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ARTICLE

Could ecological release buffer suppression efforts for non-native lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Yellowstone National Park?

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Abstract: Yellowstone Lake in Yellowstone National Park, USA, has the longest ongoing suppression program for non-native lake trout (*Salvelinus namaycush*) in the western USA. Harvest data from the suppression program, along with data from an assessment program initiated in 2011, was used to estimate lake trout abundance and mortality rates. Abundance and biomass estimates were used to estimate stock–recruitment dynamics, which were inputs to a simulation model forecasting responses to continued suppression. Abundance increased during 1998–2012 when total annual mortality exceeded 0.59 and declined thereafter. The fishing mortality rate required to reduce abundance was 67% greater than predicted by models that used prerecruit survival estimates from the lake trout's native range. Prerecruit survival in Yellowstone Lake was estimated at four to six times greater than native range survival rates. Simulated abundance continued to decline if recent suppression efforts were maintained. High prerecruit survival in Yellowstone Lake likely illustrates ecological release for an invasive species in an ecosystem containing few predators or competitors and demonstrates the potential pitfalls of assuming equal demographic rates for native and non-native populations.

Résumé : Le lac Yellowstone, dans le Parc national Yellowstone (États-Unis), est le lieu du programme de suppression continu de truites de lac (*Salvelinus namaycush*) non indigènes le plus ancien dans l'Ouest des États-Unis. Des données sur les prises issues du programme de suppression, combinées à des données d'un programme d'évaluation initié en 2011, ont été utilisées pour estimer l'abondance et les taux de mortalité des truites de lac. Des estimations de l'abondance et de la biomasse ont été utilisées pour estimer la dynamique du recrutement au stock, dont les résultats ont servi d'intrants dans un modèle de simulation qui prédit les réactions à la suppression continue. L'abondance a augmenté de 1998 à 2012, alors que le taux de mortalité annuelle totale a dépassé 0,59, pour diminuer par la suite. Le taux de mortalité par pêche requis pour réduire l'abondance est de 67 % supérieur au taux prédit par des modèles qui utilisent des estimations de la survie prérecrutement obtenues pour l'aire de répartition naturelle des truites de lac. Le taux de survie prérecrutement estimé pour le lac Yellowstone est de quatre à six fois plus grand que les taux de survie dans l'aire de répartition naturelle. L'abondance simulée continue de diminuer si les efforts de suppression récents sont maintenus. Le taux élevé de survie prérecrutement dans le lac Yellowstone reflète probablement la libération écologique d'une espèce envahissante dans un écosystème comptant peu de prédateurs ou concurrents et démontre les écueils possibles de l'hypothèse de taux démographiques égaux pour des populations indigènes et non indigènes. [Traduit par la Rédaction]

Introduction

Non-native fishes have been implicated in the decline of native fish populations worldwide (Dudgeon et al. 2006; Jelks et al. 2008), causing eradication or suppression projects to increase in frequency and scale in recent years (Britton et al. 2011). Rapid initiation of suppression efforts on initial detection of invading species has been deemed critical to curtail population expansion (Simberloff 2003). Nevertheless, baseline assessment studies and simulation modeling are useful for assessing the efficacy of management actions prior to committing to specific control policies (Hansen et al. 2010; Syslo et al. 2013; Tsehaye et al. 2013). In the early stages of a suppression program, demographic rates of a target non-native population may be difficult to accurately estimate due to a paucity of available data in the invaded system, so vital demographic rates must often be borrowed from the species' native range (Morris et al. 2011; Syslo et al. 2011). The assumption that vital rates will be similar between native and introduced populations ignores the potential for characteristics of the receiving ecosystem to alter population dynamics through differences in community structure or the abiotic environment (Ricciardi

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et al. 2013). Published studies have indicated that niche expansion can result after ecological release from predation or interspecific competition (Bolnick et al. 2010; Shedd et al. 2015); however, we are unaware of any studies examining the potential effects of ecological release on demographic rates for non-native fish populations subject to eradication or suppression efforts.

The lake trout (*Salvelinus namaycush*) is an apex predator native to northern North America that has been introduced to 15 countries and extensively within the United States (Crossman 1995). Lake trout have been introduced into large lakes and reservoirs in eight western US states (Martinez et al. 2009), where their presence has led to declines in native salmonid populations (Fredenberg 2002; Vander Zanden et al. 2003; Koel et al. 2005) and subsequently altered ecosystem structure and function (Ellis et al. 2011; Koel et al. 2019). The negative effects stemming from non-native lake trout expansion has led to the initiation of multiple suppression programs in the western USA in an effort to restore native salmonid populations (Syslo et al. 2011; Hansen et al. 2016; Ng et al. 2016; Fredenberg et al. 2017; Dux et al. 2019).

Lake trout were discovered in Yellowstone Lake, Yellowstone National Park, in 1994 (Kaeding et al. 1996) following an introduction likely occurring in the mid- to late 1980s (Munro et al. 2005). Yellowstone Lake contains the largest population of nonhybridized Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) remaining in the western USA (Gresswell and Varley 1988) and represents 89% of historical lacustrine habitat currently occupied by the species (Gresswell 2009). The Yellowstone cutthroat trout is considered a keystone species in the Greater Yellowstone Ecosystem, with four mammal and 16 bird species documented consuming Yellowstone cutthroat trout (Bergum et al. 2017). Yellowstone cutthroat trout abundance declined substantially following the establishment of lake trout in Yellowstone Lake. For example, the number of spawning Yellowstone cutthroat trout counted at the Clear Creek weir declined from 55 000 individuals in 1987 to 500 in 2007 (Koel et al. 2012). The decline in Yellowstone cutthroat trout abundance resulted in a four-level trophic cascade (Tronstad et al. 2010) and disruption of trophic linkages across aquatic–terrestrial boundaries in the Yellowstone Lake basin (Koel et al. 2019).

A lake trout suppression program was initiated in Yellowstone Lake in response to lake trout detection to decrease predation on Yellowstone cutthroat trout and reverse the population's decline (McIntyre 1995; Ruzycki et al. 2003). Removal of lake trout was initiated in 1995 with limited gillnet effort intended mostly to assess population characteristics. In 1998, gillnet effort was increased for the purpose of maximizing lake trout harvest (Syslo et al. 2011). The first assessment of the lake trout population based on data collected through 2009 suggested that lake trout abundance was increasing despite more than a decade of suppression (Syslo et al. 2011). The study used a stochastic forecasting model to predict the increase in fishing effort that would be required to reduce lake trout population growth below replacement. The model used age-0 and age-1 survival rates from the native range of lake trout and predicted that abundance would decline if total annual mortality exceeded 0.39 (Syslo et al. 2011). Since the initial assessment was completed, annual suppression effort and lake trout removals have increased, far surpassing targets recommended in 2011.

Additional years of harvest data from lake trout suppression along with data availability from an assessment program prompted a new stock assessment of the lake trout population in Yellowstone Lake and an opportunity to evaluate the assumption that prerecruit survival was commensurate with estimates from the native range of lake trout. The new stock assessment used data from the lake trout suppression and assessment programs spanning 1998–2018 to estimate abundance and mortality of lake trout in Yellowstone Lake. Age-2 abundance and spawning stock biomass estimates from the assessment model were used to quantify the stock–recruitment relationship for the lake trout population and uncertainty in stock–recruitment parameter estimates. Stock–recruitment parameter estimates were then used with parameter estimates from the stock assessment model to forecast the response of the lake trout population to future suppression efforts. Long-term data available from the 20+ year suppression program for lake trout in Yellowstone Lake provided a unique opportunity to examine stock–recruitment dynamics for a non-native lake trout population. In-depth examination of lake trout stock–recruitment dynamics in Yellowstone Lake was not possible in earlier analyses because of limited data available for assessment modeling.

Materials and methods

Study area

Yellowstone Lake is at an elevation of 2357 m and has a surface area of 34 020 ha, shoreline distance of 239 km, mean depth of 48.5 m, and maximum depth of 133 m (Morgan et al. 2003). The lake is typically ice-covered from mid-December until late May or early June. The lake thermally stratifies from late July into September, with summer surface water temperatures reaching 17 °C and a thermocline at ~15 m deep (Koel et al. 2007). The lake is considered oligomesotrophic (Theriot et al. 1997), with diatoms dominating the phytoplankton assemblage during the year (Benson 1961; Tronstad et al. 2010). The zooplankton assemblage consists primarily of the rotifer *Conochilus unicornis*, Copepoda *Diaptomus* spp. and *Cyclops* spp., and Cladocera *Daphnia* spp. (Benson 1961). The fish assemblage is relatively simple, with two native species, Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*), and three introduced species in addition to lake trout, longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*; Gresswell and Varley 1988).

Assessment model

Data

The statistical catch-at-age (SCAA) assessment model for the lake trout population in Yellowstone Lake used three data sources: (*i*) total harvest (in number) and harvest age composition of the suppression gillnet program from 1998 to 2018, (*ii*) total harvest (in number) and harvest age composition of a suppression trapnet program from 2010 to 2013, and (*iii*) total harvest (in number) and harvest age composition of a standardized assessment gillnet program from 2011 to 2018. The suppression gillnet and trapnet programs were implemented over several months, so these were treated as Type-2 fisheries. The standardized assessment gillnet program was conducted over a much shorter time period (≈2 weeks); consequently, lake trout harvest from the assessment gillnet program was treated as a Type-1 fishery that occurred ~⅔ into the fishing season. All lake trout captured in the standardized assessment program were harvested, so it was treated as a separate fishery. In addition to suppression netting efforts, an unknown amount of recreational fishing for lake trout does occur on Yellowstone Lake. The methodology for expanding self-reported catch from anglers to total lake-wide harvest has not been assessed for accuracy since the 1970s, prior to lake trout introduction. Lake trout harvest from the recreational fishery is believed to be at least an order of magnitude lower than the harvest from the suppression program and was not included in the assessment model. Details on data collection and how data were processed from each of the data sources used in the SCAA model are described in Appendix A.

Model description

SCAA assessment models include a process component that predicts abundance-at-age for the modeled population and an observation component that predicts fishery and survey harvest or catch-at-age conditional on the predicted abundance-at-age. SCAA models produce estimates of the underlying dynamics of the population and the fisheries that exploit the population, which subsequently can be used to forecast effects on a population of different harvest or suppression strategies. The lake trout SCAA model for Yellowstone Lake covered the period from 1998 to 2018 and included fish from age-2 (age of recruitment to the gear) to age-17. The age-17 age class was an aggregate group that included all fish age-17 and older. Definitions of parameters and variables used in the equations for the population and observation submodels are presented in Table 1.

Annual abundances of age-2 lake trout (i.e., annual recruitment) were estimated in the SCAA model as the product of a mean recruitment level and multiplicative annual recruitment deviations:

$$N_{y,2} = \bar{R}\exp\left(\delta^{R}_{y}\right) \tag{1}$$

with the annual recruitment deviations constrained to sum to 0. Age-3 to age-17 abundances in the first modeled year (1998) were estimated as freely varying parameters. Abundances at age for the remaining years were predicted using an exponential population model. To account for a pulse of mortality associated with the assessment gillnet program, we divided the year into two parts:

$$\dot{N}_{y,a} = N_{y,a}\exp(-0.68\cdot Z_{y,a}) \tag{2}$$

where $\dot{N}_{y,a}$ is the predicted abundance-at-age 68% into the completion of the fishing season and immediately prior to when the assessment program is conducted. Abundance in the following year at the next age was then calculated after accounting for the pulse of mortality from the assessment gillnet (AG) program and allowing for the remainder of the mortality for the current year:

$$\ddot{N}_{y,a} = \dot{N}_{y,a}\exp\left(-F^{AG}_{y,a}\right) \tag{3}$$

$$N_{y+1,a+1} = \ddot{N}_{y,a}\exp(-0.32\cdot Z_{y,a}) \tag{4}$$

Total annual instantaneous mortality excluding assessment gillnet fishing mortality was partitioned into natural causes, suppression trapnet (ST) fishing mortality, and suppression gillnet (SG) fishing mortality:

$$Z_{y,a} = M_a + \sum_{f} F^{f}_{y,a} \quad \text{for } f = \text{SG and AG} \tag{5}$$

Age-specific instantaneous natural mortalities were assumed quantities, as it can be difficult to estimate these parameters because of confounding with other mortality sources (Hilborn and Walters 1992; Quinn and Deriso 1999). Age-2 M was set equal to 0.25 based on lake trout in Lake Superior (Sitar et al. 1999). Age-3 to age-17 M was set equal to 0.16 based on Pauly's (1980) equation and von Bertalanffy growth parameters (mean $t_0 = 0.68$; mean $k = 0.13$, mean $L_\infty = 862$ mm) of lake trout in Yellowstone Lake and the mean annual water temperature for lake trout in the lake (5.1 °C; Syslo et al. 2016).

Fishing mortalities for assessment and suppression fishing were assumed to be products of fishing effort, age- and potentially year-specific selectivities (i.e., vulnerabilities), and year-specific (assessment and suppression gill netting) or constant (suppression trapnetting) catchabilities.

$$F^{SG}_{y,a} = q^{SG}_{y} s^{SG}_{y,a} E^{SG}_{y} \quad \text{for } y \geq 1998 \tag{6}$$

$$F^{ST}_{y,a} = q^{ST} s^{ST}_{a} E^{ST}_{y} \quad \text{for } 2010 \leq y \leq 2013 \tag{7}$$

$$F^{AG}_{y,a} = q^{AG}_{y} s^{AG}_{a} E^{AG}_{y} \quad \text{for } y \geq 2011 \tag{8}$$

A model-selection process was used to identify whether asymptotic (i.e., logistic function) or dome-shaped (i.e., gamma function) selectivity functions were most appropriate for the suppression and assessment gill nets and whether suppression gillnet selectivities should be time-varying (see section below on Model-based evaluation of selectivities) given changes in average mesh size through time (Appendix A). Age-specific selectivity for suppression trap nets was estimated as a logistic function of age, with the underlying coefficients of the logistic function among the parameters estimated in the SCAA model (Haddon 2011):

$$s^{ST}_{a} = \frac{1}{1 + \exp\left[-\log_e(19)\cdot\dfrac{a - a^{ST}_{50}}{a^{ST}_{95} - a^{ST}_{50}}\right]} \tag{9}$$

where a^{ST}_{50} is the age at which selectivity is 50%, and a^{ST}_{95} is the age at which selectivity is 95%.

For suppression and assessment gillnetting, we estimated annual catchabilities as the product of mean catchabilities and multiplicative annual catchability deviations with the annual catchability deviations constrained to sum to 0. To account for changes in the operation of the suppression gillnet fishery, including the addition of specialized boats for setting gill nets and an increase in average soak time, we assumed separate mean catchabilities for the years of 1998 to 2000 and 2001 to 2018:

$$q^{SG}_{y} = \bar{q}^{SG}_{1}\exp\left(\delta^{SG}_{y}\right) \quad \text{for } 1998 \leq y \leq 2000 \tag{10}$$

$$q^{SG}_{y} = \bar{q}^{SG}_{2}\exp\left(\delta^{SG}_{y}\right) \quad \text{for } 2001 \leq y \leq 2018 \tag{11}$$

For assessment gillnetting, a single mean catchability was assumed for the duration of the program:

$$q^{AG}_{y} = \bar{q}^{AG}\exp\left(\delta^{AG}_{y}\right) \quad \text{for } 2011 \leq y \leq 2018 \tag{12}$$

Estimated age-specific harvests for suppression gillnet and trapnet programs were calculated annually using the Baranov catch equation:

$$\hat{H}^{f}_{y,a} = \frac{0.68\cdot F^{f}_{y,a}}{0.68\cdot Z_{y,a}} N_{y,a}[1 - \exp(-0.68\cdot Z_{y,a})] + \frac{0.32\cdot F^{f}_{y,a}}{0.32\cdot Z_{y,a}} \ddot{N}_{y,a}\exp[1 - \exp(-0.32\cdot Z_{y,a})] \quad \text{for } f = \text{SG and ST} \tag{13}$$

Because the assessment gillnet program was treated as a Type-1 fishery, age-specific harvest for assessment gill netting was calculated as

$$\hat{H}^{AG}_{y,a} = \dot{N}_{y,a}\left[1 - \exp\left(-F^{AG}_{y,a}\right)\right] \tag{14}$$

Total annual harvest of respective fisheries was calculated by summing age-specific harvests:

$$\hat{H}^{f}_{y} = \sum_{a} \hat{H}^{f}_{y,a} \quad \text{for } f = \text{SG, ST, and AT} \tag{15}$$

Table 1. Symbols used in description of statistical catch-at-age assessment, stock–recruitment, and forward projection models for lake trout in Yellowstone Lake.

Symbol	Description	Prior
Index		
y	Year (1998–2018)	
a	Age class (2–17+)	
f	Fishery type	
SG	Suppression gill net	
ST	Suppression trap net	
AG	Assessment gill net	
Input data and assumed values		
E_y^f	Fishery-specific annual fishing effort level	
M_a	Natural instantaneous mortality	
H_y^f	Fishery-specific total observed harvest	
$P_{y,a}^f$	Fishery-specific observed harvest age composition	
$W_{y,a}$	Weight-at-age	
$m_{y,a}$	Percent mature-at-age	
$\text{Eggs}_{y,a}$	No. of eggs produced per kilogram of body weight-at-age	
n^f	No. of years that a fishery was conducted	
ESS	Effective sample size for the multinomial distributions for the harvest age compositions	
σ^{δ^f}	Standard deviation for lognormal log-prior component for fishery-specific catchability annual deviations	
σ^{δ^R}	Standard deviation for lognormal log-prior component for recruitment annual deviations	
Parameter		
$\overline{R}$	Mean recruitment	$\log_e$ scale: U(0, 15)
δ_y^R	Recruitment annual deviations	$\log_e$ scale: N(0, 4.0)
$N_{1998,3\text{ to }17+}$	Initial year abundance at age for ages 3 to 17+	$\log_e$ scale: U(0, 15)
$\overline{q}_1^{SG}$	Mean suppression gillnet catchability 1998 to 2000	$\log_e$ scale: U(−25, 0)
$\overline{q}_2^{SG}$	Mean suppression gillnet catchability 2001 to 2018	$\log_e$ scale: U(−25, 0)
δ_y^{SG}	Suppression gillnet annual deviations	$\log_e$ scale: N(0, $\sigma^{\delta^{SG}}$)
$\overline{q}^{AG}$	Mean assessment gillnet catchability	$\log_e$ scale: U(−25, 0)
δ_y^{AG}	Assessment gillnet annual deviations	$\log_e$ scale: N(0, $\sigma^{\delta^{AG}}$)
q^{ST}	Suppression trapnet catchability	$\log_e$ scale: U(−20, 0)
a_{50}^f	Fishery-specific logistic function age at which selectivity is 50% (only parameters in SCAA models with constant logistic selectivities)	$\log_e$ scale: U(−5, 5)
a_{95}^f	Fishery-specific logistic function age at which selectivity is 95% (only parameters in SCAA models with constant logistic selectivities)	$\log_e$ scale: U(−5, 5)
γ^f	Fishery-specific gamma function selectivity parameter 1 (only in SCAA models with gamma selectivities)	$\log_e$ scale: U(−5, 5)
θ^f	Fishery-specific gamma function selectivity parameter 2 (only in SCAA models with gamma selectivities)	$\log_e$ scale: U(−5, 5)
$\beta_0^{a_{50}^f}$	Intercept for relating fishery-specific logistic function age at which selectivity is 50% based on average mesh size ($\log_e$ scale) (only in SCAA models with time-varying selectivities)	$\log_e$ scale: U(−10, 10)
$\beta_1^{a_{50}^f}$	Slope for relating fishery-specific logistic function age at which selectivity is 50% based on average mesh size ($\log_e$ scale) (only in SCAA models with time-varying selectivities)	$\log_e$ scale: U(−10, 10)
$\beta_0^{a_{95}^f}$	Intercept for relating fishery-specific logistic function age at which selectivity is 95% based on average mesh size ($\log_e$ scale) (only in SCAA models with time-varying selectivities)	$\log_e$ scale: U(−10, 10)
$\beta_1^{a_{95}^f}$	Slope for relating fishery-specific logistic function age at which selectivity is 95% based on average mesh size ($\log_e$ scale) (only in SCAA models with time-varying selectivities)	$\log_e$ scale: U(−10, 10)
σ^f	Standard deviation for lognormal log-likelihood component for fishery-specific total harvest	$\log_e$ scale: U(−10, 10)
α	Intercept of linearized Ricker stock–recruit function (only in stock–recruit model)	$\log_e$ scale: U(−25, 25)
β	Slope of linearized Ricker stock–recruit function (only in stock–recruit model)	$\log_e$ scale: U(−100, 0)
σ^R	Standard deviation of the linear Ricker stock–recruit function (only in stock–recruit model)	$\log_e$ scale: U(−5, 5)
Derived variables		
$N_{y,a}$	Abundance at the start of the year	
$\dot{N}_{y,a}$	Abundances after 68% of total annual mortality has been experienced	
$\ddot{N}_{y,a}$	Abundance after 68% of total annual mortality has been experienced and after assessment gillnet harvest has been experienced	
$F_{y,a}^f$	Fishery-specific instantaneous mortality	
$Z_{y,a}$	Total instantaneous mortality	
s_a^{ST}	Fishery-specific selectivity (relative vulnerability)	
q_y^f	Fishery-specific annual catchabilities	
$\hat{H}_{y,a}^f$	Fishery-specific estimated harvest at age	
$\hat{H}_y^f$	Fishery-specific total estimated harvest	
$\hat{P}_{y,a}^f$	Fishery-specific estimated harvest age composition	
B_y	Total biomass	
Y_y^{Tot}	Total yield across all fisheries	
Y_y^{6+}	Age-6 and older yield across all fisheries	
SSB_y	Spawning stock biomass	

Table 2. Equations and descriptions of the negative log-likelihood and negative log-prior components for the lake trout statistical catch-at-age (SCAA) model for Yellowstone Lake.

Eq. No.	Equation	Description
T.2.1	$\mathcal{L}_{H^{\mathrm{SG}}} = n^{\mathrm{SG}}\log_e(\sigma^{\mathrm{SG}}) + \frac{0.5}{\sigma^{\mathrm{SG}}}\sum_y\left[\log_e\left(H_y^{\mathrm{SG}}\right) - \log_e\left(\hat{H}_y^{\mathrm{SG}}\right)\right]^2$	Total suppression gillnet harvest
T.2.2	$\mathcal{L}_{H^{\mathrm{ST}}} = n^{\mathrm{ST}}\log_e(\sigma^{\mathrm{ST}}) + \frac{0.5}{\sigma^{\mathrm{ST}}}\sum_y\left[\log_e\left(H_y^{\mathrm{ST}}\right) - \log_e\left(\hat{H}_y^{\mathrm{ST}}\right)\right]^2$	Total suppression trapnet harvest
T.2.3	$\mathcal{L}_{H^{\mathrm{AG}}} = n^{\mathrm{AG}}\log_e(\sigma^{\mathrm{AG}}) + \frac{0.5}{\sigma^{\mathrm{AG}}}\sum_y\left[\log_e\left(H_y^{\mathrm{AG}}\right) - \log_e\left(\hat{H}_y^{\mathrm{AG}}\right)\right]^2$	Total assessment gillnet harvest
T.2.4	$\mathcal{L}_{P^{\mathrm{SG}}} = -\sum_y \mathrm{ESS}\sum_a P_{y,a}^{\mathrm{SG}}\log_e\left(\hat{P}_{y,a}^{\mathrm{SG}}\right)$	Age composition of suppression gillnet harvest
T.2.5	$\mathcal{L}_{P^{\mathrm{ST}}} = -\sum_y \mathrm{ESS}\sum_a P_{y,a}^{\mathrm{ST}}\log_e\left(\hat{P}_{y,a}^{\mathrm{ST}}\right)$	Age composition of suppression trapnet harvest
T.2.6	$\mathcal{L}_{P^{\mathrm{AG}}} = -\sum_y \mathrm{ESS}\sum_a P_{y,a}^{\mathrm{AG}}\log_e\left(\hat{P}_{y,a}^{\mathrm{AG}}\right)$	Age composition of assessment gillnet harvest
T.2.7	$\mathcal{L}_{\delta^R} = n^{\delta^R}\log_e(\sigma^{\delta^R}) + \frac{0.5}{\sigma^{\delta^R}}\sum_y\left[0 - \log_e\left(\delta_y^R\right)\right]^2$	Recruitment deviation prior
T.2.8	$\mathcal{L}_{\delta^{\mathrm{SG}}} = n^{\delta^{\mathrm{SG}}}\log_e(\sigma^{\delta^{\mathrm{SG}}}) + \frac{0.5}{\sigma^{\delta^{\mathrm{SG}}}}\sum_y\left[0 - \log_e\left(\delta_y^{\mathrm{SG}}\right)\right]^2$	Suppression gillnet catchability deviation prior
T.2.9	$\mathcal{L}_{\delta^{\mathrm{AG}}} = n^{\delta^{\mathrm{AG}}}\log_e(\sigma^{\delta^{\mathrm{AG}}}) + \frac{0.5}{\sigma^{\delta^{\mathrm{AG}}}}\sum_y\left[0 - \log_e\left(\delta_y^{\mathrm{AG}}\right)\right]^2$	Assessment gillnet catchability deviation prior

while age composition of the harvest was calculated by dividing age-specific harvest by total harvest:

$$(16)\qquad \hat{P}_{y,a}^{f} = \hat{H}_{y,a}^{f}/\hat{H}_{y}^{f}\quad \text{for } f = \mathrm{SG},\ \mathrm{ST},\ \text{and AT}$$

Several other demographics of the lake trout population in Yellowstone Lake were calculated as part of the SCAA assessment model for either reporting purposes or for use in the forecasting model. These included total biomass of the population:

$$(17)\qquad B_y = \sum_a N_{y,a}W_{y,a}$$

annual total yield from the combined fisheries:

$$(18)\qquad Y_y^{\mathrm{Tot}} = \sum_f\sum_a \hat{H}_{y,a}^{f}W_{y,a}$$

and yield for fish age-6 and older from the combined fisheries:

$$(19)\qquad Y_y^{6+} = \sum\nolimits_f\sum\nolimits_{a\geq 6}\hat{H}_{y,a}^{f}W_{y,a}$$

Spawning stock biomass as indexed by the expected number of eggs produced by sexually mature females was also calculated in the SCAA model; this was calculated as the product of abundance-at-age after assessment gillnetting had been completed, weight-at-age, percent maturity-at-age, number of eggs produced per kilogram of body-weight-at-age, and an assumed 1:1 sex ratio in the population summed over all ages:

$$(20)\qquad \mathrm{SSB}_y = \sum\nolimits_a 0.5\cdot\ddot{N}_{y,a}W_{y,a}m_{y,a}\mathrm{Eggs}_{y,a}$$

Descriptions of how weight-at-age, percent maturity-at-age, and number of eggs produced per kilogram of body-weight-at-age were calculated are provided in Appendix A.

The SCAA model was programmed in AD Model Builder version 12.0 (Fournier et al. 2012). A Bayesian-based estimation approach was used, whereby point estimates of model parameters were the highest posterior density estimates (Schnute 1994). More specifically, we defined an objective function equal to the negative log-posterior (ignoring some constants) and used a quasi-Newton optimization algorithm to numerically search for the parameter estimates that minimized the objective function (Fournier et al 2012). The model was considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than 1.0×10^{-4}, which is the default in AD Model Builder. Uncertainty was characterized by full posterior probabilities for estimated parameters and derived variables.

The objective function consisted of the sum of both negative log-likelihood and negative log-prior components. Lognormal distributions were assumed for the negative log-likelihoods for suppression (eq. T.2.1; Table 2) and assessment gillnet (eq. T.2.2; Table 2) and suppression trapnet (eq. T.2.3; Table 2) total harvest. Multinomial distributions were assumed for the negative log-likelihoods for the harvest age compositions (eqs. T.2.4–T.2.6; Table 2). Lognormal distributions were also assumed for negative log-priors for the recruitment (eq. T.2.7; Table 2) and suppression (eq. T.2.8; Table 2) and assessment gillnet (eq. T.2.9; Table 2) catchability deviations. All other estimated parameters of the SCAA model were assigned uniform (on a $\log_e$ scale) priors with diffuse upper and lower bounds (Table 1).

Standard deviations for lognormal negative log-likelihood components for suppression (σ^{SG}) and assessment (σ^{AG}) gillnet total harvests were among the estimated parameters in the SCAA model. Multiple standard deviations can be difficult to estimate in SCAA models, often requiring assumptions to be made for the relative values of standard deviations for different data sources (Fielder and Bence 2014). The estimated standard deviation for the lognormal negative log-likelihood component for assessment gillnet total harvest was assumed to be the standard deviation for the negative log-likelihood component for suppression trapnet total harvest (i.e., $\sigma^{\mathrm{AG}} = \sigma^{\mathrm{ST}}$). The estimated standard deviation for the lognormal negative log-likelihood component for assessment gillnet total harvest was also assumed to be the standard deviation for the lognormal negative log-prior for the assessment gillnet catchability deviation (i.e., $\sigma^{\mathrm{AG}} = \sigma^{\delta^{\mathrm{AG}}}$). Likewise, the estimated standard deviation for the lognormal negative log-likelihood component for suppression gillnet total harvest was assumed to be the standard deviation for the lognormal negative log-prior for the suppression gillnet catchability deviation (i.e., $\sigma^{\mathrm{SG}} = \sigma^{\delta^{\mathrm{SG}}}$). Thus, we assumed that interannual variation in catchability was of similar magnitude to the observation error for catch. The standard deviation for the lognormal prior probability distribution for the annual recruitment deviations was set at 4.0, which was intended to result in a weakly informative prior on the deviations that would nevertheless constrain the deviations to being close to 0 in the absence of a strong signal. Effective sample sizes for multinomial distributions for harvest age compositions were the number of fish aged each year up to a maximum of 100 fish (Brenden et al. 2011; Tsehaye et al. 2014).

To assess uncertainty associated with parameter estimates and derived variables from the SCAA model, posterior probability distributions were obtained by Markov chain Monte Carlo (MCMC) simulations through a Metropolis–Hastings algorithm in AD Model Builder (Fournier et al. 2012). The MCMC chain was run for 1 million steps sampling every 100th step. The scaling period that the algorithm used to optimize the acceptance rate for the MCMC chain was set at 500 000 steps. The initial 5000 saved steps were discarded as a burn-in. Convergence of the MCMC chain was evaluated by constructing trace plots for each estimated parameter and derived variable and by using Z score tests to evaluate differences between the means of the first 10% and last 50% of the saved chain (Geweke 1992). All MCMC chain convergence diagnostics were conducted in R (R Core Team 2019) using the “coda” package (Plummer et al. 2006).

Model-based evaluation of selectivities

Because of uncertainty in the underlying shape of selectivity curves for suppression and assessment gillnet programs and whether suppression gillnet selectivity should be time-varying considering changes in net configurations over time, we conducted a model-based evaluation of selectivity functions for the gillnet fisheries. Evaluation of selectivity functions was based on deviance information criteria (DIC; Spiegelhalter et al. 2002), where the model with the lowest DIC was selected. Models were also evaluated by retrospective analysis that involves refitting the SCAA model after deleting recent years of observation and examining whether model predictions exhibit systematic biases in parameter estimates or model predictions. The retrospective analysis involved deleting observations as far back as 2013 and looking for systematic biases in total abundance estimates, the main performance benchmark used to evaluate success of the suppression program and to define future suppression effort.

Two different selectivity functions were evaluated for the gillnet fisheries. The first function was a logistic function, as for the assessment trapnet fishery (eq. 9):

$$(21)\qquad s_a^f = \frac{1}{1 + \exp\left[-\log_e(19)\cdot\dfrac{a - a_{50}^f}{a_{95}^f - a_{50}^f}\right]} \quad \text{for } f = \text{SG and AG}$$

The second function was a gamma function:

$$(22)\qquad s_a^f = \frac{a^{\gamma^f}\exp(-\theta^f a)}{s_{10}^f} \quad \text{for } f = \text{SG and AG}$$

where the γ and θ are gamma function parameters. The denominator in eq. 22 denotes the values that would be obtained in the numerator at age-10, which served to scale selectivity values to a reference age.

After distinguishing which selectivity function provided the best fit based on DIC values with no retrospective issues, we then evaluated whether the observed data supported using time-varying selectivities for the suppression gillnet program. Time-varying selectivities were accounted for by modeling selectivity parameters as a linear (on a $\log_e$ scale) function of the weighted average mesh size of the gill nets that were fished annually. The logistic function outperformed the gamma function (see Results below); therefore, this approach for modeling time-varying selectivities consisted of the following equations:

$$(23)\qquad a_{50_y}^{\mathrm{SG}} = \exp\left(\beta_0^{a_{50}^{\mathrm{SG}}} + \beta_1^{a_{50}^{\mathrm{SG}}}\,\overline{\mathrm{Mesh}_y}\right)$$

$$(24)\qquad a_{95_y}^{\mathrm{SG}} = \exp\left(\beta_0^{a_{95}^{\mathrm{SG}}} + \beta_1^{a_{95}^{\mathrm{SG}}}\,\overline{\mathrm{Mesh}_y}\right)$$

where β_0 and β_1 were parameters estimated as part of the SCAA model fitting process.

Annual selectivities for the suppression gillnet program were then calculated as

$$(25)\qquad s_{y,a}^{\mathrm{SG}} = \frac{1}{1 + \exp\left[-\log_e(19)\cdot\dfrac{a - a_{50_y}^{\mathrm{SG}}}{a_{95_y}^{\mathrm{SG}} - a_{50_y}^{\mathrm{SG}}}\right]}$$

Stock–recruitment estimation and uncertainty

A linearized Ricker stock–recruit function was fit to the highest posterior density estimate of age-2 lake trout abundance in year y and the estimates of spawning stock biomass (i.e., number of spawned eggs) that produced these recruits 2 years previously:

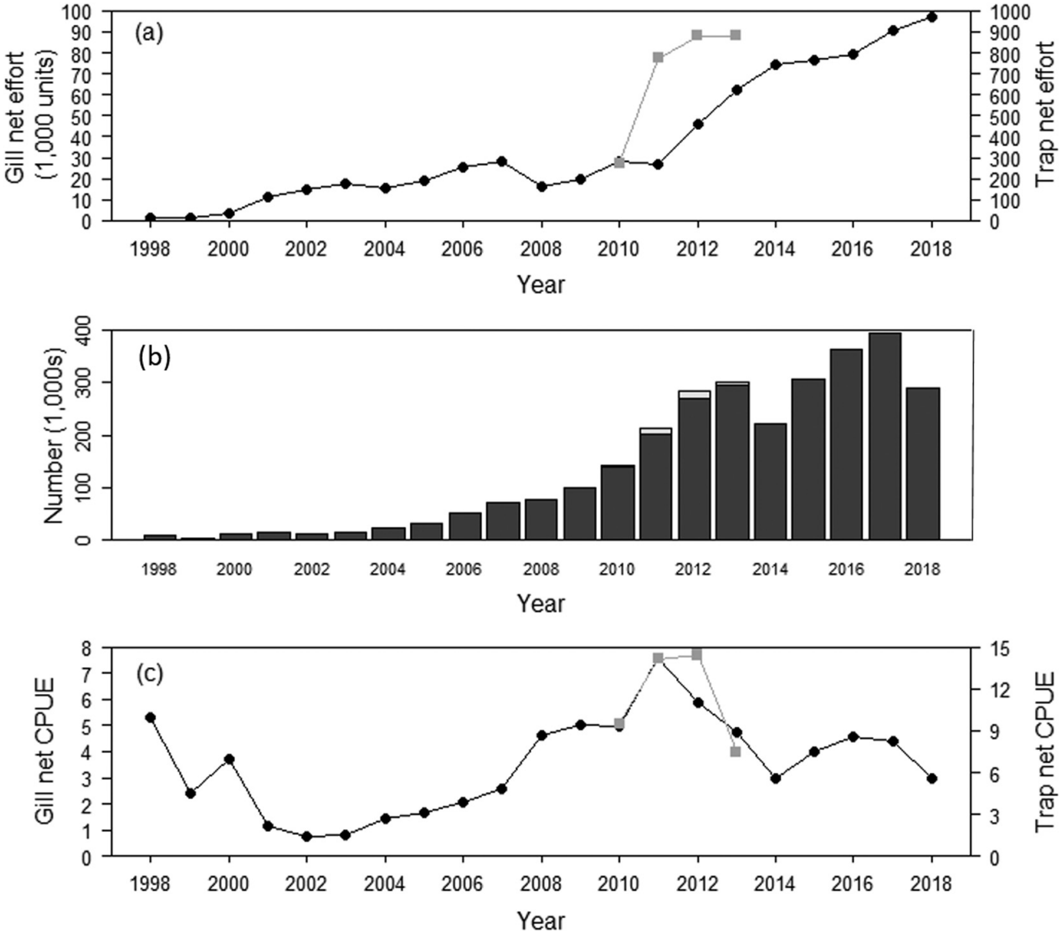
$$(26)\qquad \log_e\left(\frac{N_{y,2}}{\mathrm{SSB}_{y-2}}\right) = \log_e(\alpha) - \beta\cdot\mathrm{SSB}_{y-2} + \varepsilon_y \qquad \varepsilon_y \sim \mathrm{N}(0, \sigma^R)$$

The α estimate was corrected to account for bias stemming from linearization (Quinn and Deriso 1999). Uncertainty in the fitted stock–recruitment relationship was determined by obtaining the age-2 lake trout abundance and estimates of spawning stock biomass that resulted from the MCMC simulation of the SCAA model and fitting the linearized Ricker stock–recruit function described in eq. 26 to each set of saved values. MCMC chain diagnostics for the resulting set of stock–recruit parameter estimates were assessed using the same approaches previously described (i.e., trace plots, Z score tests). Resulting stock–recruitment functions were converted to estimates of prerecruit (i.e., age-0 and age-1) survival by dividing predicted recruitment by the corresponding number of eggs producing that recruitment over the range of egg abundances estimated for 1998 through 2018 in Yellowstone Lake. The estimate of prerecruit survival for Yellowstone Lake was compared with the product of available survival estimates for age-0 (0.0043; Shuter et al. 1998) and age-1 (0.45; Sitar et al. 1999) lake trout from the native range.

Forecasting model

A female-based Leslie matrix model was used to predict the response of the lake trout population in Yellowstone Lake to future suppression gillnet effort levels (Caswell 2001; Syslo et al.

Fig. 1. Fishing effort (*a*), number of lake trout harvested (*b*), and catch per unit effort (CPUE) (*c*) through time for suppression gillnetting (black symbols and bars) and trapnetting (gray symbols and bars) in Yellowstone Lake from 1998 to 2018. One unit of gillnet effort = 100 m of net set for 1 night; 1 unit of trapnet effort = 1 trap net set for 1 night.

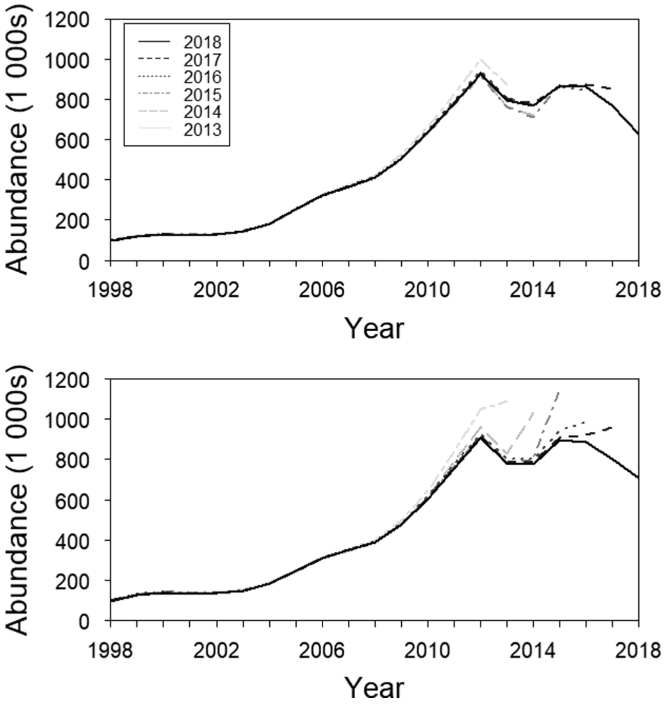


2011). The forecasting model generated 25-year projections of lake trout abundance assuming gillnet suppression levels varying from 0 to 125 000 one hundred metre net nights in 5000 one hundred metre net night increments (i.e., 26 simulated suppression effort scenarios). Suppression trapnetting was not considered in the forecasting model because this method of control was discontinued in the actual suppression program in favor of gillnetting. We also did not incorporate assessment netting in the simulation model because it is a negligible source of mortality for the actual population (see Results). The forecasting model was parameterized using results from the SCAA model, requiring the assumption that the average gillnet configuration used during 1998–2018 would be applied into the future.

The first 2 years of the projection model were initialized using abundances, age compositions, spawning stock biomass estimates, and observed gillnet suppression effort levels from the last 2 years (i.e., 2017 and 2018) of the SCAA model accounting for uncertainty in these model estimates. Initial age-specific abundances in the forecasting model were randomly generated from normal distributions using the 2017 and 2018 total abundance estimates and their associated standard errors from the SCAA assessment model. Initial age compositions for the simulations were randomly selected from the saved MCMC chain values for the 2017 and 2018 age compositions from the SCAA assessment model. Annual recruitment levels were generated from Ricker stock–recruit functions using values selected from the set of stock–recruit parameter estimates obtained from the MCMC process described in the section on Stock–recruitment estimation and uncertainty in the Results. Initial years of recruitment (i.e., 2019 and 2020) were based on randomly selected values from the saved MCMC chain values for the 2017 and 2018 spawning stock biomass estimates from the SCAA assessment model. Recruitments in later years were generated from spawning stock biomass levels calculated using the forecasted population conditions for that simulation run and eq. 20 (see below). Abundance-at-age in the simulation model was forecasted assuming the same natural mortality rates that were used in the SCAA model and suppression gillnet fishing mortality levels that depended on the suppression effort scenario being evaluated. Age-specific fishing mortality rates resulting from a particular suppression gillnet effort level were determined by randomly generating catchability from a normal distribution and logistic selectivity function coefficients from a multivariate normal distribution with mean and variance–covariance values equal to the estimates obtained from the SCAA assessment model. Instantaneous natural mortality for ages 3 and greater was generated using the meta-analysis of Pauly (1980), which predicted M as a function of mean annual environmental water temperature and a set of von Bertalanffy growth parameters that were randomly generated from a multivariate normal distribution. The von Bertalanffy growth parameters were also used to predict mean length-at-age in each simulation. Coefficients for models predicting weight-at length, probability of maturity at length, and fecundity-at-weight (Appendix A) were generated from multivariate normal distributions and used in eq. 20 to calculate spawning stock biomass.

Each simulated suppression gillnet effort scenario was repeated 1000 times to account for uncertainty in estimates of model parameters and initial abundances. For each iteration, new sets of initial abundances, initial age compositions, initial spawning stock biomass levels, stock–recruit coefficients, suppression gillnet catchabilities and selectivities, and life history characteristics (growth, length–weight relationships, maturation relationships, weight–fecundity relationships) were randomly generated from assumed distribution or by random selection from saved MCMC chains. The effects of different suppression gillnet effort levels were evaluated based on projected changes in total abundance and biomass through time. To address the feasibility of near-term objectives for the suppression program, we calculated the probability that abundance and biomass would be suppressed to less than 2018 abundance and biomass levels, less than 50% of 2018 abundance and biomass levels, and less than 100 000 fish (or the corresponding biomass) through 5- and 10-year periods at the different suppression effort levels. An additional set of simulations was used to determine the minimum level of suppression gillnet effort level required each year to maintain abundance below 100 000 fish after the target level was reached. For these scenarios, 95 000 units of effort were implemented until the population declined below 100 000 individuals and each of the 25 simulated suppression effort scenarios were implemented thereafter. Variation in simulation results was summarized with 90% confidence intervals for abundance, and the effort levels and time frames resulting in a 90% probability of suppression were reported.

Fig. 2. Retrospective pattern in total abundance for the statistical catch-at-age (SCAA) model assuming a constant logistic selectivity function for the suppression gillnet program (top panel) versus a model assuming a time-varying logistic selectivity function (bottom panel) for lake trout in Yellowstone Lake.



Results

Suppression gillnet effort (1 unit = 100 m of net set for 1 night) increased from 1447 units in 1998 to 28 327 units in 2007 and declined to 16 425 units in 2008 and 18 873 units in 2009 (Fig. 1). Gillnet effort increased slightly to 28 114 units in 2010 and 26 777 units in 2011. Gillnet effort increased more than threefold from 2011 through 2018, when 97 397 units of effort were deployed. Trapnet effort was 272 nights in 2010 and varied from 775 to 880 nights during 2011–2013. A total of 2 940 844 lake trout older than age-2 were harvested from all fisheries combined from 1998 through 2018. Suppression gill nets accounted for 98.8% (2 905 001 fish) of the harvest, followed by suppression trap nets (32 773 fish) and assessment gill nets (3070 fish). The number of lake trout harvested using suppression gill nets increased from 7659 in 1998 to 396 205 in 2017, and then declined in 2018 to 289 722 despite an increase in fishing effort that year (Fig. 1).

SCAA model

The SCAA model that assumed a logistic selectivity function for the suppression and assessment gillnet fisheries had a lower DIC (574.68) than the model that assumed a gamma selectivity function (590.60). Although the model that included a time-varying logistic selectivity for suppression gillnetting had a lower DIC (435.60) than the model that assumed a constant selectivity for suppression gillnetting, the model with time-varying selectivities exhibited a severe retrospective pattern, with terminal year abundances typically overestimated by 200 000 to 300 000 lake trout compared with when abundances were estimated for that year with added data (Fig. 2). The constant selectivity model did not exhibit a retrospective pattern in terminal year abundance estimates (Fig. 2); consequently, we elected to use the constant selectivity to assess the lake trout population.

SCAA model estimates of harvest, CPUE, and mean age matched observed temporal patterns well for all three fisheries (Fig. 3). Model estimates of trapnet harvest and mean age of trapnet harvest exhibited a somewhat poorer fit to observed data compared with the other two fisheries, likely as a consequence of the trapnet fishery being assumed to have a constant catchability.

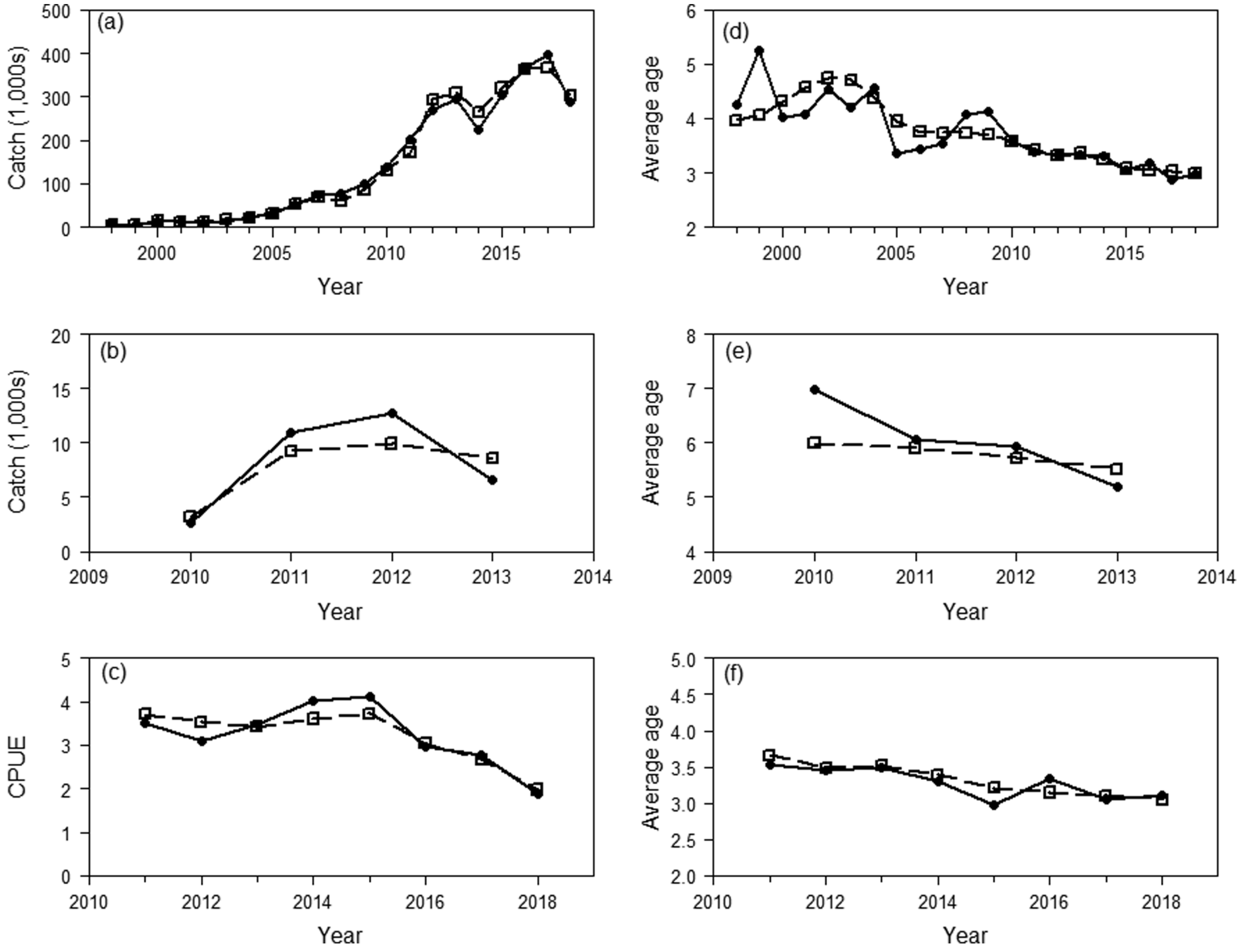
Total abundance (age-2 and older; 95% CI shown in parentheses) at the beginning of the year estimated from the SCAA model increased from 99 716 (82 372 – 120 551) lake trout in 1998 to 922 960 (759 050 – 1 123 690) in 2012 (Fig. 4*a*). Total abundance varied from $\sim$770 000 to $\sim$870 000 lake trout from 2013 through 2017 and declined to 628 203 (456 599 – 868 792) at the beginning of 2018. Total abundance at the end of the year increased from 76 548 in 1998 to 479 120 in 2012 and declined to 240 249 in 2018. Comparison of abundances between the beginning and end of the year indicated that 23% of total abundance was removed by natural and fishing mortality in 1998, 48% in 2012, and 62% in 2018 (Fig. 4*b*).

As suppression effort increased, the estimated age composition of the lake trout population shifted to younger fish. From 1998 to 2004, age-2 fish composed between 26% and 43% of total abundance. Conversely, from 2014 to 2018, age-2 fish composed between 52% and 55% of total abundance (Fig. 4*c*). The fraction of the population consisting of age-6 and older lake trout declined from between 9% and 26% in 1998–2004 to between 2% and 5% in 2014–2018. Population biomass at the beginning of the year increased from 46 832 kg (95% CI: 35 850 – 60 932 kg) in 1998 to 426 937 kg (341 846 – 528 155 kg) in 2012, before steadily declining to 232 000 kg (165 865 – 320 456 kg) in 2018 (Fig. 4*d*).

Estimated total yield increased gradually from 0.10 $\text{kg}\cdot\text{ha}^{-1}$ (95% CI: 0.07–0.15 $\text{kg}\cdot\text{ha}^{-1}$) in 1998 to 2.26 $\text{kg}\cdot\text{ha}^{-1}$ (1.54–2.94 $\text{kg}\cdot\text{ha}^{-1}$) in 2010 (Fig. 5). Implementation of suppression trapnetting and an increase in suppression gillnet effort increased annual yields after 2010. Estimated total yield peaked at 5.60 $\text{kg}\cdot\text{ha}^{-1}$ (3.82–7.24 $\text{kg}\cdot\text{ha}^{-1}$) in 2013 before declining to 3.89 $\text{kg}\cdot\text{ha}^{-1}$ (2.79–5.45 $\text{kg}\cdot\text{ha}^{-1}$) in 2018 despite an increase in gillnet effort. Estimated yield of lake trout age-6 and older increased from 0.06 $\text{kg}\cdot\text{ha}^{-1}$ (0.03–0.09 $\text{kg}\cdot\text{ha}^{-1}$) in 1998 to a peak of 1.86 $\text{kg}\cdot\text{ha}^{-1}$ (1.24–2.45 $\text{kg}\cdot\text{ha}^{-1}$) in 2012 and declined to 0.58 $\text{kg}\cdot\text{ha}^{-1}$ (0.34–0.93 $\text{kg}\cdot\text{ha}^{-1}$) in 2018.

Total instantaneous fishing mortality of all fisheries combined increased from 0.09 (95% CI: 0.05–0.13) in 1998 to 1.13 (0.72–1.53) in 2018 (Fig. 6*a*). Assuming a constant rate of $M = 0.16$, total annual

Fig. 3. Observed (solid circles) and predicted (open squares) values for data sources used in a statistical catch-at-age model for lake trout in Yellowstone Lake from 1998 to 2018. Data sources include catch in the suppression gill nets (*a*), catch in suppression trap nets (*b*), catch per unit effort (CPUE; number per 100 m of net per night) in assessment netting (*c*), and age compositions for suppression gill nets (*d*), suppression trap nets (*e*), and assessment nets (*f*).



mortality for fully selected ages was 0.25 (0.19–0.25) in 1998, 0.59 (0.52–0.68) in 2012, and peaked at 0.72 (0.58–0.81). The exploitation rate for fully selected ages was 0.08 (0.05–0.11) in 1998, increased to 0.49 (0.40–0.58) in 2012 when positive population growth ceased, and continued to increase to 0.63 in 2017 (0.51–0.70) and 2018 (0.50–0.74). Suppression gillnetting was the largest source of fishing mortality on lake trout (Fig. 6*b*). The assessment gillnet *F* ranged from 0.0015 to 0.0020. Suppression trapnetting *F* varied from 0.04 (0.03–0.055) in 2010 to 0.12 (0.09–0.17) in 2013. Lake trout were estimated to be fully selected to the suppression gillnet fishery at age-4, the suppression trapnet fishery at age-7, and the assessment gillnet fishery at age-8 (Fig. 6*c*).

Stock–recruitment estimation and uncertainty

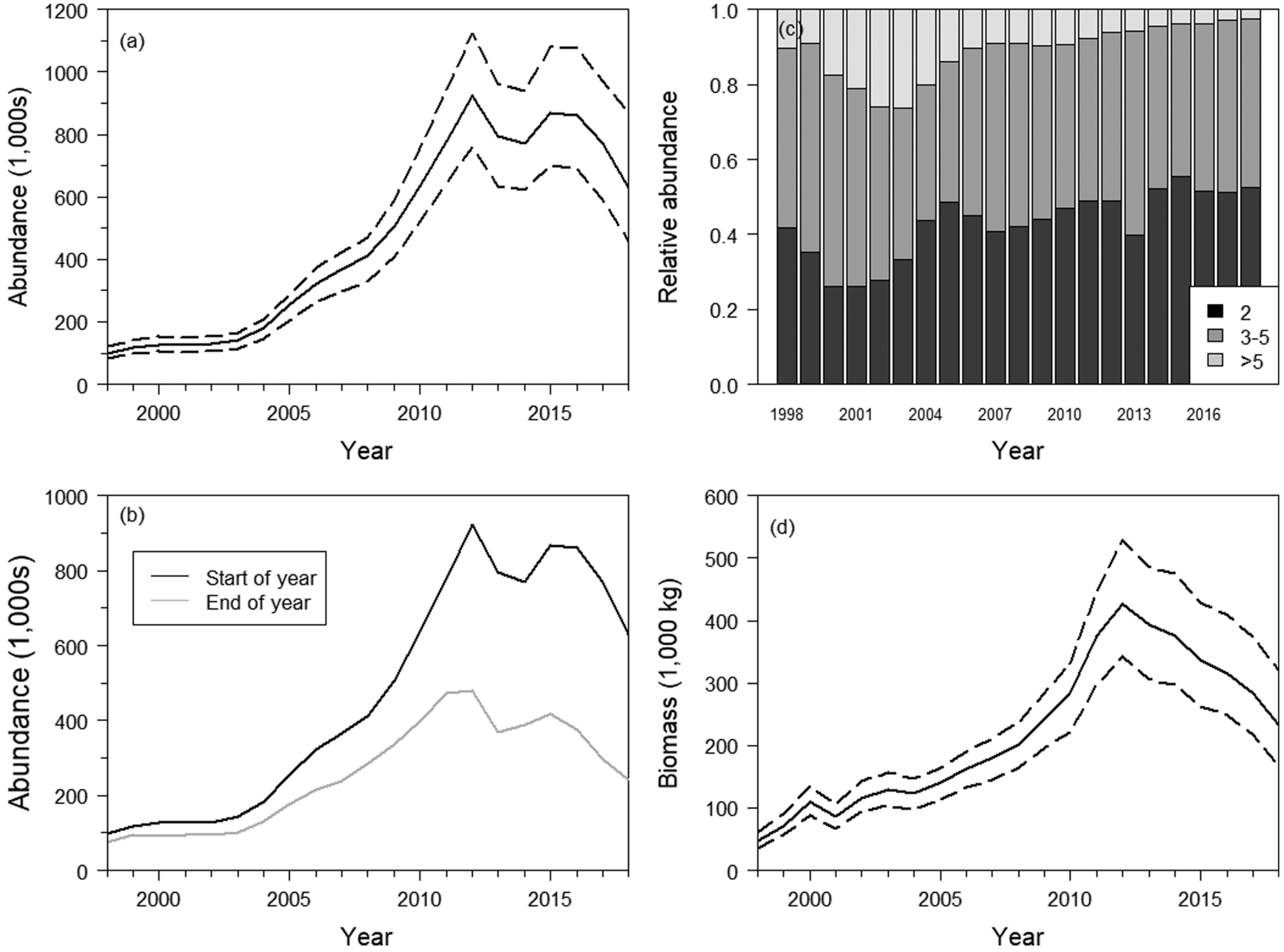
Estimated population fecundity increased from 6.3 million eggs (95% CI: 3.4–9.9 million) in 1998 to a high of 49.7 million (35.9–63.0 million) in 2010 and decreased to 21.5 million (14.4–34.3 million) in 2016. Estimated population fecundity declined to 14.3 million (9.3–24.4 million) in 2017 and 9.6 million (5.3–18.5 million) in 2018; however, fecundity values for 2017 and 2018 were not used to fit the stock–recruitment relationship given the 2-year time lag to predict recruitment. Substantial variation existed in the estimation of the stock–recruitment relationship (Fig. 7). Based on the fitted stock–recruitment relationship ($\alpha = 0.009$, $\beta = 2.14\text{e}{-09}$, $\sigma = 0.71$), the lake trout population has been on the ascending limb of the stock–recruitment curve for the 1998 to 2016 year classes. Prerecruit survival varied from 0.0076 (0.004–0.012) to 0.012 (0.006–0.023) (Fig. 7). The survival rates estimated for Yellowstone Lake were about four to six times greater than the best available estimates of survival from egg to age-2 from the native range (0.0019).

Forecasting model

The minimum level of annual gillnet effort at which median abundance declined over a 20-year period was between 35 000 and 40 000 units. The minimum level of effort causing the upper 90% confidence limit to decline over a 20-year period was between 45 000 and 50 000 units (Fig. 8). At 75 000 units of effort, median abundance declined by 84% after 5 years and 95% after 10 years. At 100 000 units of effort, median abundance declined by 93% after 5 years and 99% after 10 years. Patterns in median biomass at a given level of fishing effort were generally similar to abundance; however, the 90% confidence intervals were slightly narrower.

The probability of reducing abundance below the 2018 estimate of 628 203 fish within 10 years exceeded 90% when annual fishing effort exceeded 45 000 units of effort (Fig. 9). Annual fishing effort

Fig. 4. Estimated abundance at the beginning of the year (*a*), comparison of abundance between the beginning and end of year (*b*), estimated relative abundance by age category (*c*), and estimated biomass (*d*) from a statistical catch-at-age model for lake trout in Yellowstone Lake from 1998 to 2018. Dashed lines delineate 95% credible intervals.



of 45 000 – 50 000 units was required to cause at least a 90% probability of reducing biomass below the 2018 estimate. A 90% probability of achieving a 50% reduction in abundance and biomass relative to 2018 estimates within 10 years required between 55 000 and 60 000 units of effort, and 65 000 units of effort were required to achieve a 50% reduction in 5 years. For a 90% probability of reducing abundance below 100 000 fish, 70 000 – 75 000 units of effort were required over 10 years, and this increased to 95 000 – 100 000 units for the 5-year time frame. For a 90% probability of reducing biomass below the level equivalent to 100 000 fish within 10 years, 75 000 – 80 000 units were required. This increased to 95 000 – 100 000 units for a 5-year time frame. Once abundance was reduced to 100 000 fish, a sustained gillnet suppression effort of 50 000 – 55 000 units of effort was necessary for a greater than 90% chance of maintaining abundance at less than the target level (Fig. 10).

Discussion

High prerecruit survival for lake trout in Yellowstone Lake appears to increase the resistance of the lake trout population to suppression efforts to reduce abundance. The level of total annual fishing mortality (A) that halted the population increase in 2012 ($A = 0.60$) was 67% greater than predicted by an initial simulation study ($A = 0.36$ to 0.39) that relied on available age-0 and age-1 survival rates from the native range of lake trout (Syslo et al. 2011). Accordingly, the minimum level of fishing effort required to reduce population growth to replacement was much greater than the 29 000 suggested by the mean estimates of population growth rate from a stochastic forecasting model and catchability from an SCAA model in the 2011 study (Syslo et al. 2011). The amount of effort that ultimately halted population growth in 2012 (48 220 units) was similar to the conservative recommendation of 50 315 units from the 2011 study, which was calculated using the upper 95% confidence limit for population growth rate and lower 95% confidence limit for catchability but still ignored the potential for vital rates to differ from populations in the native range (Syslo et al. 2011). Fortunately, fishing effort was increased in excess of previously published recommendations to elicit a decline in the abundance of non-native lake trout.

The high rate of prerecruit survival for non-native lake trout in Yellowstone Lake may be an example of ecological release, wherein lake trout are no longer constrained by factors that are limiting throughout the native range. Yellowstone Lake contains a simple fish assemblage and lake trout likely face limited predation and competition. Interstitial egg predators such as sculpin (*Cottus* spp.) and crayfish (*Orconectes* spp.) are an important source of mortality for juvenile lake trout in the native range (Fitzsimons et al. 2002; Claramunt et al. 2005). Yellowstone Lake does not contain species that are known interstitial egg predators and likely does not contain any fishes that prey on fry or older lake

Fig. 5. Estimated total yield ($\text{kg}\cdot\text{ha}^{-1}$; black line) and yield of age-6 and older (gray line) from a statistical catch-at-age model for lake trout in Yellowstone Lake from 1998 to 2018. Dashed lines delineate 95% credible intervals.

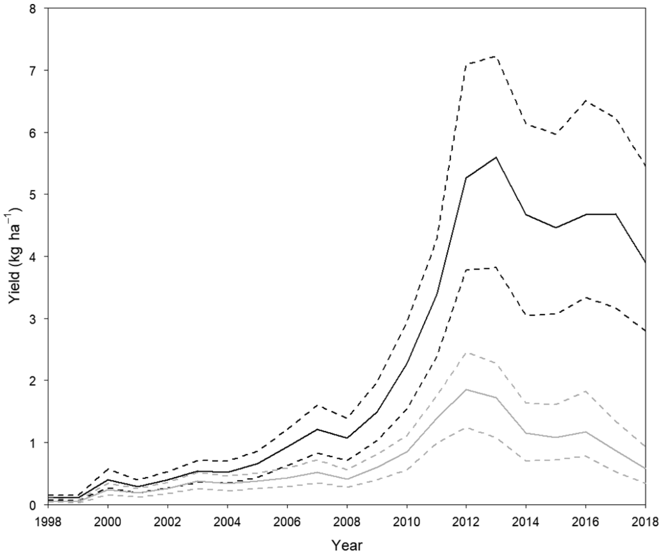


Fig. 6. Estimated total instantaneous fishing mortality (*F*) from all netting types (*a*), *F* by netting type (*b*), and age-specific selectivity by netting type (*c*) from a statistical catch-at-age model for lake trout in Yellowstone Lake from 1998 to 2018.

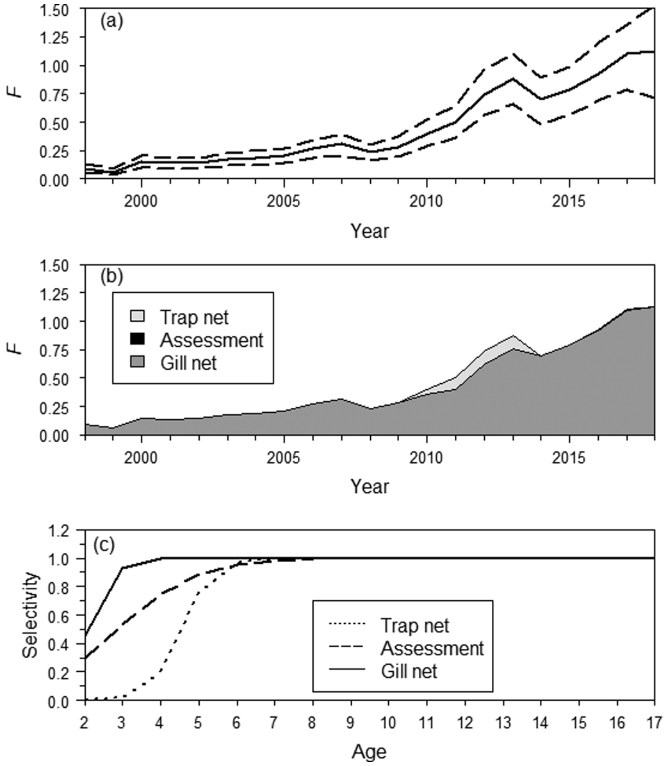
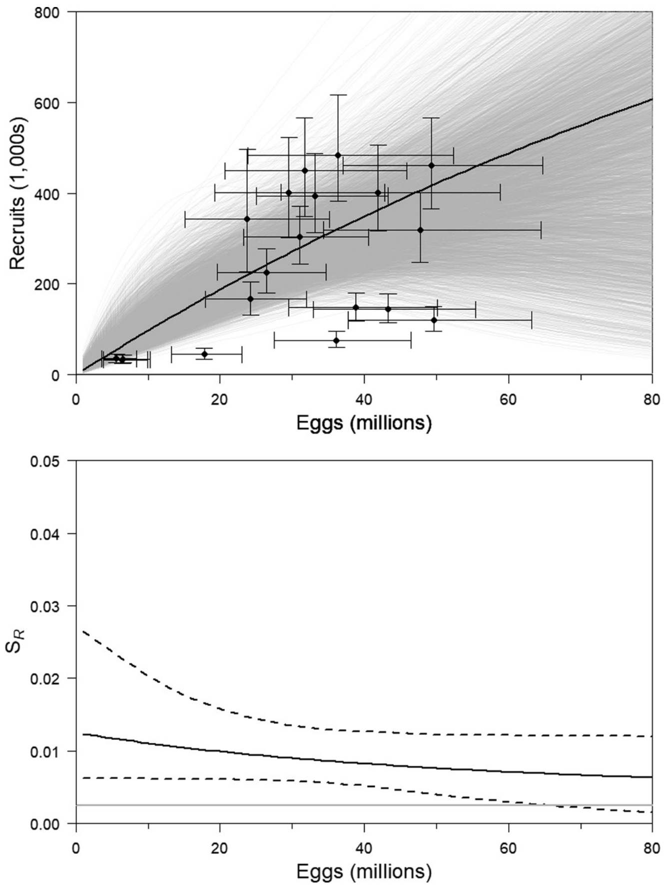


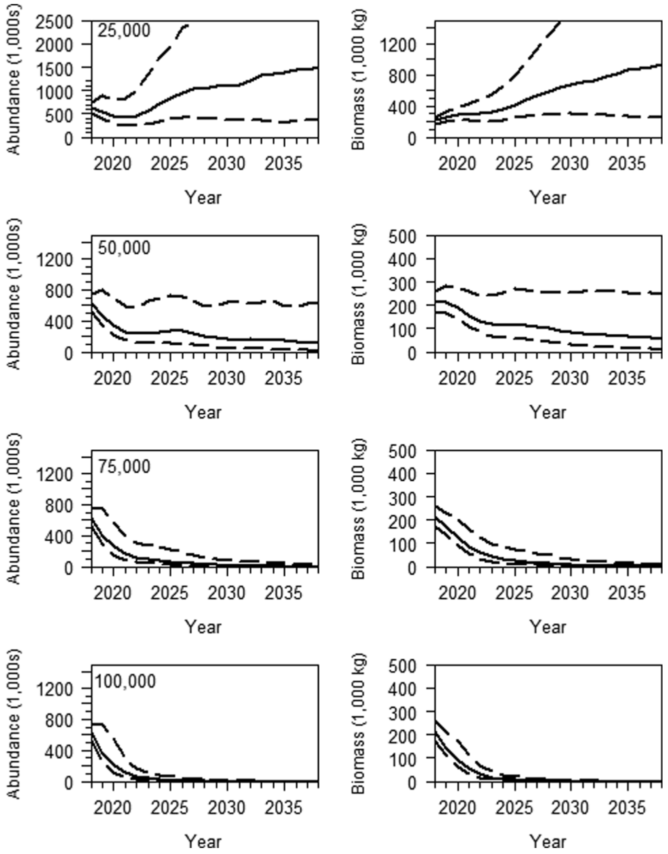
Fig. 7. Estimates of spawning stock biomass (number of eggs) and corresponding recruitment of age-2 lake trout with 95% credible intervals (bars) and 5000 random stock–recruitment relationships (gray lines; top panel) for Yellowstone Lake. The solid line in the top panel delineates the mean from 5000 posterior samples. Stock–recruitment relationship converted prerecruit survival (S_R) as a function of egg abundance (dashed lines delineate 95% credible intervals; bottom panel). Horizontal reference line indicates comparable estimate of S_R from the native range of lake trout.



trout life stages. Yellowstone cutthroat trout have been documented preying on cyprinids when Yellowstone cutthroat trout abundance was high (Jones et al. 1990; Benson 1961); however, a recent diet study did not find fish prey in Yellowstone cutthroat trout stomachs (Syslo et al. 2016). A recent study comparing feeding habits and growth of lake trout fry at a spawning location in Yellowstone Lake with those from a spawning location in Lake Champlain found that fry remained at the spawning location longer, fed at greater rates, and exhibited faster growth in Yellowstone Lake (Simard et al. 2020). The ability for fry to remain at the spawning site longer in Yellowstone Lake was hypothesized to be due to lack of potential predators and adequate availability of zooplankton (Simard et al. 2020). Lake trout are the only apex piscivore in Yellowstone Lake and face limited competition for prey. Stable isotope analysis indicates prey consumed by lake trout are from more profundal sources relative to Yellowstone cutthroat trout (Syslo et al. 2016), indicating that interspecific competition is not likely a limiting factor for the lake trout population.

Abiotic conditions in Yellowstone Lake may also be favorable for lake trout reproduction. Lake trout spawning in Yellowstone Lake occurs 1–2 months earlier in the year compared with some populations in the native range (Eschmeyer 1995; Simard et al. 2020). Earlier spawning in Yellowstone Lake is likely a function of fall turnover occurring earlier in the year and could confer benefits if earlier hatching is related to increased age-0 survival. Additionally, Yellowstone Lake is in a protected pristine watershed that has not been affected by pollution stressors hypothesized to reduce embryo survival in several populations in the native range of lake trout, such as eutrophication and associated sedimentation (Dorr et al. 1981; Sly and Widmer 1984). Thus, both biotic and

Fig. 8. Abundance (left) and corresponding biomass (right) trajectories for selected suppression gillnetting effort scenarios (number of 100 m net nights indicated in upper left) from demographic matrix model for lake trout in Yellowstone Lake. Dashed lines delineate 90% credible intervals.



abiotic characteristics may be responsible for increased prerecruit survival of lake trout in Yellowstone Lake.

The comparison of prerecruit survival between lake trout in Yellowstone Lake and populations in the native range was limited by the number of available studies in the literature. The estimate of survival for age-0 lake trout ($S_0 = 0.0043$; Shuter et al. 1998) was based on the average from four lakes throughout the native range that were all within the range of 0.0035 to 0.055 (Walters et al. 1980; Matuszek et al. 1990; Ferreri et al. 1995). However, the value we used for age-1 survival ($S_1 = 0.45$) in the native range was based on a single estimate from a SCAA model for lake trout in Lake Huron (Sitar et al. 1999). Prerecruit survival in Yellowstone Lake was a function of both S_0 and S_1, which are multiplicative. Thus, the conclusion that prerecruit survival is higher in Yellowstone Lake relative to native populations appears to be robust despite the small literature sample size for S_1 because the product of S_0 and S_1 can only be smaller than S_0, and our estimates of prerecruit survival were still two to three times greater than $S_0 = 0.0043$. We also estimated steepness (z) from the stock–recruitment relationship for lake trout in Yellowstone Lake following Myers et al. (1999) to compare with the results of their meta-analysis describing the maximum reproductive rates of fishes. The steepness estimate for Yellowstone Lake ($z = 0.93$) was greater than reported for lake trout in the meta-analysis ($z = 0.86$); however, the value in Myers et al. (1999) was based on a single lake trout population, and variability could not be estimated. The corresponding estimate of maximum annual reproductive rate at low population size ($\tilde{\alpha}$) for lake trout in Yellowstone Lake was 43, 79% greater than the value from the meta-analysis ($\tilde{\alpha} = 24$; Myers et al. 1999). Taken together, these comparisons indicate lake trout prerecruit survival in Yellowstone Lake is consistently higher than available estimates from the literature.

An alternative hypothesis for the apparent resilience of lake trout in Yellowstone Lake to harvest is that the assessment model underestimated the abundance of large, older lake trout. Underestimating the spawning stock biomass that produced a given recruitment would cause prerecruit survival to be overestimated. Modeling selectivity as a dome-shaped function of age decreases the mortality rate on older lake trout and increases the estimate of the abundance of older individuals and, thus, spawning stock biomass. Models that included dome-shaped selectivity for the suppression gillnet fishery in Yellowstone Lake provided a poorer fit to the data than models with logistic selectivity. Given the implementation of relatively high levels of fishing mortality as the lake trout population was expanding, the probability of many lake trout surviving to attain sizes at which they are no longer vulnerable to the gillnet suppression fishery appears to be low in Yellowstone Lake.

Our results suggest that studies evaluating the yield potential of lake trout populations throughout the native range are an inappropriate guide for lake trout suppression in Yellowstone Lake. Lake trout populations throughout the native range have declined when long-term yield exceeded the range of 0.5–1.0 kg·ha^{-1}·year^{-1} (Healey 1978; Martin and Olver 1980). More recent analyses evaluating lake trout yield (kg·ha^{-1}·year^{-1}) as a function of lake surface area and productivity (Marshall 1996; Shuter et al. 1998) indicate that sustainable lake trout yield in Yellowstone Lake, is likely on the order of 0.5 to 1.2 kg·ha^{-1}·year^{-1}. An exact calculation of yield using both productivity and area (Shuter et al. 1998) was not possible for Yellowstone Lake; however, sustained yield of lake trout in Yellowstone Lake was predicted to be 0.61 kg·ha^{-1}·year^{-1} based on a model predicting yield from lake surface area for populations throughout the native range (Marshall 1996). Estimated total yield of lake trout from Yellowstone Lake increased to 5.2 kg·ha^{-1}·year^{-1} in 2012 before the population began to decline. Recreational and commercial fisheries throughout the native range likely did not target lake trout as young as age-2. Therefore, we also estimated yield of adult (i.e., age-6 and older) lake trout (1.8 kg·ha^{-1}·year^{-1}), which still greatly exceeded predictions for yield based on native populations in lakes with similar surface area to Yellowstone Lake. We suspect abundance in Yellowstone Lake might not have declined without the harvest of ages 2–5 lake trout and the resulting reduction in the number of individuals surviving to maturity, as simulation studies have found the harvest of both subadult and adult stages to be advantageous for the suppression of non-native lake trout in other ecosystems (Syslo et al. 2013; Hansen et al. 2019).

The outcome of lake trout suppression programs in other ecosystems should aid in determining whether other non-native lake trout populations exhibit increased resistance to harvest or the Yellowstone Lake population is a demographic outlier. Several studies in the last decade have modeled the potential for success in suppressing non-native lake trout populations in the western USA (Hansen et al. 2010; Syslo et al. 2011; Cox et al. 2013; Ng et al. 2016; Fredenberg et al. 2017). Most studies borrowed estimates of lake trout stock–recruitment parameters or early life history survival rates from populations in the native range. For example, a simulation study evaluating the potential for a suppression program to reduce lake trout abundance in Lake Pend Oreille, Idaho, USA, used Ricker stock–recruitment parameters for lake trout in western Lake Superior while scaling the density-dependent parameter β based on habitat area (Hansen et al. 2010). The Lake Pend Oreille simulation study predicted that lake trout suppression would cause a 67% reduction in abundance within the first 10 years of the program. In contrast with the 2011 Yellowstone Lake study, the Lake Pend Oreille simulation results were validated when the observed decline in lake trout abundance closely

Fig. 9. Probability of reducing lake trout abundance (left) and biomass (right) below the 2018 estimates (top panels), 50% of the 2018 estimates (center panels), and below 100 000 fish (corresponding to an 84% reduction in biomass relative to 2018; bottom panels) for selected gillnetting effort scenarios in Yellowstone Lake. The legend delineates the amount of effort (1 unit = 100 m of net set for 1 night) per year.

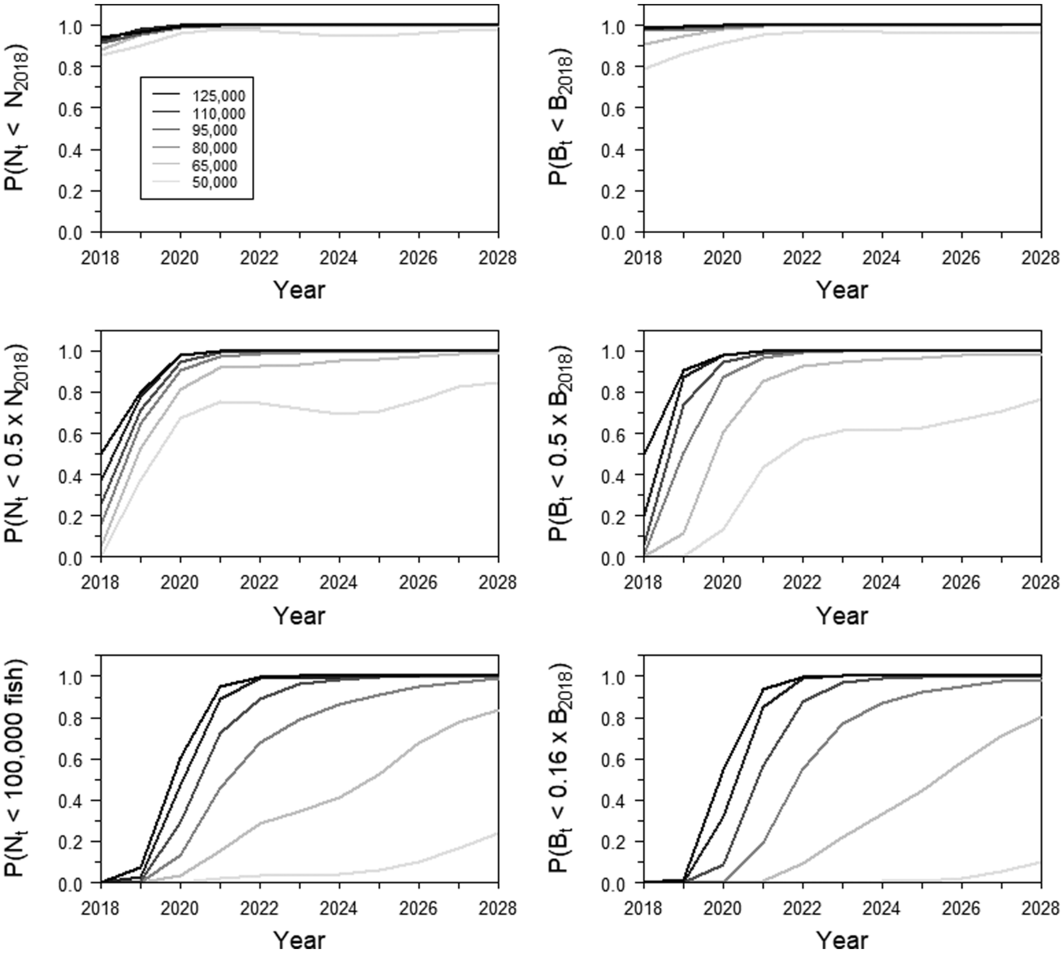
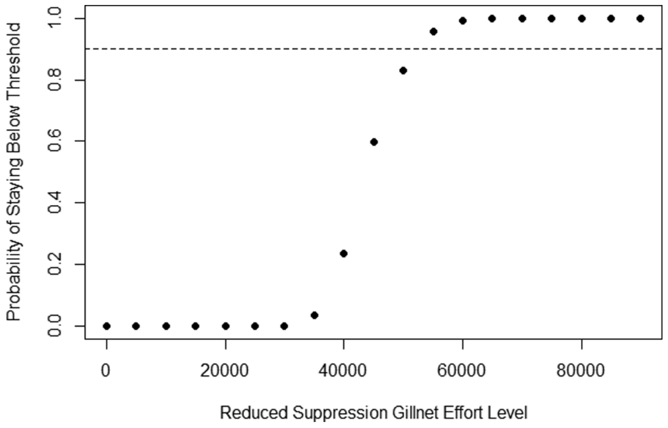


Fig. 10. Probability of maintaining lake trout abundance in Yellowstone Lake below 100 000 fish for annual levels of gillnet suppression effort (1 unit = 100 m of net set for 1 night) varying from 0 to 95 000 units. Horizontal reference line delineates a 90% probability.



matched the predicted results from the simulation study (Dux et al. 2019). The rate of total annual mortality that caused lake trout abundance to decline in Lake Pend Oreille averaged 0.31 (Dux et al. 2019), which was about half the total annual mortality rate required to reduce abundance in Yellowstone Lake. Lake Pend Oreille is a deep oligotrophic lake with limited littoral habitat and contains a more complex fish assemblage (i.e., 23 species) than Yellowstone Lake (Dux et al. 2019). Thus, it is likely that the biotic and abiotic features of Lake Pend Oreille likely resemble lakes in the native range of lake trout and that prerecruit survival rates for non-native populations are dependent on characteristics of the receiving water body.

Simulations indicated lake trout abundance will continue to decline in Yellowstone Lake at the levels of fishing effort exerted in recent years. Once abundance is reduced to the target level determined by the US National Park Service, effort can be reduced to maintain constant abundance assuming the gillnet program continues to implement the same fishing techniques as in 1998 to 2018. The minimum level of effort to keep abundance constant represents a substantial reduction relative to the level of fishing effort exerted in 2017 and 2018; however, it will continue to consume a large amount of resources through the foreseeable future.

Numerous experimental approaches for lake trout suppression have been explored to supplement gillnet removal programs by inflicting mortality on developing embryos at lake trout spawning sites in Yellowstone Lake and in other invaded ecosystems in the western USA. Approaches include seismic air guns (Cox et al. 2012), electrofishing (Brown et al. 2017), chemical and sediment application (Poole 2019), and suffocation (Thomas et al. 2019; Koel et al. 2020). The aforementioned experimental approaches have produced mixed results with respect to the resulting level of mortality and the prospect for implementation at operational scales.

Deposition of lake trout carcasses or organic pellets at spawning sites and the ensuing decomposition and hypoxia is effective at inflicting high rates of mortality on embryonic lake trout in Yellowstone Lake (Thomas et al. 2019; Koel et al. 2020). However, treating all confirmed lake trout spawning habitat in Yellowstone Lake would require large amounts of carcasses or pellets and may be limited to shallow spawning sites (Thomas et al. 2019; Koel et al. 2020). Gillnetting will remain the principal suppression method for lake trout in Yellowstone Lake; however, the level of effort to keep abundance constant may be lowered if effective embryo suppression alternatives are implemented to reduce prerecruit survival of lake trout in Yellowstone Lake.

Yellowstone cutthroat trout appear to be responding to suppression efforts for lake trout in Yellowstone Lake. Juvenile Yellowstone cutthroat trout are being detected in assessment netting after being absent for several years, and spawning adults have returned to some tributary streams (Koel et al. 2019). Total lake trout abundance remains higher than in the late 1990s when indices of Yellowstone cutthroat abundance were exhibiting the steepest decline (Koel et al. 2019). However, the estimated abundance of lake trout in age classes 10 and older began to decline in 2007 and was 86% lower in 2018 compared with 1998. The reduced abundance of old, large lake trout is substantial given the increase in predation that occurs with age (Ruzycki et al 2003; Syslo et al. 2016) and likely reduced predation mortality on Yellowstone cutthroat trout. Continued lake trout suppression will likely foster this nascent recovery in Yellowstone cutthroat trout abundance.

As the longest ongoing lake trout suppression project, Yellowstone Lake provided a unique opportunity to evaluate stock–recruitment dynamics for a non-native fish population and assess the implications for a large-scale suppression effort in a large water body. The high rates of juvenile survival estimated for lake trout in Yellowstone Lake, combined with the comparatively high yield and mortality rates required to decrease abundance, support the hypothesis that ecological release buffered the population from suppression efforts. Lake trout suppression in Yellowstone Lake illustrates difficulties associated with predicting demographic rates for non-native species and demonstrates that a cautious approach should be applied when modeling population dynamics for species outside of their native range.

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Appendix A. Description of fishery operation and data collection

Suppression gillnet program

The suppression gillnet program to remove lake trout from Yellowstone Lake was initiated in 1995 with limited gillnet effort intended mostly to assess population characteristics. In 1998, gillnet effort was increased for the purpose of maximizing lake trout harvest. Suppression gillnetting is conducted annually from late May to late October and consists of sinking gill nets composed of 25, 32, 38, 44, 51, 57, 64, 70, and 76 mm bar-measure mesh panels. Generally, gill nets were set at depths greater than 20 m to avoid Yellowstone cutthroat trout bycatch, except during peak lake trout spawning periods when nets were set in areas shallower than 20 m. Gillnet soak time varied from 1 to 7 nights. From 1998 to 2018, annual suppression gillnet effort increased from ~1450 one hundred metre net nights to 97 400 one hundred metre net nights.

Over the duration of the suppression gillnet program, the configuration of gill nets shifted with respect to the size of the mesh panels. At the beginning of the program, average bar-measure mesh size of suppression gill nets was as high as 44 and 46 mm, but in the early 2000s was reduced to as low as 32 mm. Over time, the average bar-measure mesh size increased and was 41 mm in 2018. We attempted to account for this change in average mesh size by including integrated assessment models that allowed for time-varying selectivities for the gillnet suppression program.

Total lengths of lake trout harvested in the suppression gillnet program were measured to the nearest millimetre. Lengths for fish were converted to ages for calculating suppression gillnet harvest age composition using year-specific age–length keys (Isely and Grabowski 2007). Age–length keys were constructed from sagittal otoliths taken from subsamples from both the suppression and assessment gillnet programs. See Syslo et al. (2011) for a description of the lake trout age-estimation procedures.

Suppression trapnet program

From 2010 to 2013, the lake trout suppression program included a trapnet component that targeted lake trout longer than 450 mm total length (TL). When the program was active, eight to ten trap nets were deployed at fixed locations located in Yellowstone Lake. Trapnet leads were 180 to 305 m long and 9 to 15 m deep with a 6 m × 6 m × 12 m pot (Koel et al. 2012). Trapnet soak times varied from 1 to 4 nights. Annual suppression trapnet effort ranged from 270 net nights in 2010 to 880 net nights in 2013. Total lengths of each lake trout harvested in suppression trap nets were measured to the nearest millimetre. Lengths for fish were converted to ages for calculating suppression trapnet harvest age composition using the same year-specific age–length keys that were used to convert lengths to ages for suppression gillnetting.

Standardized assessment gillnet program

The standard assessment gillnet program has occurred annually since 2011. Twelve fixed sites and twelve random sites were sampled annually in early August with six experimental gill nets (two gillnet configurations fished at each of three depth strata) deployed at each site. The three depth strata that are sampled are epilimnion (3 to 10 m in depth), metalimnion (10 to 30 m in depth), and hypolimnion (>40 m). The two gillnet configurations are a small-mesh gill net that is 2 m deep and 76 m long and consists of 13.7 m panels of 19, 25, 32, 38, 44, and 51 mm bar-measure mesh and a large-mesh gill net that is 3.3 m deep and 68.6 m long and consists of 13.7 m panels of 57, 64, 70, 76, and 89 mm bar-measure. Gill nets are set perpendicular to shore with the small-mesh and large-mesh nets set parallel about 100 m apart. All lake trout caught in assessment gillnets were measured for TL. Total lengths of fish were converted to ages using the same year-specific age–length keys that were used to convert lengths to ages for the suppression gillnet and trapnet programs.

Life history variables

Growth in length, weight, and maturity of lake trout in Yellowstone Lake did not change as abundance increased, suggesting that the lake trout population had not reached the lake's carrying capacity (Syslo 2015). Consequently, life history variables were considered to not vary over time either for the assessment model or for the forecasting prediction. Mean length-at-age was calculated from aged samples of lake trout and converted to weight-at-age using coefficients from a $\log_{10}$-transformed length–weight regression ($\beta_0 = -5.20$; $\beta_1 = 3.07$; $r^2 = 0.98$; $p < 0.001$; df = 11 965) for samples collected from 1998 through 2013 (Syslo 2015). Maturity-at-age was calculated using coefficients from a logistic regression model to predict female probability of maturity at length ($\beta_0 = -13.71$; $\beta_1 = 0.025$; $p < 0.001$; df = 971) for samples from 1998 through 2013 (Syslo 2015). Probabilities of maturity-at-age were determined using the mean length-at-age and the mean predicted probability of maturity at that length. Female lake trout were 50% mature at 541 mm and 6.7 years. The number of eggs produced per kilogram body weight was calculated using coefficients from a weight–fecundity regression model ($\beta_0 = 245.8$; $\beta_1 = 1\,458.9$; $r^2 = 0.74$; $p < 0.001$; df = 194) for samples in 2006 and 2007 (Syslo et al. 2011). The number of eggs produced per kilogram body weight was multiplied by mean weight-at-age, probability of maturity-at-age, sex ratio (assumed to be 0.5), and age-specific abundance in the calculation of spawning stock biomass (eq. 20).

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