oj})^2. \quad (5)$$

Unlike Kaeding (2010), the objective function did not include the mean TL of run fish because that metric showed little variation across the fitted years (Kaeding 2013a). All coding and subsequent analyses were in MATLAB (MathWorks 2016).

An adaptive Metropolis–Hastings algorithm that used Markov chain Monte Carlo (MCMC) simulation (Laine 2017) was used to fit model to data. To propagate uncertainty from each Table 1 parameter, 5000 unique MCMC runs were conducted—each run consisting of a 250-iteration burn-in, followed by 250 saved iterations. That burn-in period was initially indicated by visual inspection of the *SST* traces of numerous preliminary runs and then substantiated by calculating Geweke’s convergence diagnostic (Geweke 1992; Brooks and Roberts 1998), which compared the first 10% of the chain with the last 50%. Each run began with a random draw from the normal probability distribution for each Table 1 parameter; the chosen values were maintained throughout the run and retained for subsequent analyses. The two climate-based age-0 survival parameters and that for their separating climate index parameter were those examined using the Metropolis–Hastings algorithm. Thus, the model had three estimated parameters and 10 additional parameters that were fixed in any given run. That modeling approach was necessary. Had those 10 parameters instead been assigned their informative prior probabilities in model fitting, their influence in

the likelihood function overwhelmed the estimation of plausible posterior probabilities for the three remaining parameters (i.e., the effect of variance inflation).

## Model convergence and assessment

In addition to the use of Geweke’s diagnostic, model convergence was assessed by visual inspection of the *SST* chain plot across the 1.25 million saved iterations, the overall histogram of *SST*, and the posterior density plots for the three estimated parameters. Thus, as recommended by Gelman and Shirley (2011), a range of diagnostics was used to determine convergence or—perhaps more precisely—no “lack of convergence,” which those authors considered was the only reliable use of convergence diagnostics.

Assessment of model performance was based on the ability of a middle proportion of the 1.25 million predicted runs, based on their *SST*, to encompass most observed runs. This was considered another test of model convergence. That middle proportion began at 40% and was adjusted upward in increments of 10% until the largest predicted populations became unrealistic. These and subsequent analyses used the parameter and *SST* estimates from a random sample of 50,000 of the saved iterations.

## Forecasting

Using the selected model, the simulated population was likewise projected through the subsequent forecast period (1994–2007, the final empirical data year) and the resulting data were similarly examined. In addition, Spearman’s rank correlation was used to assess the model’s forecasting performance. Spearman’s was not unduly influenced by the anticipated nonlinear association between observed and predicted YCT populations portended by the growing predation effect.

## Results

### Convergence diagnostics

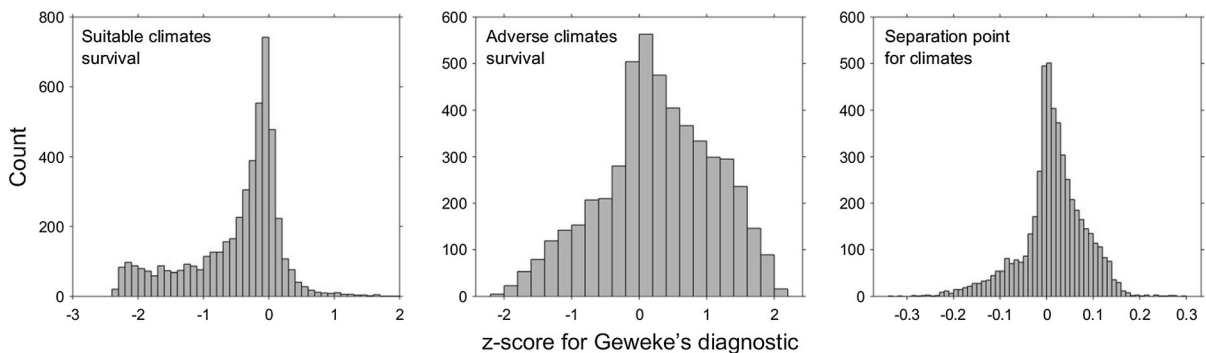
The histograms of *z*-scores for Geweke’s diagnostic supported model convergence and indicated the burn-in period was suitable. Specifically, almost none of the *z*-scores fell outside the estimated parameter’s 95%

prediction bounds, except for 5.8% of those for the suitable climates survival (Fig. 3). The chain plot and overall histogram of *SST* for the saved iterations likewise indicated model convergence and *SST* between 10.9 and 14.6 for the middle 50% of model fits (Fig. 4). Even so, the histogram's minor peaks suggested perhaps two local minima in the overall parameter space.

The suitable climates age-0 survival probability had its middle 50% of values between 0.0401 and 0.0689, that for adverse climates between 0.0030 and 0.0073, and for the climate index separation point between 1464 and 1551 (Fig. 5). However, the plot shape for the separation point was contrastingly abrupt and mostly rectangular.

### Model assessment

The model performed well in its prediction of the observed run sizes across the fitted-years period. At middle *SST* proportions of 40 to 80%, the predicted runs encompassed 12 to 14 of the 14 observed runs, respectively. However, for the middle 60%, the largest predicted runs were about 110,000 fish, considered an unrealistic size. Thus, the middle 50% proportion met the prescribed criteria by encompassing most observed runs (12), while the largest predicted populations remained realistic ( $\sim 100,000$  fish). That particular model closely predicted the observed population decline to the lows of the early 1980s, its increase in the late 1980s, and the subsequent decline in the early 1990s (Fig. 6). The two observed runs that fell outside the predicted runs did so only nominally and occurred in 1985 and 1989.



**Fig. 3** Histograms of the z-score test statistic for Geweke's convergence diagnostic for the model parameters estimated using the Metropolis–Hastings algorithm: age-0 survival in the

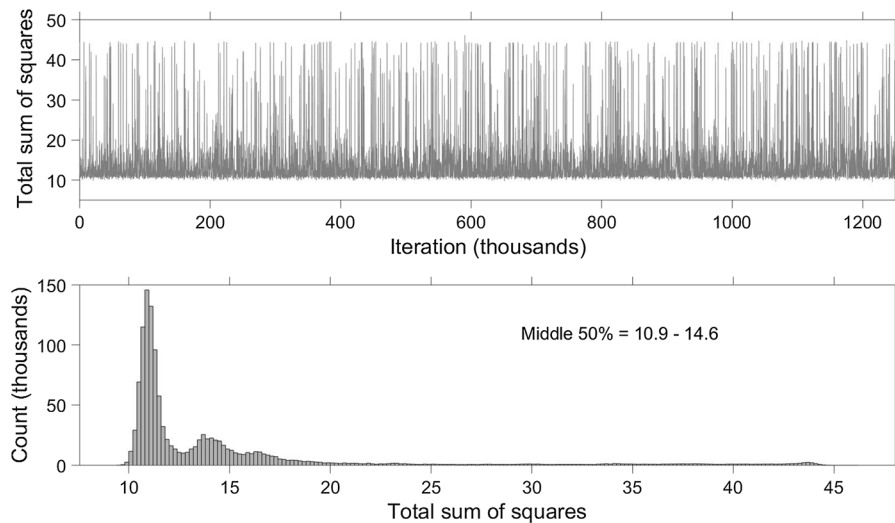
### Forecasting

In contrast, during the subsequent projected-years period, none of the 14 observed spawning runs was larger than the median predicted run or smaller than the smallest predicted runs (Fig. 6). Even so, the predicted population trajectories closely paralleled that of the observed runs across the projected-years period, including their increase in the late 1990s. More specifically, Spearman's rho had a mean 0.765 (95% CI 0.653, 0.890) and *p* value of 0.004 (95% CI 0.000, 0.014). Thus, when the anticipated nonlinearity due to the growing predation effect was accounted for, the model explained nearly 60% ( $\rho^2 = 0.59$ ) of the variation in observed run size.

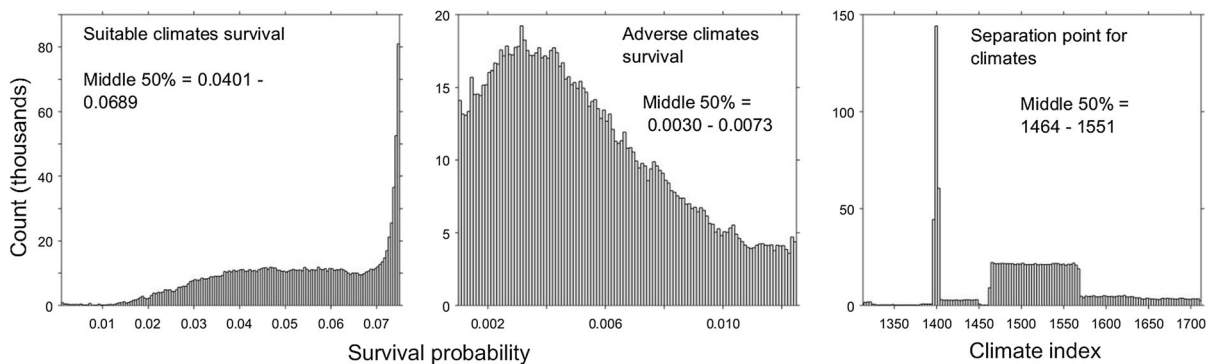
### Discussion

This study was conducted in a remarkably uncommon environment—one where the typical human impacts of fishery over-harvest, water pollution and water removal, and habitat degradation did not exist and thus were not potential confounding factors in the examination of YCT population dynamics. It showed the trend toward higher climate indexes in the Yellowstone Lake region that began in the 1970s had an overarching, negative effect on YCT reproduction. The particular characteristics of Clear Creek's environment that affected YCT reproduction success are unknown and may themselves be negatively associated, as Kaeding (2013b) showed when developing the climate index. Specifically, the climate index captured

suitable and adverse climates, and the climate index that separated those climates. Data are for the 5000 model runs



**Fig. 4** Chain plot (upper panel) and overall histogram (lower panel) for the total sum of squares (SST) for the 1.25 million saved iterations



**Fig. 5** Density plots for the 1.25 million saved iterations for the three model parameters estimated using the Metropolis–Hastings algorithm: age-0 survival in the suitable and adverse

climates, and the climate index that separated those climates. The *x*-axis limits are the upper and lower bounds for the parameters' uniform prior densities

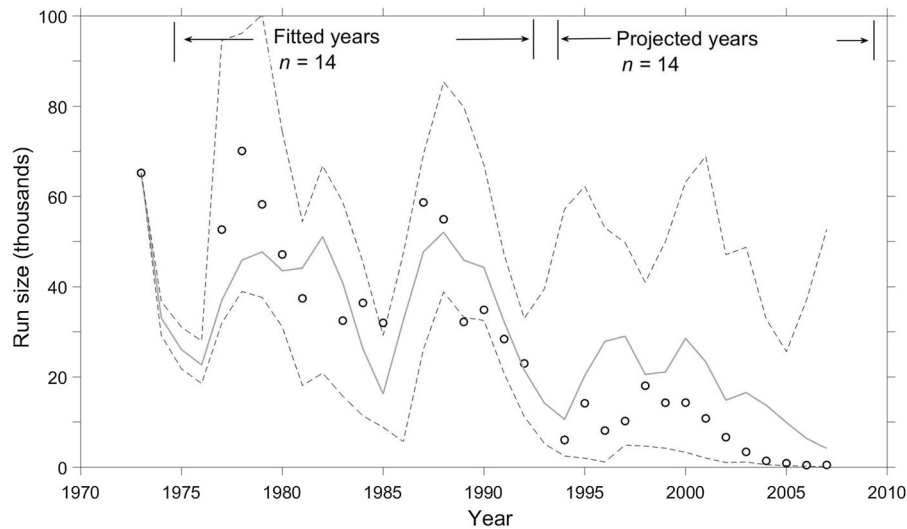
that negative association for creek discharge and temperature.

But none of the observed spawning runs during the forecast period were larger than the median predicted run, which suggested lake trout predation began to negatively affect the YCT population's climate-driven trajectory soon after the lake trout were discovered (cf. Kaeding 2010). Moreover, that emerging predation effect was evidently forestalled by climatic conditions more favorable to YCT reproduction that followed the particularly warm and dry years 1987 and 1988, Yellowstone National Park's epic wildfire year. Finally, if compared to the median predicted YCT population, lake trout predation resulted in an

approximate 90% reduction in the spawning run across recent years and thus—according to Kaeding's (2013a) correlations—in the YCT population of Yellowstone Lake.

Because the precise timing of lake trout introduction (and, more important, their initial reproduction and population growth) to the lake is unknown, it could be argued that a predation effect occurred across the entire Clear Creek YCT time series. But to speculate a predation effect large enough to *measurably* influence that population would require—as dismissed in "Introduction"—that perhaps a few hundred lake trout began to *measurably* diminish a lake-wide YCT population numbering several million





**Fig. 6** Observed and predicted size of the annual Yellowstone cutthroat trout spawning run in Clear Creek for the “fitted”-years (1977–1992) and the “projected”-years (1994–2007)

in the 1970s. That belief is untenable. Moreover, Kaeding (2010) presented a YCT population model driven entirely by a hypothetical, growing predation effect but it did not fit the observed data nearly as well as did his climate model.

Recognizing the prominent climate effect on these YCT is important, particularly to assessments of management actions intended to protect them by controlling the lake trout population (Ruzycki et al. 2003; Koel et al. 2005; Syslo et al. 2011). For example, if those actions are effective, Clear Creek’s YCT spawning run size should trend toward the median values predicted by this study’s model. Although the Clear Creek trap was not replaced after its destruction in 2008, an annual gill-net sampling program has continued to measure the lake’s YCT population trend (Arnold et al. 2017). This study’s model could be modified to examine those gill-net data. In any case, the present model could be used to predict climate-driven, post-2007 YCT population “bump-ups” in data trends that may otherwise be attributed to reduced lake trout predation.

But, absent long-term movement toward climatic conditions more favorable to YCT reproduction, even a greatly reduced lake trout population may not result in an increasing YCT population because the cold Yellowstone Lake temperature regime invariably favors the nonnative lake trout over the native YCT (Kaeding 2012). Furthermore, recent studies showed

periods. The observed data appear as open circles. The dashed lines delimit the extremes and the solid line the median of the predicted values for the middle 50% of model fits based on SST

historic climate warming in the Western US region that included the park was associated with anthropogenic global warming and that a return to the early 1970s climates, i.e., those most favorable to YCT reproduction, was highly unlikely (Vose et al. 2017).

The temporal trend in the climate index reported here and by Kaeding (2010, 2013b) suggested a climate shift in the Yellowstone Lake region in the late 1970s. Mantua et al. (1997) reported a 1977 shift in the Pacific Decadal Oscillation (PDO), a robust index of North Pacific Basin climate. Based on subsequent analyses of 31 climatic and 69 biological time series, Hare and Mantua (2000) confirmed the 1977 shift and provided a comprehensive review of the numerous supporting studies. That 1977 shift heralded a new climatic regime in the North Pacific and North America regions.

Annual variation in regional climate and stream flows in the Western USA, including the Yellowstone Lake region, is mainly driven by the North Pacific climate (Redmond and Koch 1991; see also Graumlich et al. 2003). Thus, the temporal trend in this study’s climate index was attributable to the climate shift and subsequent climatic regime documented by Hare and Mantua (2000) and other researchers. Furthermore, that trend is part of a broader, ongoing pattern of climate warming, especially evident in Western North America (Vose et al. 2017). Since the investigation of Hare and Mantua (2000), the PDO has undergone

substantial variations between “cool” and “warm” phases, yet much of Western North America (including the Yellowstone Park region) has shown a general warming trend, accompanied by substantial variation in annual precipitation (Easterling et al. 2017; Vose et al. 2017).

This study also indicated the climate shift reported by Hare and Mantua (2000) was the driver of a broader “regime” shift of the Yellowstone Lake ecosystem, i.e., from one relatively stable state to another (in the sense of Steele 1996; Folke et al. 2004). The pre-1977 stability was provided by climatic conditions favorable to YCT reproduction, in contrast to the subsequent, post-1977, climatic regime. Tronstad et al. (2010) described a concurrent shift in the Yellowstone Lake ecosystem but attributed it entirely to lake trout predation, largely based on a narrow examination of the climate data and its possible effect on YCT population dynamics. Instead, the present study showed the regime shift began with the 1977 North Pacific Basin climate shift that harmed YCT reproduction and was only later enhanced by the growing predation effect.

This study’s modeling approach to uncertainties (e.g., Hilborn and Mangel 1997) was an improvement over that used by Kaeding (2010) for this YCT population. Stochastic simulation of the 10 known model parameters and simultaneous use of Bayesian analysis to estimate the remaining three parameters accounted for process uncertainty. Although the measurement uncertainty associated with the observed spawning run sizes was unknown, assessment of model performance based on the ability of a middle proportion of the predicted runs to encompass most observed runs was a conservative approach that accounted for some of that uncertainty. The model’s structure (i.e., the issue of model uncertainty) accounted for the known variation in YCT somatic growth, fecundity, survival, maturity, and membership in the spawning run, along with a plausible environment effect on age-0 survival. A more simple but applicable model was not evident. Absent the environment effect, the simulated YCT population would have grown without limit—an impossible explanation for the empirical data. Finally, fitting the model to the pre-predation data precluded possible confounding of the climatic and predation effects in the analyses.

Koel et al. (2005) hypothesized reduced Yellowstone Lake surface elevations in dry years exposed natural alluvial deposits at tributary mouths that

blocked YCT fry emigration to the lake and the trapped fry consequently died. They also provided an aerial photograph of such a barrier on Columbine Creek (another Yellowstone Lake tributary) in which creek discharge appears entirely within those deposits. The posterior density plots for the three estimated parameters supported that hypothesis for Clear Creek. Specifically, the plot for the climate index separation point for the suitable and adverse climates age-0 survival probabilities was abrupt and mostly rectangular. Although such a posterior density would be expected because the empirical climate indexes were discrete rather than continuous values, it would also indicate an effective, climate-dependent physical barrier that had a “door-like” effect on YCT fry emigration to the lake. Furthermore, the marked contrast between the estimated suitable and adverse climates age-0 survival probabilities suggested the barrier effect greatly reduced age-0 YCT survival, perhaps by an order of magnitude. The barrier effect may not need to be complete to greatly reduce the survival of blocked YCT fry.

This study showed identifying and accounting for the overarching population drivers is important to structuring statistical models intended to detect and assess the effects of new and emerging population impacts across historic data sets. Those overarching drivers should be considered population specific, but identifying them may be problematic because the available data time series are often short compared to those of this study; few environments have experienced the paucity of human impacts like that characteristic of Yellowstone Lake; and few aquatic environments are as simple ecologically. Consequently, to reach the desired management outcomes for most fish populations today, adaptive management (in the sense of Walters 1986) is required to identify contemporary population drivers and use appropriate population models to determine the efficacy of actions intended to mitigate or enhance the drivers’ effects. For this YCT population, those management experiments should consider the evident climate-dependent, “barrier” effect on age-0 survival and management planning should consider probable future climates.

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