Demography of Adfluvial Bull Trout in Lake Pend Oreille, Idaho
Project Completion Report

Clark Fork Settlement Agreement Dissolved Gas Supersaturation Control, Mitigation, and Monitoring Program

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ABSTRACT

Lake Pend Oreille, Idaho, historically supported a prominent Bull Trout *Salvelinus confluentus* fishery prior to the listing of Bull Trout as threatened under the Endangered Species Act. Although Bull Trout population declines were documented in parts of the western United States in the late 20th century, Lake Pend Oreille remains a stronghold for adfluvial Bull Trout. Nonnative Lake Trout *S. namaycush* are the primary threat to Bull Trout in Lake Pend Oreille and have been actively removed from the system since 2006. A Bayesian integrated population model was used to estimate lifestage-specific demographic parameters, predict population responses to potential management actions, and generally assess the population status of Bull Trout in Lake Pend Oreille following over a decade of Lake Trout suppression. Mean estimated apparent survival from 2010 through 2018 was 0.39 (0.32–0.46, 95% credible interval [CI]) for the adult stage, 0.59 (0.51–0.66, 95% CI) for the subadult stage, and 0.18 (0.13–0.24, 95% CI) for the juvenile stage. Estimated annual population growth rates were oscillating but stable over the assessed timeframe (i.e., 1983–2018), with a geometric mean population growth rate (λ) of 1.01. Projected intrinsic growth rates (r) for modeled management scenarios remained positive (i.e., 0.16) under a 5% increase in exploitation, but were negative (i.e., -0.08) under a 15% increase in exploitation. Reducing incidental gill netting mortality by 50% led to a minor change in r (i.e., $\Delta = 0.14$). Modeling results indicate the Lake Pend Oreille Bull Trout population remains robust and stable. In addition, model predictions suggest Lake Trout netting operations are not leading to a substantial decrease in Bull Trout abundance and this population could support additional harvest mortality. Therefore, the Lake Pend Oreille Bull Trout population may be biologically capable to support a limited harvest fishery under current conditions.

INTRODUCTION

Bull Trout *Salvelinus confluentus* are native to northwestern North America and are often a focus of conservation efforts due to their stenothermic habitat requirements (Rieman and McIntyre 1993) and population declines from historical abundances (Rieman and McIntyre 1996). Population declines of Bull Trout have been primarily associated with habitat loss and fragmentation, fish passage barriers, and negative interactions with introduced species (USFWS 2008). Further, climate change may pose an additional threat to some populations of Bull Trout (Rieman et al. 2007; Wenger et al. 2013; Kovach et al. 2017) due to their distinctly low upper thermal tolerance (Selong et al. 2001). Declines in abundance and distribution led to the 1999 listing of Bull Trout as threatened in the conterminous United States under the Endangered Species Act (ESA; USFWS 1999). While Bull Trout remain a focal species for fisheries management, their distribution has remained relatively constant since the ESA listing and the species is currently considered stable range-wide (USFWS 2015a).

The lower Clark Fork-Pend Oreille Basin of Idaho and Montana supports a lake migratory (adfluvial) population of Bull Trout that utilize Lake Pend Oreille (LPO) and surrounding tributaries throughout their lifecycle. Despite hydroelectric dams on the lower Clark Fork and the Pend Oreille rivers resulting in considerable habitat fragmentation of the migratory corridor in this region, the LPO basin remains a stronghold for adfluvial Bull Trout. The ability of LPO to support a robust Bull Trout population is due to the abundance of high-quality habitat present in the system coupled with the availability of ample food resources in the lake (USFWS 2015b). Lake Pend Oreille is an oligotrophic lake where hypolimnetic temperatures average around 9°C during stratification (Rieman 1977), thus serving as a cold-water refuge for this adfluvial population.

Historically, LPO supported a world-renowned Bull Trout fishery. In 1949, the LPO Bull Trout population produced the world record fish (14.5 kg). This, in part, can likely be attributed to an abundant kokanee *Oncorhynchus nerka* population at the time. The LPO kokanee population historically provided the largest kokanee fishery in the state of Idaho and serves as a rich forage base for Bull Trout and other predators in the lake. However, kokanee abundances have substantially declined from historical levels, partially attributable to over-predation by introduced Lake Trout *S. namaycush*. In the early 2000s, the LPO kokanee population was predicted to completely collapse within a decade unless a substantial increase in production or decrease in predation occurred (Hansen et al. 2010). The potential collapse of kokanee not only threatened an important fishery in itself, but also served as a significant threat to the Bull Trout population and other predators that rely on kokanee as their primary food resource.

A predator suppression program was implemented in 2006 in LPO to recover fisheries and benefit Bull Trout (Hansen et al. 2010; Dux et al. 2019). Initially, suppression activities targeted both Rainbow Trout *O. mykiss* and Lake Trout, but eventually focused on reducing Lake Trout abundance. This predator suppression program (partially funded by the Clark Fork Settlement Agreement) utilizes incentivized angler harvest and annual targeted netting efforts to selectively capture and remove Lake Trout from the system. Since its implementation, the abundance of age-8+ Lake Trout has declined by 64% and the kokanee population has rebounded (Dux et al. 2019). However, the current population status of LPO Bull Trout, and the impact of the predator suppression program on this population are not fully understood.

Lakewide abundance estimates of the LPO Bull Trout population were conducted in 1998 (Vidergar 2000) and 2008 (McCubbins 2016). These estimates suggested the population remained stable over this decade. However, these estimates occurred prior to or during the initial years of suppression netting. While Lake Trout suppression has been conducted as a Bull Trout conservation measure, netting efforts lead to incidental catch (annual average of 1,555) and mortality (28% of catch) of Bull Trout. Nonetheless, it is expected the Bull Trout population may have collapsed without netting intervention based on observations in other regional systems (Kovach et al. 2017). Redd counts declined from 2006 to 2016 during suppression but remained within the range of counts observed prior to netting (Dux et al. 2019). An estimate of current abundance is needed to assess the status of LPO Bull Trout following over a decade of predator suppression netting.

Redd counts, combined with live capture events of Bull Trout during Lake Trout suppression netting efforts and other Bull Trout monitoring activities provide a large sample of encounters that can be used to evaluate demographic rate parameters in this population. These count and demographic data can be incorporated in an integrated population model (IPM; Besbeas et al. 2002) to obtain a comprehensive assessment of Bull Trout population demographics in the system. Integrated population models provide more precise parameter estimates than traditional models that evaluate datasets independently, while appropriately accounting for uncertainty in the data and enabling the estimation of additional parameters that could not be estimated through independent analyses (Schaub and Abadi 2011). Furthermore, IPMs can be used to analyze historical data and conduct population projections under the same model, thus providing a powerful tool for population management (Arnold et al. 2018).

Here, an IPM is employed to concurrently analyze several multi-year datasets for the LPO Bull Trout population. This model is applied to estimate current and past demographic parameters, as well as to predict future demographic parameters under various management scenarios. Furthermore, as LPO presents an opportunity to provide a world class Bull Trout fishery, the IPM was used to assess the biological capability of this population to support various levels of angler harvest. The specific objectives of this study are to:

1) Estimate the survival, abundance and population growth of LPO Bull Trout through time;
2) Evaluate the effects of netting bycatch on the LPO Bull Trout population; and
3) Develop an IPM that can be used for future Bull Trout monitoring. Full development of this IPM will include the identification and rectification of any current data gaps.

METHODS

Count Data

Starting in 1983, Bull Trout redds have been located and enumerated annually in October in standardized spawning tributaries of LPO (Figure 1; see Jakubowski and Bouwens 2019 for detailed methods). Redds were defined as areas of clean gravels at least 0.3 x 0.6 m in size with gravels at least 76 mm in diameter having been moved by the fish and with a mound of loose gravel downstream from a depression (Pratt 1984). Redds were visually identified by trained individuals walking standardized tributary transects. Only redd count data from tributaries where fish are known to display adfluvial life history strategy were used in the IPM. This restricted data utilization to redd counts from 20 tributaries downstream of Cabinet Gorge Dam where all Bull Trout individuals are considered migratory (Jakubowski and Bouwens 2019).

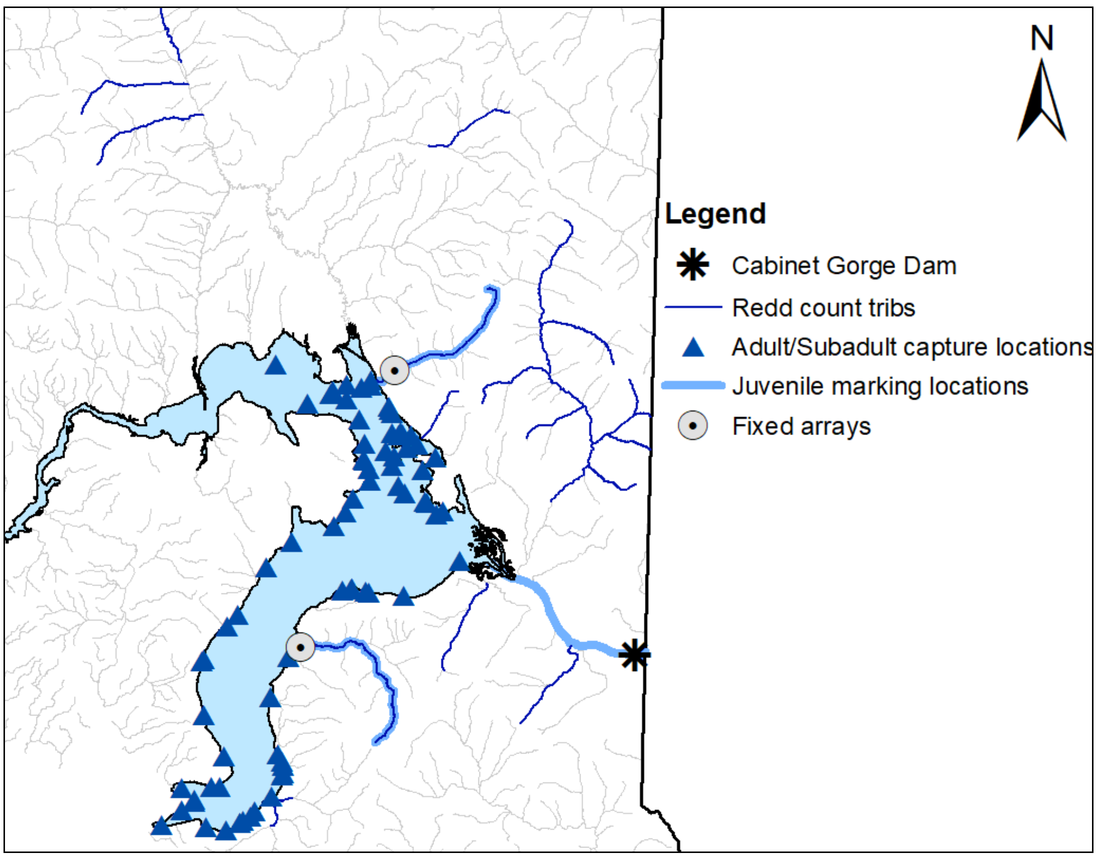

Figure 1. Collection locations of data used in the Integrated Population Model (IPM). Redd count data was collected from the dark tributaries. Active capture events of adult and subadult Bull Trout occurred approximately at indicated locations within the lake proper. Juveniles were captured, marked, and released within highlighted tributaries. Passive capture events occurred at fixed arrays located near the inflow of two documented spawning tributaries (Granite and Trestle creeks).

Mark-Recapture Data

Bull Trout are encountered as incidental bycatch during annual Lake Trout removal gill and trap netting operations (see Rust et al. 2020 for detailed methods). Upon capture, Bull Trout were interrogated for passive integrated transponder (PIT) tags and previously unmarked individuals received a 12 mm half-duplex (HDX) PIT tag prior to release if alive at time of capture. In addition, individual total length (mm) and capture information (e.g., capture location, mesh size, fish condition, etc.) was recorded during these encounters.

Juvenile Bull Trout were captured in Trestle and Granite creeks via electrofishing from late-June through mid-September in 2011, 2012, 2014, and 2015 (Figure 1; see Ryan and Jakubowski 2013 for detailed methods). Captured individuals were measured for total length and marked with 12 mm HDX PIT tags prior to release. In 2011, remote HDX PIT tag antenna arrays were installed near the mouths of Trestle and Granite creeks to passively detect PIT tagged individuals travelling over the arrays. These arrays allow for the detection of marked juveniles emigrating into LPO as well as marked adults returning to these tributaries during spawning migrations.

Bull Trout are captured annually in Montana tributaries of the lower Clark Fork River (LCFR) via traps and electrofishing. Since 2000, juvenile Bull Trout that measured between 100 mm and 299 mm were implanted with PIT tags and transported downstream of the Cabinet Gorge Dam into the Idaho portion of the LCFR (see Lacy et al. 2016 for detailed methods). Select adult Bull Trout that were captured emigrating from the East Fork Bull River or Graves Creek following spawning events were also transported and released downstream of Cabinet Gorge Dam (Bernall and Duffy 2018).

Annually since 2001, Bull Trout have also been captured downstream of the Cabinet Gorge Dam in the Idaho portion of the LCFR via traps, electrofishing, and hook-and-line sampling (see Bernall and Duffy 2016 and Bernall and Duffy 2018 for detailed methods). Captured Bull Trout were interrogated for PIT tags, measured for total length, implanted with a PIT tag if no prior tag was detected, and transported to a holding facility to await genetic assignments. Following genetic assignment, Bull Trout were transported to their stream of origin and released. Bull Trout that genetically assigned to a tributary downstream of Cabinet Gorge Dam were released into the Idaho section of the LCFR.

Model Development

Central to the analysis, a population process model (see Figure 2 for a representative directed acyclic graph) was developed to describe the mechanisms responsible for demographic changes in the LPO Bull Trout Population. This process model, a stage structured exponential growth projection matrix (Caswell 2001), estimated the annual abundances of each life stage as follows:

$$N_{\mathrm{juv},t+1} \sim \mathrm{Poisson}\left(\frac{N_{sp,t}}{2}\ \bar{x}_{eggs} S_{eggs:age1}\right)$$
$$N_{\mathrm{sub},t+1} \sim \mathrm{Poisson}\left(N_{\mathrm{juv},t} S_{\mathrm{juv},t} + N_{\mathrm{sub},t} S_{\mathrm{sub},t}(1-\Psi_{\mathrm{SA}}) - h_{sub,t}\right)$$
$$N_{adt,t+1} \sim \mathrm{Poisson}\left(N_{sub,t} S_{sub,t} \Psi_{SA} + N_{adt,t} S_{adt,t} - h_{adt,t} + dm_t\right)$$
$$N_{sp,t} \sim \mathrm{Poisson}(N_{adt,t} R_t)$$
$$dm_t = \bar{x}_{mort} n,$$

where:

t = time step (i.e., year)
N_{sp} = the total number of spawning adults
$\bar{x}_{\mathrm{eggs}}$ = the mean number of eggs per redd
$S_{\mathrm{eggs:age1}}$ = the mean annual survival of eggs through age one
N_{juv} = the number of juveniles
S_{juv} = the mean apparent survival for juveniles
N_{sub} = the number of subadults
S_{sub} = the mean apparent survival for juveniles
Ψ_{SA} = the annual probability that a subadult transitions into the adult life stage
h_{sub} = the number of subadults removed from the population via harvest
N_{adt} = the number of adults
S_{adt} = the mean apparent survival for adults
h_{adt} = the number of adults removed from the population via harvest
dm = the annual reduction in the number of direct gill netting mortalities
R = the probability that an adult successfully spawns
$\bar{x}_{mort}$ = the average annual number of direct gill netting mortalities in the system to date
n = a netting reduction factor (ranging from 0 to 1, with 1 indicating 100% reduction in direct gill netting mortalities).

The harvest parameters, $h_{\mathrm{sub},t}$ and $h_{\mathrm{adt},t}$, and the direct netting mortality reduction parameter, dm_t, were incorporated into this process model to allow for the evaluation of hypothetical future management scenarios. Population sizes were modeled as Poisson processes to account for demographic stochasticity.

Redd counts were linked to the latent abundance of spawning adults ($N_{sp,t}$) in an observation model as follows:

$$y_t \sim \mathrm{normal}\left(\frac{N_{sp,t}}{2}, \sigma_y^2\right)$$

$$\sigma_y \sim \text{uniform}(10, 20),$$

where y_t is the totaled number of redds in year t, τ_y is an estimate of the sampling precision, and σ_y is the standard deviation of the observation process. The annual count of redds was assumed to represent half the total number of spawning individuals in a given year, thus assuming a 50:50 sex ratio in the population. While the associated error around redd counts was unknown, the uniform prior for the standard deviation of the observation process was selected to be an informative parameter because the model failed to converge without this parameterization. However, model estimates of this parameter did not approach the upper or lower limit of the distribution, indicating that the selected uniform prior adequately described the error in the dataset.

An informative prior provided information on the number of eggs per redd in the population. This was modeled as:

$$\bar{x}_{eggs} \sim \text{normal}\left(\bar{x}, \frac{1}{\sigma^2}\right)$$

$$\bar{x} = 4{,}927$$
$$\sigma = 353,$$

where $\bar{x}$ is the mean and σ^2 is the variance of egg counts conducted by Brunson (1952) in the Clark Fork River.

To estimate the state-specific apparent survival of LPO adfluvial Bull Trout, PIT tag data was summarized in a multistate encounter history and was applied in a state-space formulation (see Gimenez et al. 2007; Royle 2008; Kéry and Schaub 2012) of an open population multistate capture-mark-recapture (CMR) model. The Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), a widely used open population CMR model, allows for the estimation of apparent survival (φ) and detection probability (p) from multiple live recapture events of individuals. Multistate models are an extension of the CJS model that allow for state-specific estimates of apparent survival (S), detection probability (p), and the transition probability (ψ) between defined states (see Lindberg 2012 for a review of CMR study designs).

Three states were defined for this model based on the life stages of marked Bull Trout (i.e., juvenile, subadult, and adult). Due to incomplete data and limited sample sizes in earlier years, only PIT tag data collected from 2010 through 2019 were utilized. Combined data provide information on individuals across various life stages ranging from 97 mm to 939 mm in length. Individual encounter histories were condensed to represent an annual time-step from July 1 in a given calendar year to June 30 the following year. Therefore, each individual received a single notation indicating its observed state during that annual time-step. If an individual Bull Trout had multiple capture events during a single time-step, capture information (e.g., total length, location of capture, etc.) was retained from the individual's last capture event in that time-step. The July through June time-step was selected because the lowest number of marking events occurred in the months of May and June, and July precedes the annual spawning timeframe for this population (i.e., August through October; Rieman and McIntyre 1996).

At each occasion in the encounter history, an encountered Bull Trout was assigned a life stage based on designated criteria and all marked individuals were coded as either a 'juvenile', 'subadult', 'adult', or 'not-detected'. Bull Trout were assigned to the juvenile life stage at a capture event if they were actively captured in a tributary and measured less than 299 mm in length. Bull Trout were assigned to the subadult life stage at a capture event if they were actively captured in LPO or the LCFR and measured less than 425 mm in length, or if they were passively captured moving over PIT tag antenna arrays while out-migrating into the lake. Bull Trout were assigned to the adult life stage at a capture event if they were actively captured in LPO or the LCFR and measured greater than or equal to 425 mm in length, or if they were passively captured moving over PIT tag antenna arrays while migrating into the tributaries for an assumed spawning event. The 425 mm threshold for the adult life stage designation was determined based on the average length at maturity for this population (see McCubbins et. al 2016). See Table 1 for a summary of the number of annual Bull Trout captures by designated life stage.

Table 1. Number of annual encounters of individual Bull Trout by life stage from 2010 through 2019. Encounters are reported for July through June.

Stage	2010–2011	2011–2012	2012–2013	2013–2014	2014–2015	2015–2016	2016–2017	2017–2018	2018–2019
Juvenile	285	564	252	299	411	387	268	175	195
Subadult	1	418	446	395	483	468	289	311	336
Adult	0	367	538	751	769	897	615	796	811

The detection probability for the juvenile state was manually set to zero within the model because recapture events did not occur while individuals were in this life stage. As such, we assumed all individuals within the juvenile life stage transition to the subadult life stage by the time-step following that of initial capture (i.e., t+1). Therefore, the probability of a juvenile staying in this state for more than an annual time-step (i.e., juvenile-to-juvenile) was fixed to zero and the probability of a juvenile transitioning to the subadult state was fixed to one within the model. This is a reasonable assumption of the model, as 99% of the Bull Trout that were detected via arrays while emigrating out of the tributaries were detected doing so within or before the time-step following that of their marking event. The annual transition probability was also manually fixed to zero for all biologically impossible state-to-state movements (i.e., juvenile-to-adult, adult-to-juvenile, adult-to-subadult, and subadult-to-juvenile) and was manually fixed to one for all biologically required state-to-state movements (i.e., adult-to-adult). The detection probabilities for the subadult and adult state and the transition probability of a Bull Trout moving from the subadult state to the adult state were estimated within the model.
State and observation models were defined as components of the state-space multistate models. Here, the state model describes the true state of an individual at time t+1 ($z_{i,t+1}$) given its state at time t ($z_{i,t}$) as a categorical distribution defined as:

$$z_i, f_i = fs_i$$

$$z_{i,t+1} | z_{i,t} \sim \text{categorical}(\boldsymbol{\Omega}_{z_{i,t},1 \ldots S,i,t})$$

where z_{i}, f_{i} is the assigned state at first encounter and is equal to the true state at first encounter, fs_{i}. The state-transition matrix ($\boldsymbol{\Omega}$) is four-dimensional, where the first dimension is the state of departure, the second dimension is the state of arrival, the third dimension is the individual (i) and the fourth dimension is time (t). Here, states are denoted 1 through S, where S is the number of true states. An observation model was used to link the multistate encounter history to the true state of each individual and was defined as:

$$y_{i,t} | z_{i,t} \sim \text{categorical}(\boldsymbol{\Theta}_{z_{i,t},1 \ldots O,i,t})$$

where $y_{i,t}$ is the observed state of individual i at time t, $\boldsymbol{\Theta}$ is the four dimensional observation matrix, and O is the number of observed states (see Kéry and Schaub 2012).

A set of candidate models were developed from *a priori* hypotheses to estimate the apparent survival for all three states and the detection and transition probabilities of non-fixed states (Table 2). A random effect of year on survival was include in the models to account for annual variation in survival probabilities. The potential differential survival of juvenile Bull Trout that were initially tagged in connected LPO tributaries (i.e., Granite and Trestle creeks) versus those that were tagged in Montana prior to being transported downstream of Cabinet Gorge Dam and released into the LCFR was of specific interest in this study. Models that included a location of first capture covariate on survival were assessed using a multiplicative and additive model structure to assess if survival probabilities differed between these two groups. However, because 95% credible intervals for parameter estimates from these models overlapped with those from the model that omitted this covariate, the location covariate was excluded from the final model structure to minimize the number of estimated parameters. The resulting selected model included a life stage covariate on all parameters (g), a random effect of year on survival (t), and constant detection and transition probabilities and can be represented as:

$$\{S_{gt} p_{g} \psi_{g}\}.$$

Stage-specific survival (i.e., S_{juv}, S_{sub}, and S_{adt}) and transition (i.e., Ψ_{SA}) probabilities were not estimated within the IPM itself. Instead, these parameters were first generated in the multistate CMR model and then the mean and standard error of these posterior distributions were provided as informative priors. Stage-specific survival was modeled as described on page 200 of Kéry and Schaub (2012).

Table 2. Candidate model set for multi-state capture-mark-recapture (CMR) models to estimate Bull Trout apparent survival (S), detection probability (p), and transition probability (ψ). The asterisk (*) denotes the selected model used in data analyses.

Model	**Description**
$S_g p_g \psi_g$	Constant model with life stage covariate (g)
$S_{gt} p_g \psi_g{}^*$	Random effect of year on survival
$S_{gtloc} p_g \psi_g$	Random effect of year and individual location covariate on survival
$S_{gt+loc} p_g \psi_g$	Random effect of year and individual location covariate on survival (additive)
$S_{gt+loc} p_{g+loc} \psi_g$	Random effect of year and individual location covariate on survival and detection (additive)

An informative beta prior was used for the annual probability of a subadult individual transitioning into the adult state (Ψ_{SA}) and was modeled as:

$$\Psi_{SA} \sim \text{beta}(\alpha_{\Psi}, \beta_{\Psi})$$
$$\alpha_{\Psi} = \left(\frac{1-\psi_{SA}}{\sigma^2_{\psi_{SA}}} - \frac{1}{\psi_{SA}}\right)\psi^2_{SA}$$
$$\beta_{\Psi} = \alpha_{\Psi}\left(\frac{1}{\psi_{SA}} - 1\right),$$

where ψ_{SA} is the mean and $\sigma_{\psi SA}$ is the standard error of the mean of the transition probability posterior distribution generated by the multi-state CMR model.

Two parameters in the process model, $S_{eggs:age1}$ and R_t were not able to be informed by empirical data. Furthermore, because IPM abundance estimates are intrinsically linked to both parameters, model convergence could not be achieved without utilizing an informative prior for one of these two parameters. Therefore, an informative prior was developed to describe the unknown survival of eggs to age-1. This beta prior was modeled as:

$$S_{eggs:age1} \sim \text{beta}(\alpha_{Seggs:age1}, \beta_{Seggs:age1})$$
$$\alpha_{Seggs:age1} = \left(\frac{1-\mu_{Seggs:age1}}{\sigma^2_{Seggs:age1}} - \frac{1}{\mu_{Seggs:age1}}\right)\mu^2_{Seggs:age1}$$
$$\beta_{Seggs:age1} = \alpha_{Seggs:age1}\left(\frac{1}{\mu_{Seggs:age1}} - 1\right)$$
$$\mu_{Seggs:age1} = 1 \times 10^{-2}$$
$$\sigma^2_{Seggs:age1} = 1 \times 10^{-6},$$

where $\mu_{\text{Seggs:age1}}$ is the designated value for the mean survival of eggs to age-1 and $\sigma^2_{\text{Seggs:age1}}$ is the designated value for the variance of egg to age-1 survival. The annual probability of an individual in the adult state spawning in a given year (R_t) was modeled as an uninformative beta prior:

$$R_t \sim \text{beta}(1,1).$$

Model fitting

The CMR models and IPM were implemented in a Bayesian framework using programs R 3.6.3 (R Core Team 2020) and JAGS (Plummer 2015), and the R2jags package (Su and Yajima 2015). The CMR multi-state model was fit by running three chains in parallel with 40,000 Markov chain Monte Carlo (MCMC) iterations per chain. A burn-in period of 10,000 iterations and a thinning rate of 6 was used, thus retaining 5,000 samples per chain. Model convergence was assessed using the Gelman-Rubin statistic (*Rc*) (Gelman and Rubin 1992) and parameter convergence was considered achieved when the maximum value of *Rc* was ≤ 1.1 (Gelman et al. 2013). Posterior distributions for model parameters (i.e., S, ψ, and p) from the converged model were retained to generate annual estimates of life stage-specific survival for juvenile, subadult, and adult Bull Trout from 2010 through 2018.

To fit the IPM, three MCMC chains were run in parallel with 25,000,000 iterations each. A burn-in period of 20,000,000 iterations and thinning rate of 1,000 were used, thus retaining 5,000 samples per chain. Model convergence was considered achieved when all parameters had an *Rc* value ≤ 1.1. Uniform priors were used to establish the initial cohort sizes in the first year of study and were specified as:

$$N_{juv,1} \sim \text{uniform}(0, 1 \times 10^5)$$
$$N_{sub,1} \sim \text{uniform}(0, 50{,}000)$$
$$N_{adt,1} \sim \text{uniform}(0, 8{,}000)$$
$$N_{sp,1} \sim \text{uniform}(0, 3{,}000)$$

These values were selected because they were biologically reasonable given what is known about the LPO system.

The harvest parameters, $h_{\text{sub},t}$ and $h_{\text{adt},t}$, and the direct mortality reduction parameter, dm_t, were manually set to zero for the initial model run and posterior distributions from the converged IPM were used to generate annual estimates of life stage specific abundances for juvenile, subadult and adult Bull Trout in Lake Pend Oreille from 1983 through 2018. Interannual changes in total abundance (N_{tot}) were evaluated to assess population growth rates (λ) over the course of the study and were estimated as:

$$\lambda_t = \frac{N_{tot,t+1}}{N_{tot,t}}$$

Harvest Scenarios
The IPM forecasted future abundances of adult Bull Trout by projecting process model parameters under varying hypothetical management scenarios. This was done using a truncated dataset starting in year 2010. The IPM cannot concurrently predict future abundances and estimate annual spawning probability from an uninformative prior. Therefore, an informative prior was developed for the parameter R_t for these predictive model runs. This beta prior included the posterior mean and variance of the parameter R_t from the initial IPM run and was modeled as:

$$R \sim \mathrm{beta}(\alpha_R, \beta_R)$$
$$\alpha_R = \left(\frac{1-\hat{R}}{\sigma^2_{\hat{R}}} - \frac{1}{\hat{R}}\right)\hat{R}^2$$
$$\beta_R = \alpha_R\left(\frac{1}{\hat{R}} - 1\right),$$

where $\hat{R}$ is the posterior mean and $\sigma^2_{\hat{R}}$ is the posterior variance from the converged IPM.

The restructured IPM was used to estimate the annual abundance of adult Bull Trout from 2010 through 2018 and to project abundance forward in time on an annual time-step through 2025. This relatively short projection timeframe was selected to limit exponential growth and not exceed predictive capabilities of the model. Similar to the initial IPM parameterization, annual survival and transition probabilities from the CMR model were provided to the IPM as informative priors. The mean values for these parameters were used during model forecasting (i.e., 2019–2025).

Adult harvest, subadult harvest, and gill netting direct mortality reduction scenarios were assessed using the forecasting parameterization of the IPM. Harvest scenarios discussed here include: a status quo management scenario, where predator suppression netting is assumed to continue at current effort levels with no angler harvest of Bull Trout occurring in the population; a 5% annual adult harvest management scenario, where predator suppression netting is assumed to continue at current effort levels with additional angler harvest of 5% of the total adult Bull Trout population; a 15% annual adult harvest management scenario, where predator suppression netting is assumed to continue at current effort levels with additional angler harvest of 15% of the total adult Bull Trout population; and a 15% annual adult harvest concurrent with 50% reduction in direct gill netting mortality management scenario, where direct mortalities from predator suppression netting efforts are assumed to be reduced by 50% concurrent with 15% annual angler harvest of the total adult Bull Trout population. In each scenario that deviates from the status quo, modeled management changes are initiated in 2019 and are implemented annually in subsequent years. Geometric mean population growth rates (λ) and intrinsic growth rates (r) were calculated for each modeled scenario to evaluate forecasted changes is the population size.

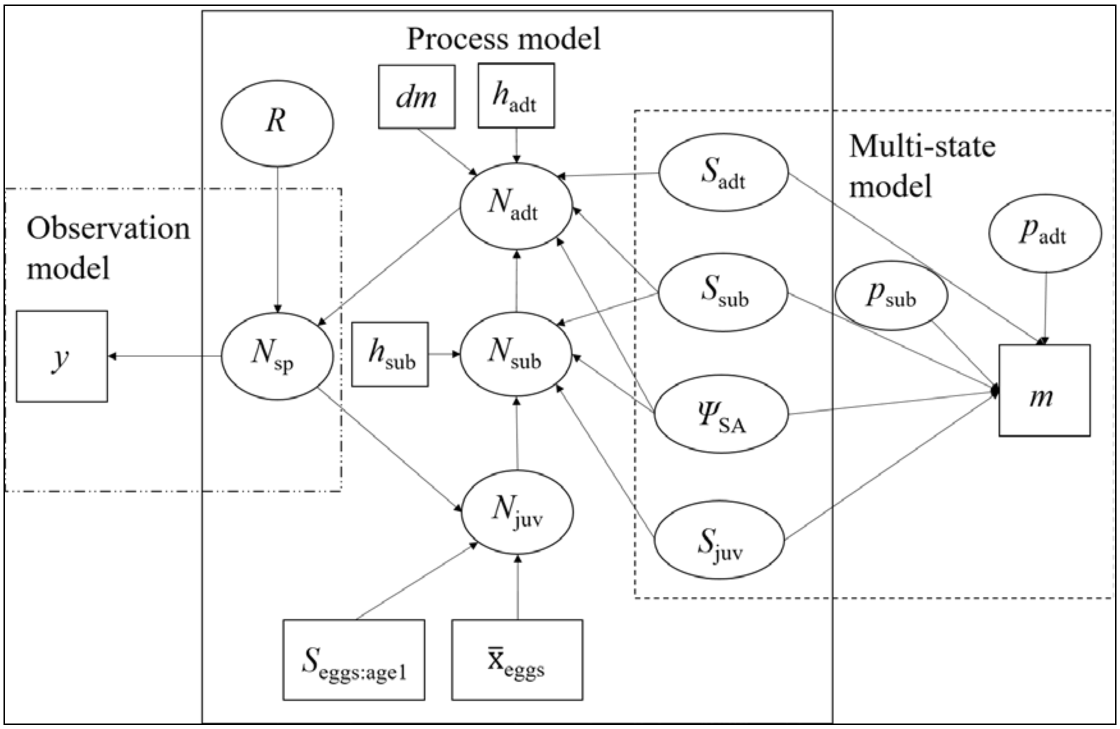

Figure 2. Directed acyclic graph (DAG) depicting the structure of the Bull Trout IPM. Ovals represent estimated parameters and rectangles represent input data. Arrows denote node dependencies. Data and parameter abbreviations are defined in Table 3.

Table 3. Definitions of data and parameter abbreviations.

Symbol	**Definition**
y	annual count data of Bull Trout redds in the system
$\bar{x}_{eggs}$	estimate of mean number of eggs per redd
R	estimate of annual probability of an adult spawning
p_{sub}	estimate of mean detection probability of subadults
p_{adt}	estimate of mean detection probability of adults
$S_{eggs:age1}$	estimate of mean egg through age one survival probability
S_{juv}	estimate of annual juvenile survival probability
S_{sub}	estimate of annual subadult survival probability
S_{adt}	estimate of annual adult survival probability
Ψ_{SA}	estimate of annual transition probability from the subadult to adult stage
N_{juv}	estimate of annual juvenile population size
N_{sub}	estimate of annual subadult population size
N_{adt}	estimate of annual adult population size
N_{sp}	estimated annual number of spawning adults in the population
h_{adt}	annual number of adults removed from the population via harvest
h_{sub}	annual number of subadults removed from the population via harvest
dm	annual reduction in the number of direct gill netting mortalities

RESULTS

Survival, Detection, and Transition Probability

Estimated stage-specific apparent survival varied annually from 2010 through 2018 (Figure 3). Apparent survival for adult Bull Trout ranged from 0.32 (0.28–0.36, 95% credible interval [CI]) in the 2015–2016 annum to 0.48 (0.42–0.54, 95% CI) in the 2012–2013 annum (Table 4). Mean apparent survival for the adult stage was 0.39 (0.32–0.46, 95% CI). Apparent survival for subadult Bull Trout ranged from 0.51 (0.46–0.56, 95% CI) in the 2015–2016 annum to 0.67 (0.62–0.73) in the 2012–2013 annum. Mean apparent survival for the subadult stage was 0.59 (0.51–0.66, 95% CI). Apparent survival for juvenile Bull Trout ranged from 0.14 (0.11–0.18, 95% CI) in the 2015–2016 annum to 0.24 (0.19–0.31, 95% CI) in the 2012–2013 annum. Mean apparent survival for the juvenile stage was 0.18 (0.13–0.24, 95% CI). Estimated detection probability was 0.08 (0.07–0.24, 95% CI) for subadult Bull Trout and 0.4 (0.36–0.44, 95% CI) for adult Bull Trout. The annual probability of a subadult individual transitioning to the adult stage was estimated at 0.36 (0.32–0.42, 95% CI).

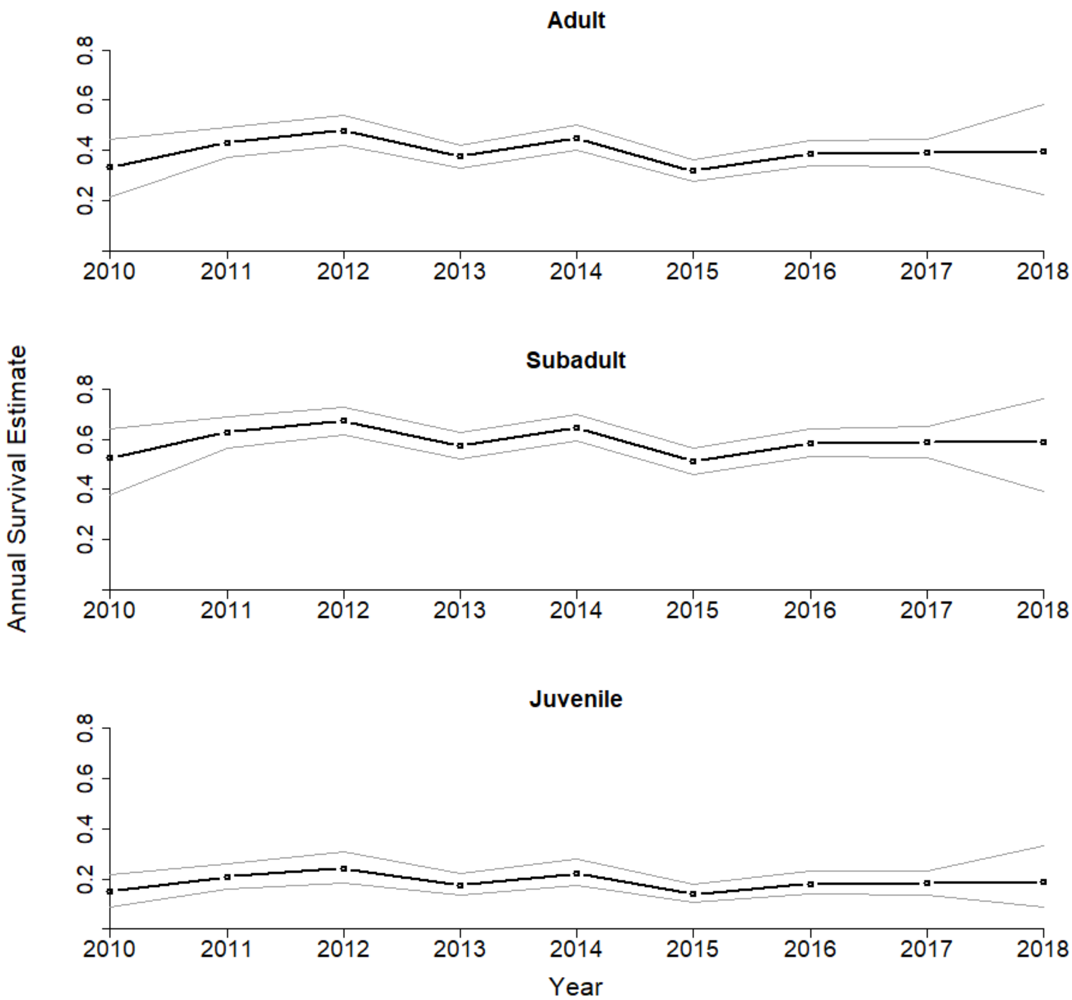

Figure 3. Estimated annual apparent survival with 95% CIs by life stage for Bull Trout in Lake Pend Oreille, 2010–2018.

Table 4. Estimated annual apparent survival with 95% credible intervals (CIs) of Bull Trout in Lake Pend Oreille by life stage. Mean apparent survival was 0.39 (0.32–0.48) for the adult life stage, 0.59 (0.51–0.67) for the subadult life stage, and 0.18 (0.14–0.24) for the juvenile life stage.

Year	**Adult Survival**	**Subadult Survival**	**Juvenile Survival**
2010–2011	0.33 (0.21–0.44)	0.53 (0.38–0.64)	0.15 (0.09–0.22)
2011–2012	0.43 (0.37–0.49)	0.63 (0.57–0.69)	0.21 (0.16–0.26)
2012–2013	0.48 (0.42–0.54)	0.67 (0.62–0.73)	0.24 (0.19–0.31)
2013–2014	0.38 (0.33–0.42)	0.57 (0.52–0.63)	0.17 (0.13–0.22)
2014–2015	0.45 (0.40–0.50)	0.65 (0.59–0.70)	0.22 (0.17–0.28)
2015–2016	0.32 (0.28–0.36)	0.51 (0.46–0.56)	0.14 (0.11–0.18)
2016–2017	0.39 (0.34–0.44)	0.59 (0.53–0.64)	0.18 (0.14–0.23)
2017–2018	0.39 (0.34–0.45)	0.59 (0.53–0.65)	0.18 (0.14–0.23)
2018–2019	0.40 (0.23–0.58)	0.59 (0.39–0.76)	0.19 (0.19–0.33)

Abundance and Population Growth

Estimated annual abundance of Bull Trout in Lake Pend Oreille varied annually and by life stage (see Appendix Table A-1 for annual abundance estimates). Adult Bull Trout abundance estimates ranged from 2,885 (1,753–4,395, 95% CI) in 1995 to 6,105 (3,713–9,356, 95% CI) in 2009, and averaged 4,255 individuals over the assessed timeframe (Figure 4). Subadult Bull Trout abundance estimates ranged from 9,087 (5,776–13,423, 95% CI) in 1997 to 22,687 (14,143–34,099, 95% CI) in 2008, and averaged 14,205 individuals (Figure 5). Juvenile Bull Trout abundance estimates ranged from 22,896 (17,520–28,621, 95% CI) in 1996 to 89,997 (69,899–109,953, 95% CI) in 2007 and averaged 48,348 individuals (Figure 6). Estimated annual population growth rates were oscillating but stable over the assessed timeframe (i.e., 1983–2018), with a geometric mean population growth rate (λ) of 1.01 (Figure 7).

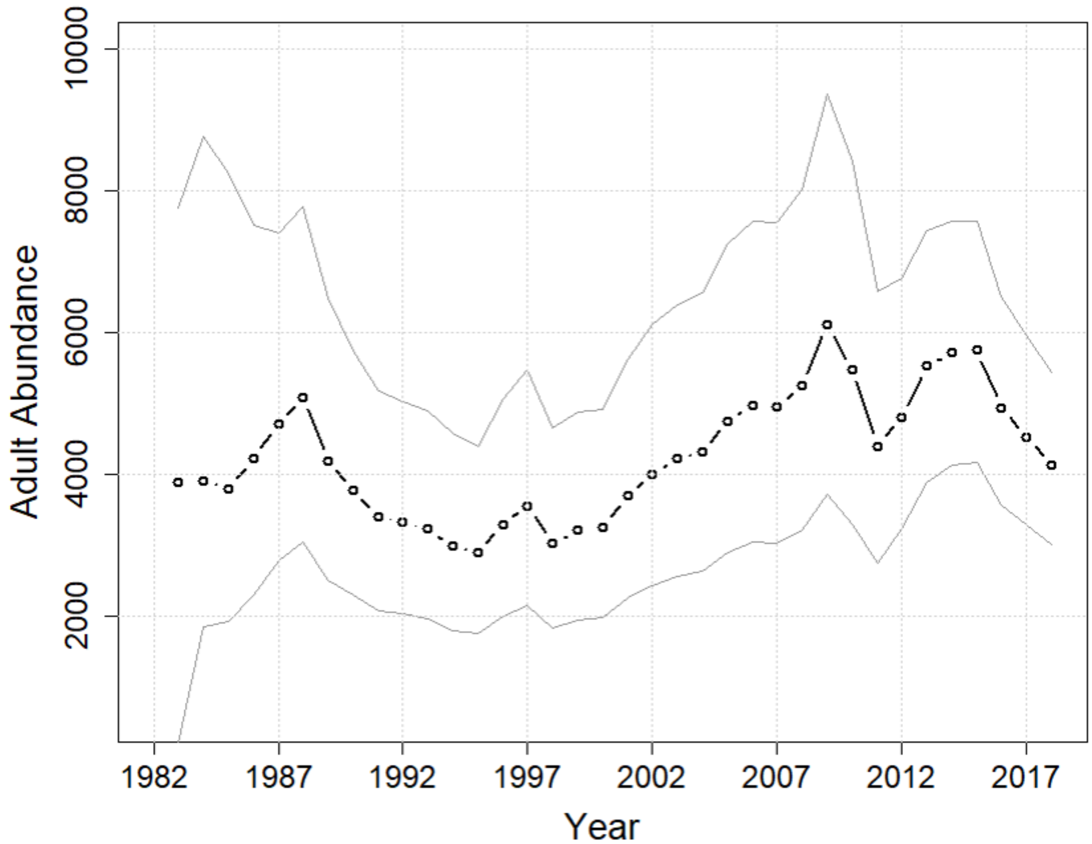

Figure 4. Estimated annual adult abundance with 95% CIs for Bull Trout in Lake Pend Oreille, 1983–2018.

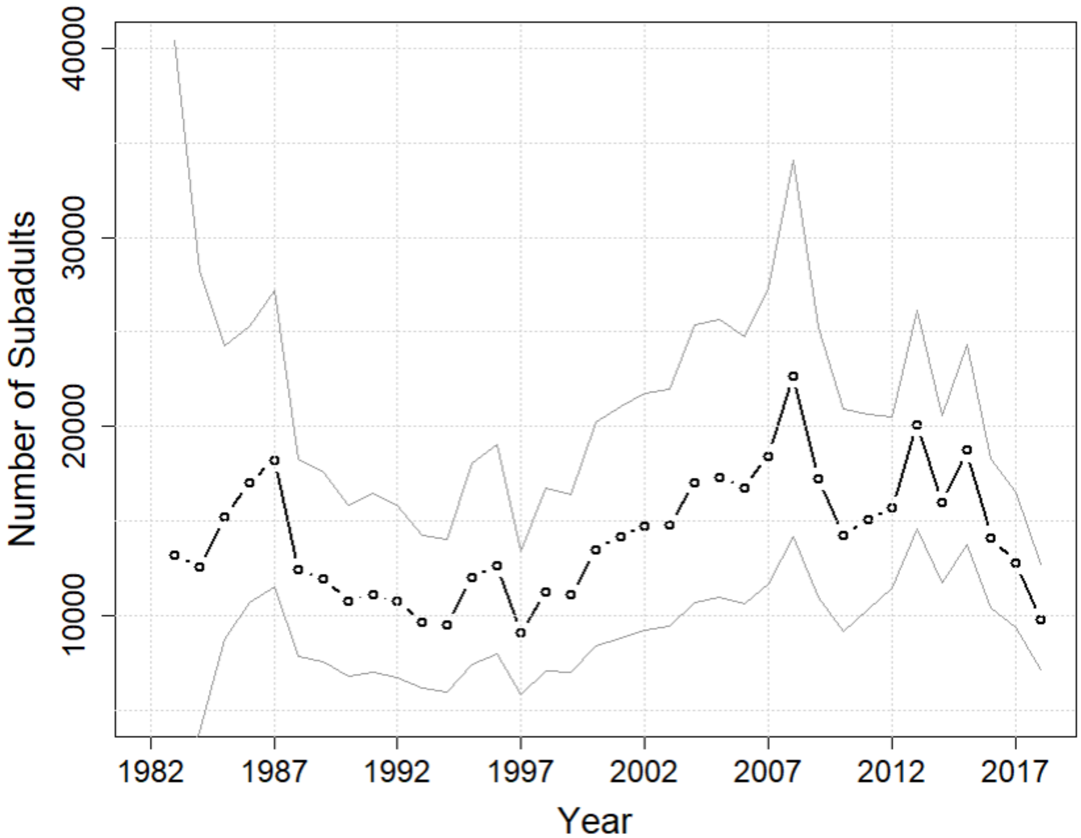

Figure 5. Estimated annual subadult abundance with 95% CIs for Bull Trout in Lake Pend Oreille, 1983–2018.

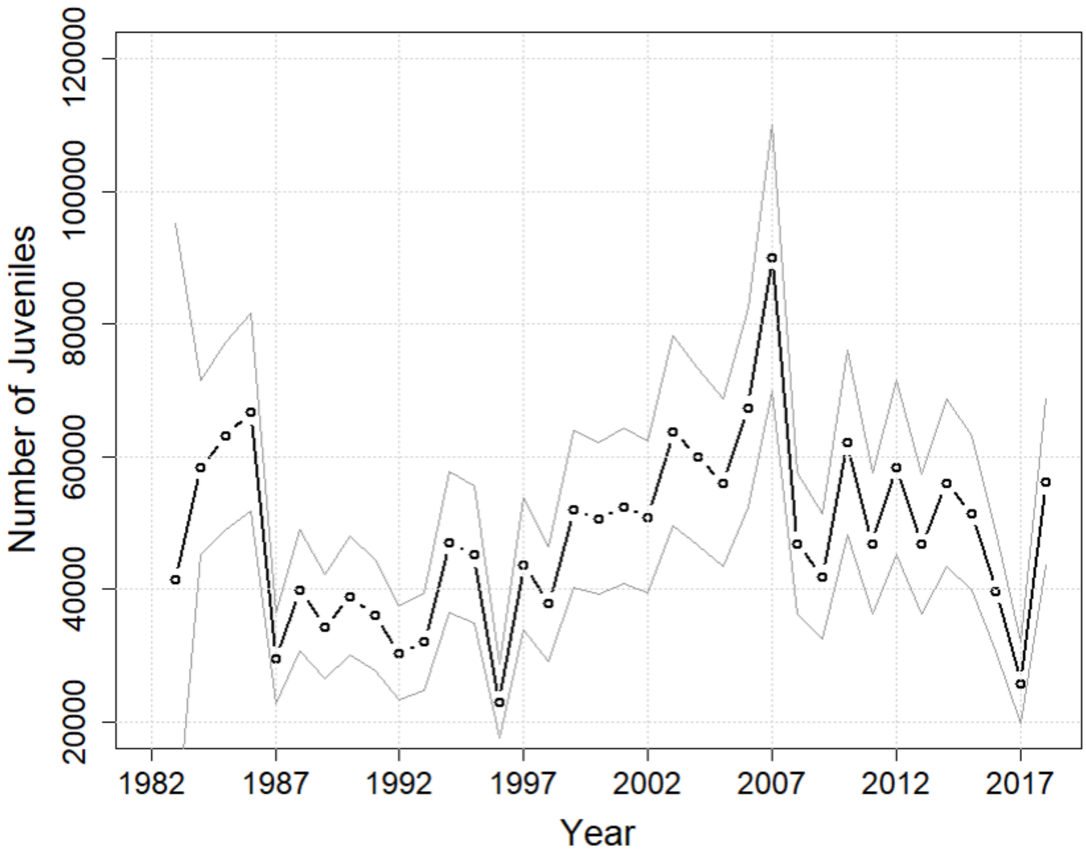

Figure 6. Estimated annual juvenile abundance with 95% CIs for Bull Trout in Lake Pend Oreille, 1983–2018.

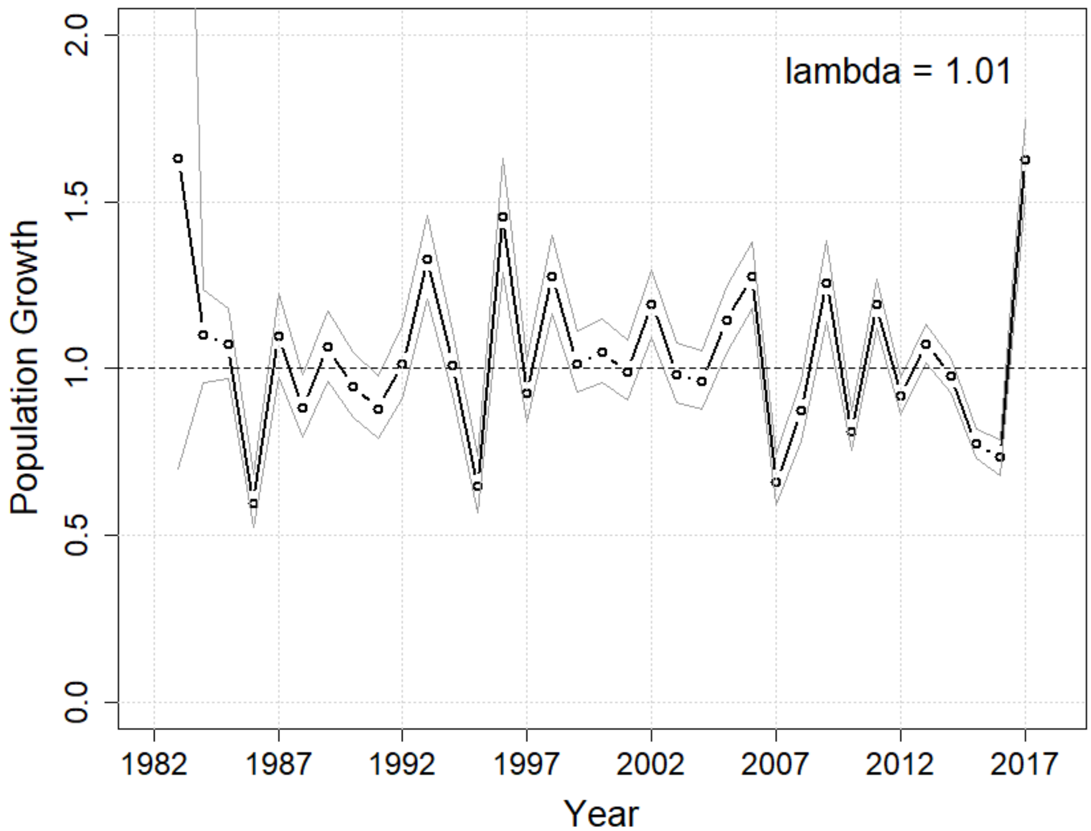

Figure 7. Estimated annual population growth rate for the Lake Pend Oreille Bull Trout population, 1983–2018. The geometric mean population growth rate (λ) over the course of the study was 1.01.

Modeled Harvest Scenarios

The terminal projected adult abundance estimate was highest under the status quo management scenario and lowest under the 15% adult harvest management scenario. However, prediction intervals (PI) overlapped for terminal abundance estimates from all scenarios. When adult Bull Trout abundance was projected forward under the status quo management scenario, estimated abundance steadily increased from 3,636 (2,948–4,373, 95% PI) in the first year of projection (i.e., 2019) to 5,496 (3,085–8,950, 95% PI) in the final projected year (i.e., 2025; Figure 8). Under this scenario, the intrinsic growth rate during the projection interval (i.e., 2019–2025) was 0.29 and the predicted geometric mean population growth rate for the entire modeled period (i.e., 2010–2025) was estimated at 1.07. When adult Bull Trout abundance was projected forward under the 5% annual adult harvest management scenario, estimated abundance increased from 3,431 (2,740–4,166, 95% PI) in the first year of projection to 4,760 (2,603–7,930, 95% PI) in the final projected year (Figure 9). Under this scenario, the intrinsic growth rate over the projection interval was 0.16 and the predicted geometric mean population growth rate for the entire modeled period was estimated at 1.06. When adult Bull Trout abundance was projected forward under the 15% annual adult harvest management scenario, estimated abundance varied slightly annually from 3,035 (2,350–3,778, 95% PI) in the first year of projection to 3,605 (1,856–6,244, 95% PI) in the final projected year (Figure 10). Under this scenario, the intrinsic growth rate during the projection interval was -0.08 and the predicted geometric mean population growth rate for the entire modeled period was estimated at 1.04. When adult Bull Trout abundance was projected forward under the 15% annual adult harvest concurrent with a 50% reduction in direct netting mortality scenario, estimated abundance increased from 3,260 (2,580–4,014, 95% PI) in the first year of projection to 4,256 (2,346–7,057, 95% PI) in the final projected year (Figure 11). Under this final scenario, the intrinsic growth rate during the projection interval was 0.06 and the predicted geometric mean population growth rate from over the entire modeled period was estimated at 1.05.

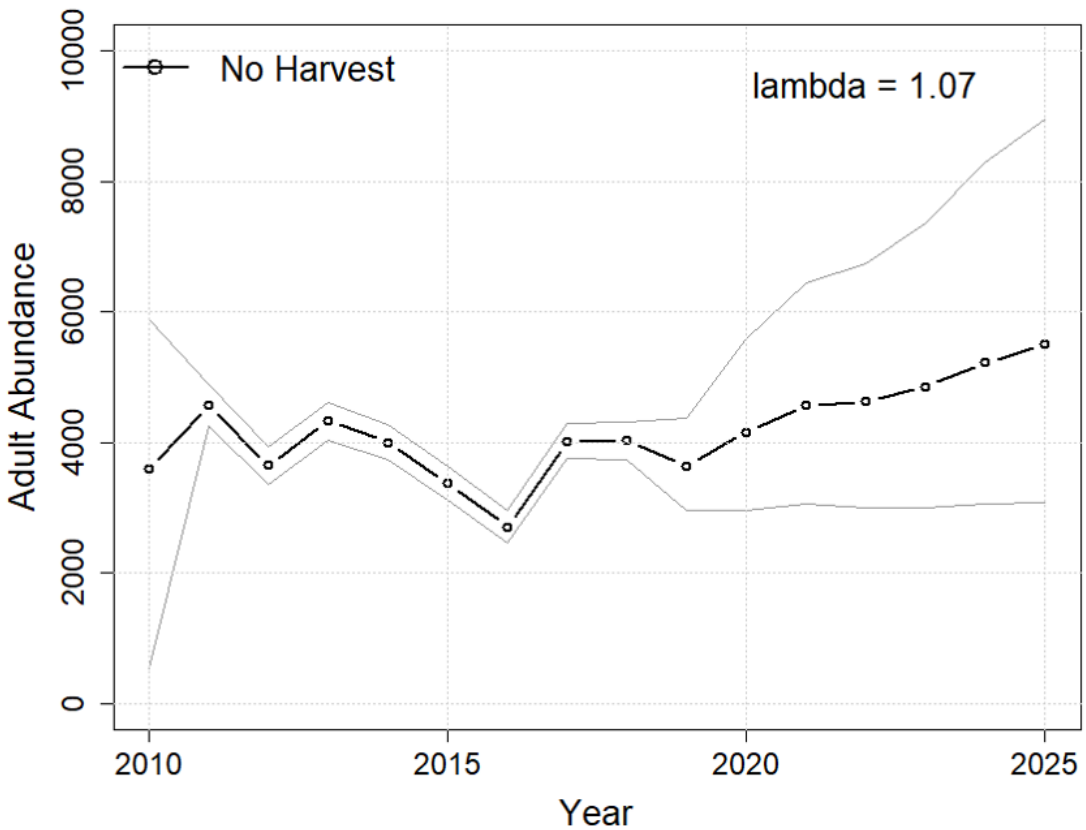

Figure 8. Estimated annual projected abundance of adult Bull Trout in Lake Pend Oreille modeled under a status quo management scenario. The geometric mean population growth rate (λ) over the course of the entire modeled period is 1.07.

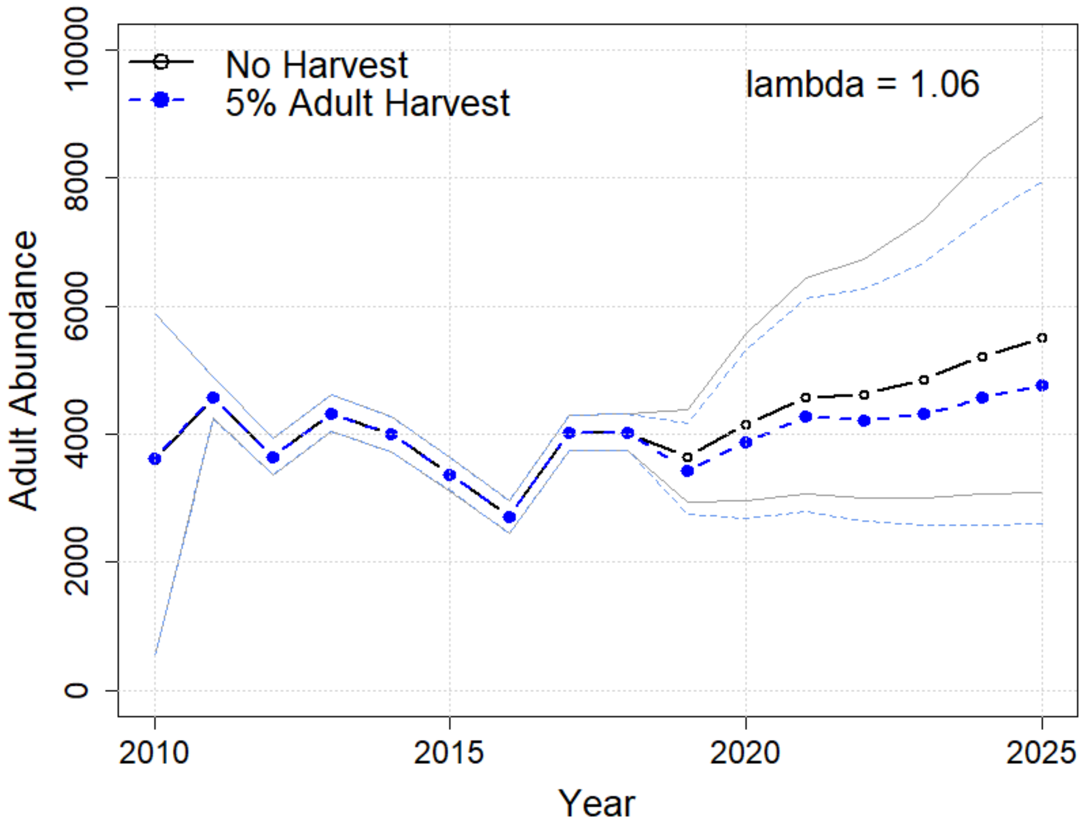

Figure 9. Estimated annual projected abundance of adult Bull Trout in Lake Pend Oreille modeled under status quo and 5% adult harvest management scenarios. Modeled harvest is initiated in 2019 and is implemented annually in subsequent years. The geometric mean population growth rate (λ) over the course of the entire modeled period is 1.06.

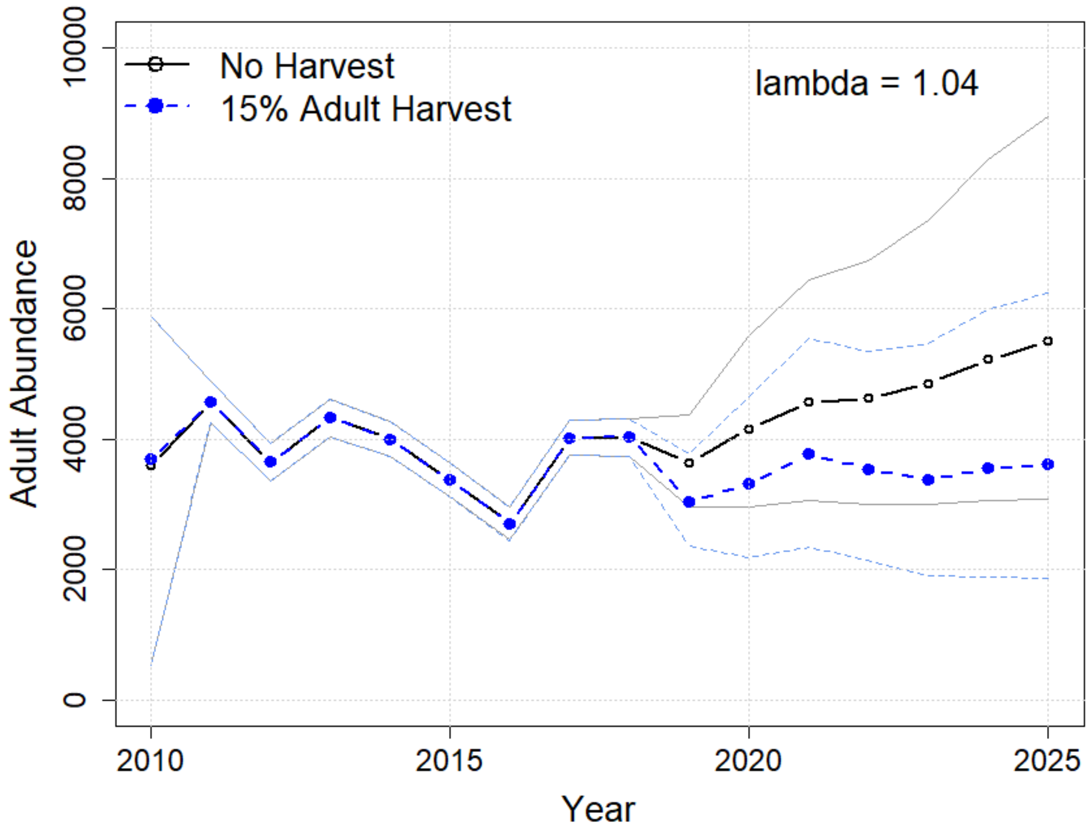

Figure 10. Estimated annual projected abundance of adult Bull Trout in Lake Pend Oreille modeled under status quo and 15% adult harvest management scenarios. Modeled harvest is initiated in 2019 and is implemented annually in subsequent years. The geometric mean population growth rate (λ) over the course of the entire modeled period is 1.04.

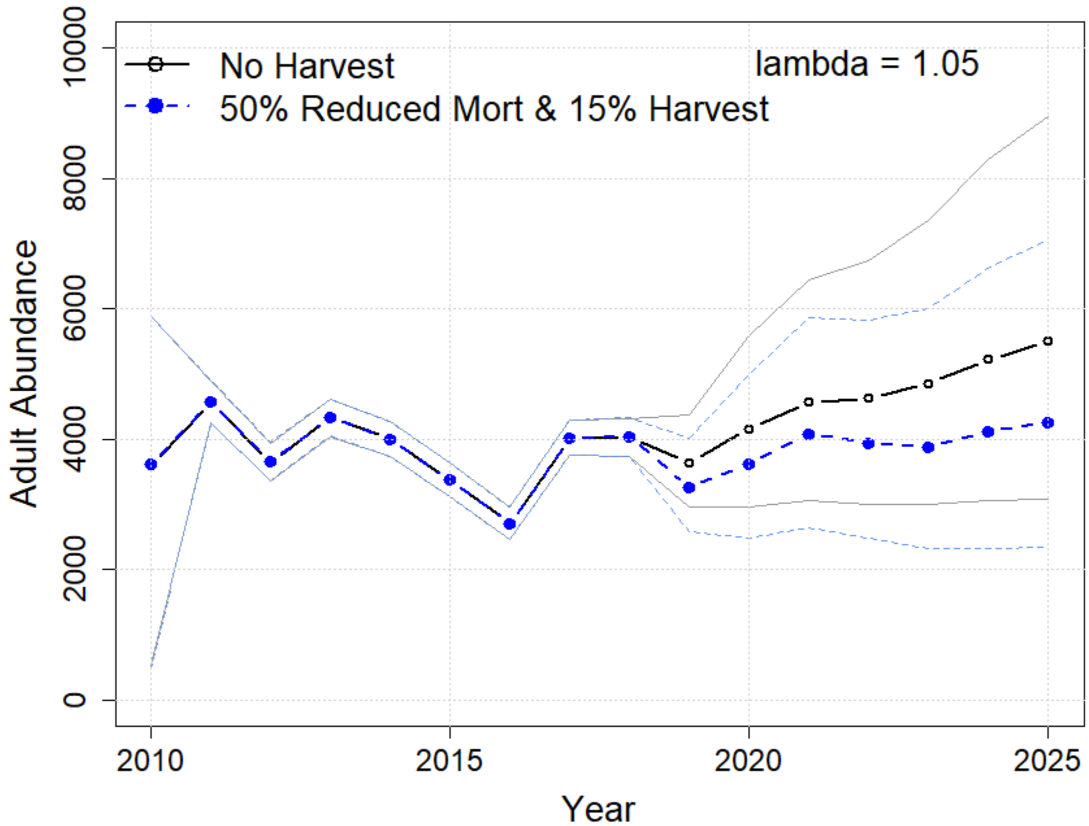

Figure 11. Estimated annual projected abundance of adult Bull Trout in Lake Pend Oreille modeled under status quo and a management scenario with 15% adult harvest and a 50% reduction in direct mortality related to netting operations. Modeled harvest and reduced netting mortality are initiated in 2019 and is implemented annually in subsequent years. The geometric mean population growth rate (λ) over the course of the entire modeled period is 1.05.

DISCUSSION

While the abundance of Bull Trout in Lake Pend Oreille has fluctuated over time, growth rates were unchanged over the past few decades. Previous work demonstrated that the trend in abundance of Bull Trout in LPO was not increasing or decreasing from 1998 through 2008 (McCubbins et al 2016). Results from the current study corroborate this finding. Lowest abundances were estimated in the mid-1990s, concomitant with the designation of Bull Trout as threatened under the ESA (USFWS 1999). This is consistent with what previous studies have found for Bull Trout populations in Idaho, where intrinsic rates of population change were estimated to be either decreasing (High et al. 2008) or stable (Meyer et al. 2014) prior to 1994, and increasing thereafter (High et al. 2008; Meyer et al. 2014).

The conclusion that annual stage-specific apparent survival does not notably vary between juvenile fish that were initially captured downstream of Cabinet Gorge Dam in Trestle and Granite creeks versus those first captured upstream of the dam and transported into the mainstem of the LCFR is a notable finding of this study. Fish from populations upstream versus downstream of Cabinet Gorge Dam likely experience different sources of mortality in different times and locations, so this finding, while allowing us to simplify the model by removing a parameter, also raises interesting questions about limiting factors for these populations. For instance, this finding suggests that transported fish (which represent the majority of tagged fish from above Cabinet Gorge Dam) are not at a survival disadvantage relative to fish that migrate directly from their natal stream to the lake. This indicates that transporting fish to avoid mortality in Cabinet Gorge and Noxon reservoirs is likely successful. While an encouraging finding, more research is necessary to understand the mechanisms that led to this observation.

Modeled harvest scenarios demonstrate that the LPO Bull Trout population could biologically support additional harvest mortality. Intrinsic growth rates for projected abundances were estimated to be positive for all scenarios except under 15% annual adult harvest. Therefore, moderate annual harvest rates under 15% are not predicted to cause a population decline. Intuitively, reducing direct mortality associated with predator suppression netting operations resulted in a slight increase intrinsic growth rates. However, increases in population growth rates were minor even under a 50% reduction in netting mortality, suggesting incidental bycatch mortality is not driving population dynamics in this system. Scenarios that evaluated the effects of harvest on the subadult population were initially assessed during preliminary model runs. However, these scenarios were not included in the final analyses because preliminary results showed population responses to changes in subadult abundance were redundant with responses that occurred due to manipulation of the adult population.

It is of note that while demographic parameters in Bull Trout populations such as early juvenile survival (Johnston et al. 2007) and spawning probability (Johnston and Post 2009) are density dependent, a density independent, exponential growth model was used for all analyses. This was done because models did not converge using a logistic model. Although exponential growth is an unrealistic assumption for this population, this is a conservative approach to evaluating harvest feasibility. Harvest mortality would likely be compensatory under density dependence (Miranda and Bettoli 2007) and therefore the effects of harvest on the population may be exaggerated in the model. Further, predicted increases in abundance related to reduced netting mortality are likely overstated assuming there is density dependence in this population.

A principal advantage to utilizing IPMs is their capacity to enable inference on a parameter that is not directly informed by empirical data (see Kéry and Schaub 2012). However, because two parameters (i.e., spawning probability and age-0 survival) were lacking empirical data in the current analysis, model generated estimates of spawning probability were conditional upon the arbitrary assigned value for age-0 survival and it was not appropriate to evaluate estimates of these parameters independently. When assessed in conjunction, estimates of spawning probability and age-0 survival demonstrate considerable interannual variability. Therefore, it is probable that one or both of these parameters largely fluctuated across years. Incorporating empirical data on spawning probability in subsequent model runs may further improve the precision of estimates and allow for egg through age-1 survival to be directly assessed. This would help address current data gaps around a lifestage that is notoriously difficult to empirically assess.

The current analysis relies on an index of abundance to provide population count information in the IPM. Previous studies have demonstrated the utility of employing index data in IPMs (e.g., Besbeas et. al 2002; Davis et al. 2014), particularly when true abundance data is not available. However, it is of note that the observation error associated with redd count data is unknown and could not be freely estimated within the IPM due to difficulties with model convergence. The constraint of redd count observation error to facilitate model convergence is likely valid, as redd count observation error was estimated to be minimal in previous studies (Meyer et al. 2014) and constrained model estimates of observation error did not approach the ceiling of the prior. Nevertheless, an improved estimate of sampling error around LPO redd counts may further refine parameter estimates in successive model runs.

At present, the joint likelihood calculated within the IPM is conditional on point estimates from the multistate CMR model. While this parameterization of the IPM improves processing speed and previous analyses illustrate the efficacy of this approach (see Arnold et al. 2018), we may not have fully accounted for uncertainty due to process variability and sampling error. It is also of note that the CMR dataset violates the model assumption of instantaneous capture, as capture events occurred year-round. However, previous studies suggest that violations of this assumption likely have inconsequential effects on survival estimates (see Hargrove and Borland 1994). As previously mentioned, it is also notable that apparent survival estimates here should not be identified as true survival, as they are the combination of survival and latent emigration (Schaub and Royle 2014).

Despite the noted limitations, the IPM developed here will serve as an essential tool in the evaluation of current and future management practices of the LPO Bull Trout population. Addressing the identified data gaps will even further improve model parameter estimates and enhance resulting inferences about LPO Bull Trout population demographics. This study demonstrates the utility of employing IPMs to concurrently evaluate standing population demographics and assist in the assessment of potential fisheries management scenarios. Results from this study indicate that the LPO Bull Trout population continues to exhibit stability over multiple decades. As noted in previous studies (e.g., Vidergar 2000; McCubbins et al. 2016), this enduring and projected stability may justify permitting a limited harvest fishery. The tool developed here will provide a means for subsequent standardized assessments of the LPO Bull Trout population, thus promoting the ability to evaluate and adaptively manage this population as new information comes to light and potential future management strategies are implemented.

RECOMMENDATIONS

- Incorporate Bull Trout and Lake Trout catch-at-age models as well as kokanee abundance data to enhance the model to investigate Bull Trout bycatch with respect to interactions between these species.
- Install additional PIT arrays in LPO tributaries to increase the number of interrogation sites to further refine the model.
- Where possible, continue to provide empirical data for parameters that are currently estimated or provided by the literature, such as fecundity, maturity, spawning frequency, redd observation error, region of origin, etc.

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APPENDIX

Table A-1. Estimated annual abundance with 95% CIs of adfluvial Bull Trout by life stage.

Year	Adult Abundance	Subadult Abundance	Juvenile Abundance	Total Abundance
1983	3,890 (204–7,760)	13,217 (805–40,390)	41,333 (18,95–95,170)	58,440 (17,233–118,915)
1984	3,903 (1,839–8,773)	12533 (3,856–28,225)	58,300 (45,267–71,443)	74,735 (56,902–97,662)
1985	3,795 (1,914–8,249)	15,190 (8,706–24,285)	63,108 (49,053–77,198)	82,094 (63,633–102,528)
1986	4,218 (2,295–7,518)	17,014 (10,655–25,309)	66,613 (51,757–81,519)	87,846 (67,806–109,018)
1987	4,699 (2,772–7,392)	18,208 (11,496–27,176)	29,492 (22,661–36,498)	52,399 (39,275–67,402)
1988	5,085 (3,050–7,776)	12,396 (7,825–18,281)	39,729 (30,709–49,006)	57,211 (43,600–71,922)
1989	4,193 (2,493–6,481)	11,925 (7,527–17,604)	34,227 (26,401–42,155)	50,345 (38,265–63,468)
1990	3,773 (2,301–5,741)	10,773 (6,777–15,801)	38,881 (30,058–47,896)	53,428 (40,901–66,660)
1991	3,402 (2,071–5,181)	11,094 (6,958–16,466)	36,026 (27,764–44,428)	50,521 (38,504–63,196)
1992	3,321 (2,025–5,023)	10,742 (6,734–15,824)	30,280 (23,218–37,525)	44,344 (33,529–55,672)
1993	3,224 (1,954–4,896)	9,623 (6,149–14,201)	32,000 (24,639–39,423)	44,846 (34,074–56,224)
1994	2,986 (1,797–4,572)	9,509 (5,972–14,018)	46,990 (36,480–57,711)	59,486 (45,779–73,943)
1995	2,885 (1,753–4,395)	11,980 (7,430–18,091)	45,180 (34,915–55,562)	60,045 (45,864–75,255)
1996	3,283 (1,989–5,060)	12,646 (7,952–19,007)	22,896 (17,520–28,621)	38,825 (28,935–50,119)
1997	3,555 (2,140–5,471)	9,087 (5,776–13,423)	43,677 (33,766–53,684)	56,318 (43,208–69,998)
1998	3,016 (1,825–4,653)	11,250 (7,062–16,764)	37,730 (29,091–46,450)	51,997 (39,783–65,093)
1999	3,207 (1,948–4,883)	11,100 (7,018–16,359)	51,998 (40,304–63,852)	66,305 (50,912–82,220)
2000	3,252 (1,978–4,913)	13,457 (8,388–20,201)	50,490 (39,154–62,040)	67,198 (51,359–83,900)
2001	3,696 (2,250–5,628)	14,186 (8,836–21,086)	52,434 (40,754–64,263)	70,317 (53,798–87,408)
2002	3,996 (2,420–6,150)	14,755 (9,240–21,785)	50,855 (39,388–62,309)	69,606 (53,215–86,806)
2003	4,218 (2,557–6,388)	14,789 (9,405–21,938)	63,777 (49,510–78,134)	82,784 (63,552–102,814)
2004	4,312 (2,623–6,566)	17,040 (10,656–25,373)	59,900 (46,492–73,320)	81,252 (62,236–101,614)
2005	4,752 (2,892–7,242)	17,283 (10,978–25,677)	55,939 (43,357–68,585)	77,974 (59,669–97,786)
2006	4,965 (3,043–7,564)	16,735 (10,583–24,732)	67,331 (52,255–82,373)	89,032 (68,354–110,903)
2007	4,954 (3,032–7,542)	18,441 (11,632–27,349)	89,997 (69,899–109,953)	113,393 (87,418–140,391)
2008	5,251 (3,206–8,020)	22,687 (14,143–34,099)	46,857 (36,276–57,529)	74,795 (56,365–95,194)
2009	6,105 (3,713–9,356)	17,228 (10,971–25,202)	41,837 (32,362–51,433)	65,170 (49,149–82,149)
2010	5,469 (3,280–8,417)	14,263 (9,161–20,953)	62,042 (48,087–75,930)	81,774 (62,793–101,408)
2011	4,396 (2,740–6,586)	15,068 (20,625–46,837)	46,837 (36,306–57,620)	66,301 (50,828–82,225)
2012	4,809 (3,232–6,763)	15,713 (11,420–20,523)	58,381 (45,218–71,484)	78,903 (61,010–97,017)
2013	5,521 (3,891–7,437)	20,084 (14,609–26,120)	46,688 (36,168–57,352)	72,293 (55,599–88,984)
2014	5,722 (4,119–7,576)	15,958 (11,697–20,593)	55,931 (43,319–68,667)	77,611 (59,978–95,166)
2015	5,759 (4,170–7,572)	18,733 (13,757–24,304)	51,368 (39,816–63,011)	75,860 (58,726–93,110)
2016	4,928 (3,559–6,498)	14,126 (10,382–18,254)	39,625 (30,720–48,784)	58,679 (45,333–72,357)
2017	4,516 (3,279–5,957)	12,753 (9,346–16,530)	25,749 (19,690–31,985)	43,018 (33,005–53,440)
2018	4,124 (2,999–5,436)	9,793 (7,160–12,717)	56,033 (43,520–68,670)	69,950 (54,151–85,999)