Estimating bull trout spawner-recruitment relationships for the tributaries of the Flathead and Swan River Basins

Submitted to Montana Fish, Wildlife and Parks by:

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Executive Summary

We used a Montana Fish, Wildlife & Parks (MFWP) long-term (10-32 years) dataset of redd and juvenile densities to estimate spawner-recruitment relationships, understand environmental influences on recruitment, and establish biological benchmarks for bull trout.

Bull trout spawner-recruitment relationships did not support evidence for depensation at low spawner abundances and were best estimated using a Ricker spawner-recruitment model, where overcompensatory density-dependent dynamics existed at high spawner abundances. We were able to incorporate variation in recruitment productivity for the different bull trout populations. Populations overall had similar estimates of productivity, though a difference existed between Ole and Granite Creeks, both in the Middle Fork Flathead River, and between Goat (Swan River drainage) and Granite Creeks.

Additionally, we found no evidence of environmental effects (i.e., fine sediment, summer streamflow, winter flooding frequency, and summer temperature) on recruitment.

We derived population-specific biological reference points for the number of spawners that produced maximum recruitment and that produced 50% maximum recruitment. Goat, Lion, and Squeezer Creeks had the highest percentages of years where the number of redds surveyed exceeded the maximum recruitment benchmark (36%, 56%, and 66%, respectively), whereas Big, South Fork Coal, and (MWFP site name) north fork Coal Creek had the lowest percentages (7%, 4%, 0%, respectively). By contrast, 49% of years in Coal Creek and 52% of years South Fork Coal Creek had redds below the 50% maximum recruitment benchmark.

This work, as well as past research regarding bull trout spawner-recruitment dynamics, demonstrate that the species is productive at low spawner abundances (compensation), suggesting that bull trout have the ability to recover from environmental disturbances or overharvest. Evidence of overcompensation from this and past research suggests that bull trout recovery may be limited by habitat quantity or quality, which is consistent with the complex life history needs of the species and responses to anthropogenic habitat alterations.

We derived biological reference points from the spawner-recruitment models that could be used as recovery objectives or precautionary benchmarks, which is a novel approach for the conservation of bull trout. The population-specific reference points provide a bull trout conservation framework grounded in biological relationships and could be extended to objectives relating to historical dynamics. By using these benchmarks, declines or recovery of bull trout can be better anticipated, and the cost and effect of management actions on meeting recovery goals can be clearly evaluated. As additional data become available over time, these benchmarks can be refined, likely improving the efficiency and cost-effectiveness of bull trout recovery efforts.

Background

Purpose and Need:

Bull trout (*Salvelinus confluentus*) have declined throughout much of the species native range (Rieman et al., 1997) and are currently listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service, 1998). Montana Fish, Wildlife & Parks highly value the species for its ecological significance and recreational value (where fishing is legally permitted; Dickinson, 2018). The federal listing of bull trout and high susceptibility to anthropogenic influences and fishing pressure (Post & Johnston, 2002; Rieman & Mclntyre, 1993; Rodtka et al., 2009) have made empirically deriving benchmarks a priority for population recovery. Given the vulnerability of bull trout to disturbance, estimating stock-recruitment relationships, and understanding whether density-dependent relationships exist, can support realistic recovery benchmarks and critical thresholds for triage management actions. Despite the importance of understanding spawner-recruitment dynamics, the spawner-recruitment relationship has rarely (e.g., Chudnow et al., 2019) been quantified for the species.

This research focused on using existing datasets to establish a stock-recruitment relationship for bull trout. Since the early 1980s, Montana Fish, Wildlife & Parks have surveyed bull trout redds and sampled juvenile bull trout in the tributaries of the Flathead, Swan, and Stillwater River basins. Redd data have previously been used to understand population trends and effects of biotic and abiotic factors on population dynamics (e.g., Kovach et al., 2017, 2018), but few efforts have leveraged the extensive juvenile monitoring data. Merging these datasets represents a unique opportunity to further inform bull trout population dynamics and other metrics related to bull trout recovery. Furthermore, data were explored to understand anthropogenic or environmental influences on bull trout recruitment. Bull trout recruitment metrics could guide management decisions and directly aid in the recovery of the species.

This project aimed to determine whether the current bull trout redd and juvenile data contained the appropriate structure to estimate stock-recruitment relationships. Additionally, abiotic data (e.g., temperature, streamflow, fine sediment) were used to understand recruitment drivers. The project will compile bull trout monitoring data collected by Montana Fish, Wildlife & Parks from the Flathead and Swan River basins to provide insight into the application and utility of long-term monitoring data and bull trout stock-recruitment dynamics.

Objectives:

1. Estimate stock-recruitment relationships for bull trout.

2. Conduct analyses to understand drivers of bull trout recruitment.

3. Derive biological reference points related to redd counts to inform bull trout recovery efforts.

Methods

Data

Montana Fish, Wildlife & Parks (MFWP) provided redd counts and juvenile abundance estimates collected using depletion electrofishing from 13 survey areas in the Swan and Flathead River basins. Though many populations in the Swan and Flathead River basins have redd counts conducted on a yearly basis, fewer have both redd and juvenile surveys needed to estimate spawner-recruitment relationships. Migratory bull trout tend to be large (>500 mm) and construct easily discernible redds that can be accurately counted by trained field biologists (Al-Chokhachy et al., 2005; Brooks et al., 2024; Dunham et al., 2001; Howell & Sankovich, 2012; Muhlfeld et al., 2006). Redd count accuracy is, however, influenced by several factors, including observer experience, abiotic or biotic environmental conditions (e.g., flooding, heterospecific fall spawners), timing of counts, and habitat characteristics (Dunham et al., 2001; Muhlfeld et al., 2006). Redd counts included here were observed in "index" reaches, where redds were counted on a routine basis and may have included only part of the total creek length but were consistently surveyed within the upper and lower limits of a defined redd survey reach (Table 1). To minimize potential bias, we communicated with biologists from MFWP to determine survey areas with greatest survey confidence and removed those with potential habitat or personnel bias from inclusion in our study (n=2). Redd counts are strongly correlated with spawner abundance in migratory bull trout (Johnston et al., 2007); consequently, we considered redd counts as a proxy for adult bull trout abundance in our analyses. MFWP surveyed juvenile bull trout (total length < 300 mm) in the same tributaries as redd counts according to their standardized backpack electrofishing protocol (Weaver et al., 2006). We used age-1 abundance estimates as our measure of recruitment due to inconsistent capture of age-0 bull trout during juvenile surveying events and because juvenile emigration before age-1 was likely limited (Pinto et al., 2013). A total of 11 survey areas (Figure 1; hereafter populations) were included in this investigation with the median time-series including 25 years of data (mean 22.5 years), totalling 248 observations (Table 1).

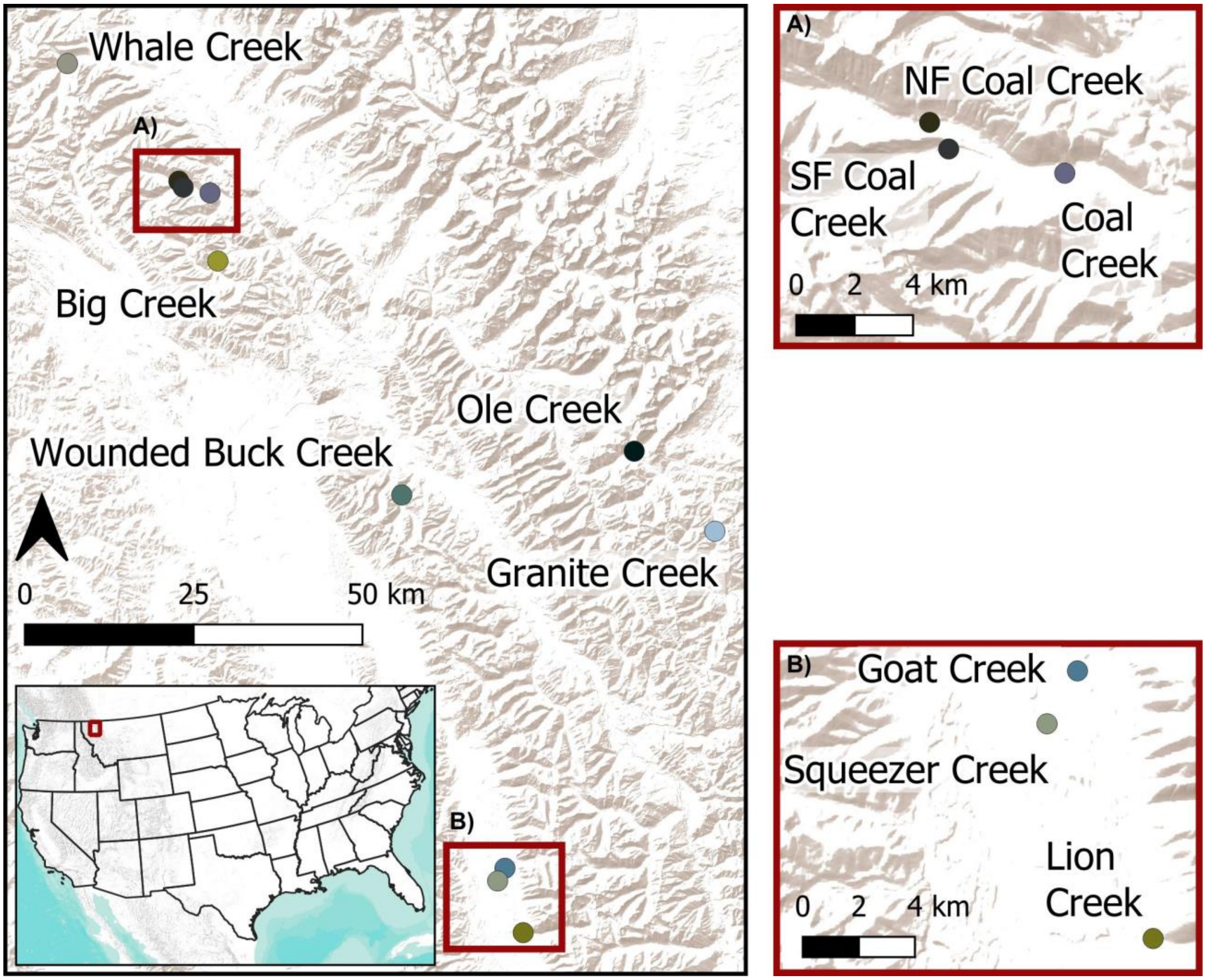

Figure 1. Bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations used for spawner-recruitment modeling in the Flathead River drainage of northwestern Montana, U.S.A. Selected locations in A) Coal Creek (SF= South Fork and NF= north fork) and B) the Swan River subbasins are shown for further sampling location context. ESRI basemap.

Table 1. Information relating to bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations and datasets used for spawner-recruitment modeling in the Flathead River drainage of northwestern Montana, U.S.A. Amount of habitat, drainage area, and August temperature from the Native Trout Climate Change Vulnerability Explorer (https://www.usgs.gov/apps/ecosheds/#/). Montana Fish, Wildlife & Parks identifies a sampling site in Coal Creek as "north fork" Coal Creek.

Population name	Subbasin	Redd survey length (km)	Stream habitat (km)	Drainage area (km^2)	Timeseries length (years)	August mean water temperature (˚C)
Goat Creek	Swan Lake	7.5	23.0 (Goat & Squeezer)	72	26	8.9
Squeezer Creek		7.0			26	
Lion Creek		10.5	11.0	29	25	9.2
Wounded Buck Creek	South Fork Flathead	5.2	6.6	14	18	7.8
Big Creek	North Fork Flathead	6.1	35.7	199	32	9.0
Coal Creek		6.1	45.7 (Coal & Forks)	156	28	9.2
South Fork Coal Creek		4.8			20	
north fork Coal Creek		4.0			10	
Whale Creek		12.8	27.3	125	30	8.4
Granite Creek	Middle Fork Flathead	5.6	13.1	74	18	9.3
Ole Creek		5.5	12.7	113	15	10.9

Spawner-recruitment relationship

We initially compared the utility of different plausible spawner-recruitment relationships. Specifically, we considered the Shepherd model (Shepherd, 1982), which included an additional parameter, *c*, that assessed the strength of density-dependent dynamics; that is, whether the spawner-recruitment relationship for each population had tendencies of Ricker (median c >1, overcompensatory density-dependent; Ricker, 1954) or Beverton-Holt (median c = 1, compensatory density-dependent; Beverton & Holt, 1957) models. We also explored a Beverton-Holt model that included depensatory dynamics (Myers et al., 1995), where per capita population growth is slowed at very small population sizes. We considered the populations to have depensatory dynamics if the median depensatory parameter, q, was <0. We fit all models using a hierarchical Bayesian framework (Cahill et al., 2018, 2020; Myers & Mertz, 1998) to account for observation error, random population effects, and to improve precision in model fit. We used diffuse priors to allow the data to inform posterior distributions. No evidence existed to support depensation in the Beverton-Holt model (Figure S1). Additionally, results from the Shepherd model indicated more instances of overcompensatory density-dependent dynamics than compensatory density-dependent dynamics (Figure S2).

Therefore, we investigated potential environmental drivers of spawner-recruitment relationships and derivation of conservation benchmarks using the Ricker spawner-recruitment model (Ricker, 1954), where recruitment (R) was modelled as:

$$R_i = \alpha_i \cdot S_i e^{-\beta_i S_i}$$

and i is each individual observation and S is spawning stock (i.e., redd density). Log-transforming the observed recruitment introduces an error term, with the likelihood specified as:

$$\log(R_i) \sim \mathrm{N}(\log(\alpha_i \cdot S_i e^{-\beta_i S_i}) - \frac{\sigma_{obs}^2}{2}, \sigma_{obs}^2),$$

where σ_{obs} is the standard deviation of observation error. The parameters α_i and β_i are derived as:

$\log(\alpha_i) = \log(\alpha_m) + \alpha_{stream[j]}$ and

$\log(\beta_i) = \log(\beta_m)$.

Parameter α represents the slope of the stock-recruitment curve near the origin (i.e., recruitment productivity) and is density-independent, where α_m is global mean productivity and $\alpha_{stream[j]}$ is a variable intercept for each population, j. Parameter β is related to carrying capacity and is density-dependent. We were unable to include a variable intercept on both the productivity parameter, α, and the density dependent parameter, β, due to data limitations. Understanding population-level variability in production of recruits at low spawner abundances can be of more interest than understanding population-level variability in overcompensation because most bull trout populations have low adult abundance in recent years. Therefore, we included a random effect on α only. The variable slope for each population is modelled as:

$$\alpha_{\mathrm{stream}[j]} \sim \mathrm{N}(0, \sigma_\alpha^2),$$

where σ_α is the standard deviation of the variable intercept.

Environmental drivers of spawner-recruitment relationships

Next, we included covariates (env) to understand the potential effects of environmental influences on recruitment production with γ_m representing the coefficient for the environmental covariate, specifically influencing the productivity of recruits at low adult spawning abundances, where:

$$\log(\alpha_i) = \log(\alpha_m) + \alpha_{stream[j]} + \gamma_m \cdot \mathrm{env}_i$$

We hypothesized that bull trout recruitment would be negatively influenced by fine sediment (<6.35 mm), summer temperature, winter flooding, and positively influenced by summer streamflow (Fig. S3-S7). Due to the inclusion of population random effects, we did not include covariates representing habitat patch size and habitat complexity as done in other analyses in this region (i.e., Kovach et al., 2015) but include habitat metrics for reference in Table 1.

Fine sediment can affect bull trout recruitment through multiple mechanisms, and previous regional research has found a negative relationship between fine sediment and juvenile bull trout densities in Swan River (Leathe, 1985) and Flathead River tributaries (Weaver & Fraley, 1991). Fine sediment accumulations can reduce pool depth, cause channel braiding or dewatering, and reduce interstitial spaces among larger streambed particles (Beschta & Platts, 1986; Bowerman et al., 2014; Bryce et al., 2010; Everest et al., 1987; Lisle, 1982; Thurow, 1997). MFWP has collected annual sediment core samples to monitor substrate for a subset of populations in the Swan and Flathead River drainages (Shepard et al., 1984; Weaver, 2005). Here, we included the median percentage of substrate < 6.35 mm in each set of samples from each year-population combination in our analysis (n=12). However, data were not available for Ole Creek; consequently, we assumed that the fine sediment timeseries was analogous to that of Granite Creek because both creeks are tributaries to the Middle Fork Flathead River.

Various thermal and hydrologic conditions are known to influence bull trout populations at the spawning and recruitment stages. We used the annual mean and minimum August streamflow, frequency of winter flood events, and annual mean August air temperature for each population to represent environmental conditions – thermal and hydrologic stressors – thought to influence bull trout (e.g., Al-Chokhachy et al., 2016; Bell et al., 2021; Dunham et al., 2003; Kovach et al., 2017; Wenger et al., 2013). We used mean August air temperature from Daymet

(Thornton et al., 2016) to represent the thermal regimes experienced by bull trout populations within the survey areas during the summer (e.g., Rieman et al., 2007; Wenger et al., 2011); observed or predicted annual stream temperatures were unavailable for local populations. Generally, air temperatures are strongly correlated with water temperatures during summer months (Isaak et al., 2010), but the degree of correlation can vary across space (Luce et al., 2014) or due to groundwater inputs (O'Driscoll & DeWalle, 2006). Then, we used the HUC-10 predicted (Hoylman, 2025) average summer streamflow (DOY=day of year; DOY > 196, DOY < 245), minimum summer streamflow (DOY > 196, DOY < 245), and frequency of high winter flow events (the number of days that exceeded the 95th percentile days of annual streamflow DOY > 305 | DOY < 91; Kovach et al., 2015; Wenger et al., 2010, 2013) to represent hydrologic conditions for each population.

We included the influence of fine sediment, August temperature, average summer streamflow, and minimum summer streamflow as covariates during the spawning year (year of covariate data collection, year of redd count), the age-0 (year of redd count +1), and age-1 year (year of redd count +2). We included the influence of high winter flow events on the age-0 and age-1 year. All covariates were standardized prior to analyses by subtracting the mean value and dividing by the standard deviation. We considered a covariate to have a significant influence on the productivity parameter of the spawner-recruitment relationship if the 80% credible intervals of the covariate-influenced productivity parameter estimate did not overlap compared to the productivity estimate without covariates (base model).

Posterior calculation

Posterior density functions for parameters of interest were approximated using the Markov chain Monte Carlo (MCMC) algorithm implemented using JAGS software (Just Another

Gibbs Sampler; version 4.3.1; available from http://mcmc-jags.sourceforge.net/) implemented through R (v4.4.2; R Core Team, 2024) using the R2jags package (version 0.8-9; Su et al., 2015). Three chains were run for 30,000 iterations after a burn-in of 15,000, and the final posterior estimates were thinned by 10. We visually inspected trace plots for convergence and verified Rhat was < 1.05 (Gelman et al., 2004). Evaluation of the Ricker hierarchical model using trace plots demonstrated model convergence with all Rhat values <1.05. Little to no observed autocorrelation existed after thinning in the posterior MCMC chains for the model.

Biological reference points

Biological reference points can be derived from spawner-recruitment models and are usually calculated in relation to harvested fisheries, often salmon stocks (e.g., Staton et al., 2017). Due to bull trout having an iteroparous life history strategy and being a federally threatened species, goals for maximum recruitment may result in recovery. Therefore, we included a reference point of spawner abundance that produce maximum recruitment (S_{MAX}) and a reference point that would indicate precautionary (i.e., 50% S_{MAX}; Mace, 1994; e.g., Overholtz, 1999) recruitment levels (S_{CAU}):

$$S_{MAX} = \frac{1}{\beta};$$

$$S_{CAU} = 0.5 \cdot \frac{1}{\beta}$$

We derived an estimate of S_{MAX} and S_{CAU} for each survey area and transformed the estimate from redd density (redds·km^{-1}) to a value relevant to the specific survey area length. We transformed the S_{MAX} and S_{CAU} to a value most translatable to redd counts within the survey area (i.e., no longer standardized to redds·km^{-1}), in which case, variability in the biological reference points across survey areas becomes more recognizable.

Results

Spawner-recruitment relationship and environmental drivers

Overall, fits of the Ricker model described the mean relationship between spawning stock size and recruitment abundance for each population with some populations demonstrating overcompensation at high redd densities (Figs. 2, S8). The random effect of population had no influence on the differences in the productivity estimate for most survey areas (Fig. 3). However, a difference existed between Ole and Granite Creeks, both in the Middle Fork Flathead River, and between Goat (Swan River drainage) and Granite Creeks (Fig. 3). Granite Creek was estimated to have the most recruitment production at low spawner abundances, whereas Ole and Goat Creeks were estimated to be the least productive of the areas surveyed (Fig. 3; Table 2).

No differences existed across any of the productivity parameter estimates incorporating environmental drivers compared to the base model without covariates (Fig. S9-S10). Granite Creek had the largest uncertainty around productivity estimates of any survey area, whereas Ole and Goat Creeks had the least uncertainty independent of model (Fig. S10).

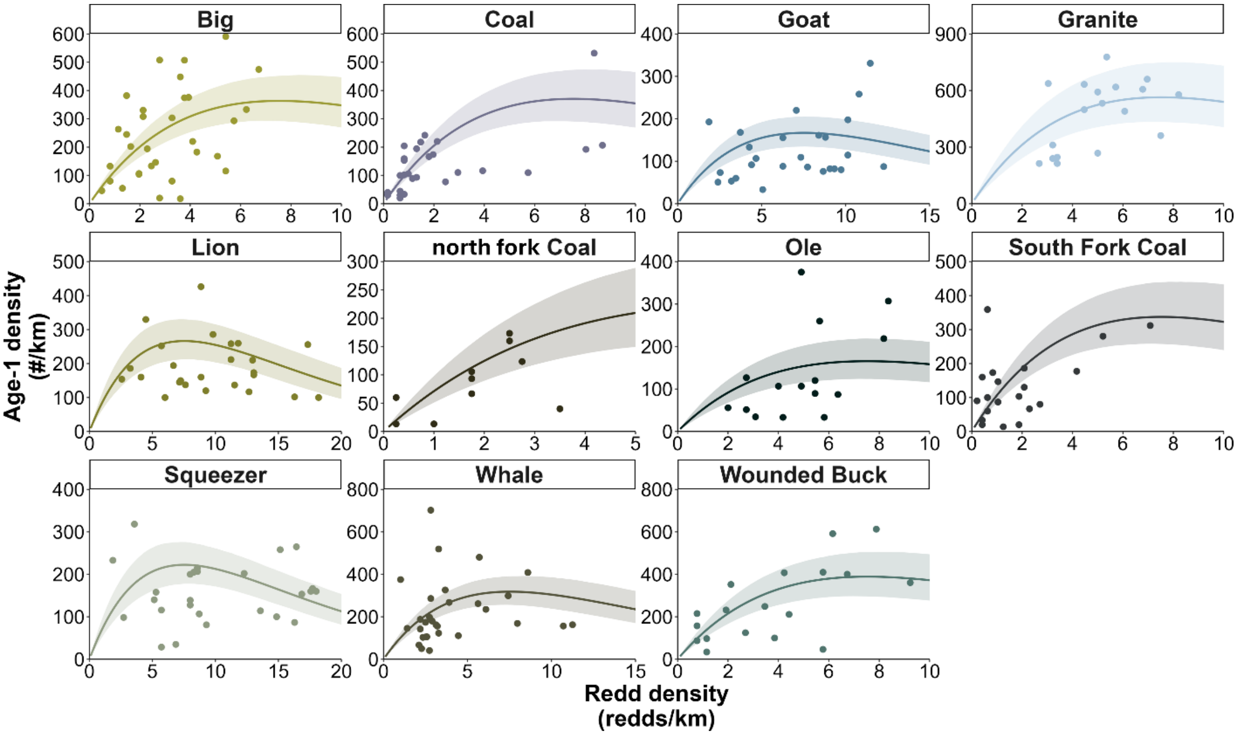

Figure 2. Ricker spawner-recruitment curves for bull trout in the Swan and Flathead River basins, Montana, U.S.A., where each panel represents a different survey area. Points are observed redd and age-1 densities collected by Montana Fish, Wildlife & Parks during field surveys. Curve is median model including the stream effect on the productivity parameter. Shaded polygon represents 90% credible interval.

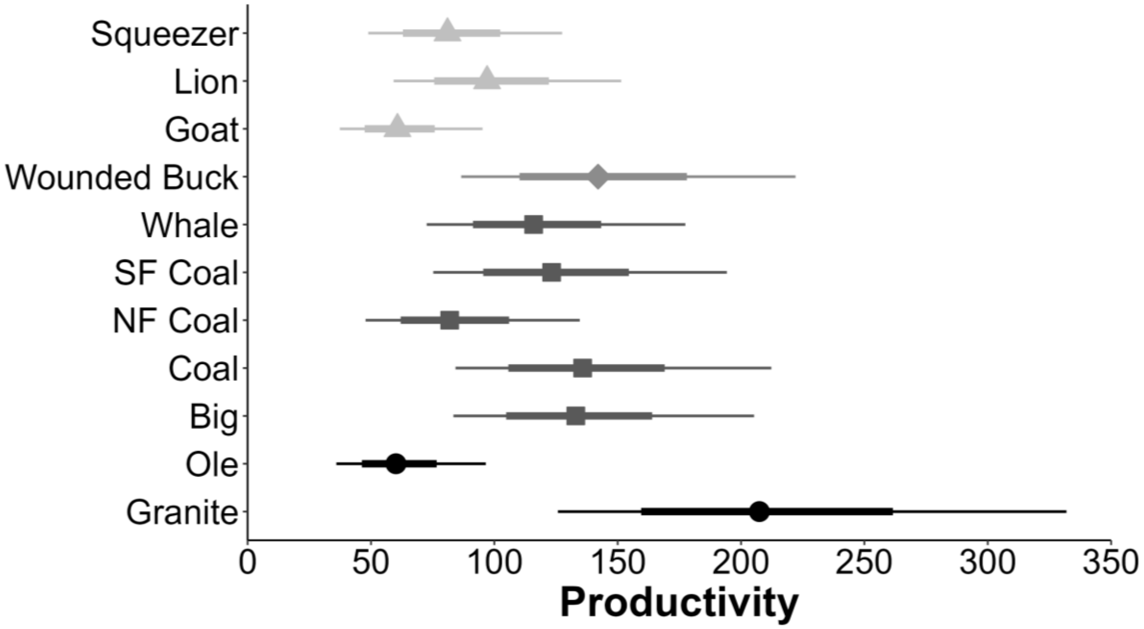

Figure 3. Comparison of the survey area random effect on the productivity parameter (α) across populations for bull trout (*Salvelinus confluentus*) in the Flathead River basin of Montana, U.S.A. Color and shape combination represents subbasin, where: light grey triangle is Swan River, grey diamond is South Fork Flathead River, dark grey square is North Fork Flathead River, and black circle is Middle Fork Flathead River. Point is mean, thick line is 50% credible interval, thin line is 80% credible interval. SF= South Fork, NF= north fork.

Table 2. Ricker spawner-recruitment model mean productivity parameter estimates and maximum recruitment biological benchmarks derived from the spawner-recruitment model for populations of bull trout (*Salvelinus confluentus*) in the Flathead River basin of northwestern Montana, U.S.A. Montana Fish, Wildlife & Parks identifies a sampling site in Coal Creek as "north fork" Coal Creek.

Population	Productivity parameter, α (80% credible interval)	Estimated redd count within survey area that produces maximum recruitment	Estimated redd count within survey area that produces 50% maximum recruitment
Goat Creek	60.73 (37.39 – 95.21)	56 (47 – 67)	12 (9 – 17)
Squeezer Creek	81.02 (48.89 – 127.49)	52 (44 – 63)	11 (8 – 17)
Lion Creek	97.06 (59.19 – 151.43)	78 (66 – 95)	17 (12 – 24)
Wounded Buck	142.05 (86.57 – 222.09)	38 (32 – 46)	8 (6 – 11)
Big Creek	133.03 (83.42 – 205.29)	45 (38 – 55)	10 (8 – 12)
Coal Creek	135.80 (84.27 – 212.29)	45 (38 – 55)	10 (8 – 12)
South Fork Coal Creek	123.23 (75.25 – 194.26)	35 (30 – 43)	7 (5 – 10)
north fork Coal Creek	81.91 (47.82 – 134.63)	29 (25 – 35)	6 (4 – 9)
Whale Creek	115.94 (72.59 – 177.42)	85 (81 – 116)	21 (17 – 27)
Granite Creek	207.43 (125.77 – 331.91)	41 (34 – 50)	12 (6 – 9)
Ole Creek	60.13 (35.96 – 96.56)	40 (34 – 49)	9 (6 – 13)

Biological reference points

We only derived biological reference points for the base model (the model without covariates) given the lack of environmental covariate influence on spawner-recruitment relationships. Due to only the productivity parameter having a random effect for survey area, the density dependence parameter estimate was the same value for every survey area, 0.13, which resulted in the same S_{MAX} for each survey area of 7.53 redds·km^{-1}. When transformed relative to the survey area, Whale Creek had the highest S_{MAX} (rounded to the nearest whole number) of 85 redds compared to north fork Coal Creek with an S_{MAX} of 29 redds (Fig. 3; Table 2). This contrast in S_{MAX} when transformed to total survey area increases proportionately with the total survey area length (Tables 1 & 2). Goat, Lion, and Squeezer Creeks had the highest percentages of years where the number of redds surveyed exceeded the maximum recruitment benchmark (36%, 56%, and 66%, respectively), whereas Big, South Fork Coal, and north fork Coal Creek had the lowest percentages (7%, 4%, 0%, respectively; Fig. 4). Only Lion Creek had no years where the number of redds were below the precautionary benchmark, and Goat, Squeezer, Whale, Granite, and Ole Creeks stayed above the precautionary benchmark 95% of years or more (Fig. 4). However, 49% of years in Coal Creek and 52% of years in South Fork Coal Creek had redds below the precautionary benchmark (Fig. 4).

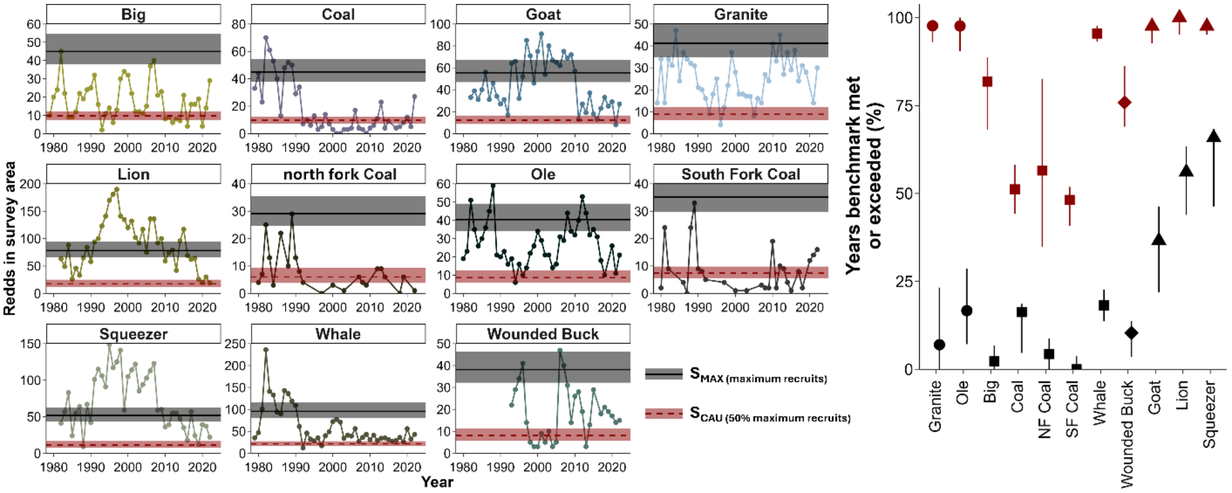

Figure 4. Left: Timeseries of observed bull trout (*Salvelinus confluentus*) redd counts completed by Montana Fish, Wildlife & Parks in Swan and Flathead River basins, Montana, U.S.A, where each panel represents a different survey area. Black, solid line represents the transformed, estimated redd count within survey area that produces maximum recruitment with shaded area representing 80% credible interval (CI), derived from the Ricker spawner-recruit relationship (β^{-1}; S_{MAX}). Red, dashed line represents 50% of the transformed, estimated redd count within survey area that produces maximum recruitment with shaded area representing 80% CI, derived from the Ricker spawner-recruit relationship ($0.5*\beta^{-1}$; S_{CAU}). Right: percentage of years the benchmark was met or exceeded for S_{MAX} (black; point is median, bars are 80% CI) and S_{CAU} (red; point is median, bars are 80% CI). Point shape represents subbasin (circle: Middle Fork Flathead, square: North Fork Flathead, diamond: South Fork Flathead, triangle: Swan Lake). SF= South Fork, NF= north fork. Montana Fish, Wildlife & Parks identifies a sampling site in Coal Creek as "north fork" Coal Creek.

Conclusions

With this work, we demonstrate that understanding the relationship between breeding adults and recruits can provide vital information needed to conserve threatened species. Long-term data from 11 populations of bull trout in the Flathead River drainage revealed spawner-recruitment relationships (as measured by redd densities and age-1 densities) with no evidence to support the influence of environmental disturbances included in this study (i.e., summer streamflow, winter flooding, August air temperature, percentage of fine sediment in substrate) on recruitment productivity. Differences in recruitment productivity did exist for some populations within the same subbasin and for two populations not sharing a subbasin, indicating source-sink dynamics (Carroll, 1994; McCullough, 1996) common in metapopulation structure. Furthermore, populations within subbasins exhibited consistency regarding meeting or exceeding biological benchmarks derived from spawner-recruitment relationships. Redd counts from one subbasin (North Fork Flathead River) were consistently below the maximum and precautionary recruitment benchmarks. Using spawner-recruitment relationships to understand the capacity of at-risk species to exhibit compensation (i.e., ability to respond to population declines) and overcompensation at large population sizes is essential for evaluating harvest rates and estimating recovery targets (Pine III et al., 2013; Walters & Martell, 2004).

Spawner-recruitment relationship

For populations investigated in the Flathead River drainage, bull trout appear to have strong recovery potential via recruitment at low adult abundances (i.e., compensation), as evidenced by the productivity parameter of the Ricker spawner-recruit relationship. The apparent compensation (i.e., compensatory reserve; Christensen & Goodyear, 1988) is supported by estimation of compensation ratios in other bull trout populations (Chudnow et al., 2019), as well as recovery of populations after reduced harvest (Erhardt & Scarnecchia, 2014; Johnston et al., 2007). Only populations (Goat, Lion, and Squeezer Creeks) from one subbasin (Swan Lake) contained enough contrast in spawning stock abundance to show clear overcompensatory recruitment dynamics at high spawner abundances consistent with the Ricker function. Despite the median timeseries being 25 years, populations generally included only data for small spawning stock abundances, which adds uncertainty in estimating the true spawner-recruitment relationship (Hilborn & Walters, 1992). However, bull trout have been shown to exhibit overcompensation, where high spawning biomass resulted in decreased recruitment (Johnston et al., 2007). This evidence of overcompensation suggests that bull trout recovery may be limited by habitat quantity or quality, which is consistent with the complex life history needs of the species and responses to anthropogenic habitat alterations (Haas & McPhail, 1991; Hagen & Decker, 2011; Post & Johnston, 2002).

Environmental drivers

Clear evidence exists for the environmental drivers we chose to influence bull trout (Al-Chokhachy et al., 2016; Bell et al., 2021; Dunham et al., 2003; Thurow, 1997, among others); however, these covariates did not have an influence on recruitment productivity. The possibility exists that the bull trout populations included in this analysis can compensate when the environmental drivers we included fluctuate beyond the average conditions. For example, redd formation inherently cleans substrate of fine sediment (Chapman, 1988), and fish spawning in areas with high fine sediment loads compensate by building larger redds and depositing eggs at shallower depths (compared to those areas with low fine sediment loads; Everest et al., 1987). Adaptations in behavior may explain the resilience to environmental drivers included but environmental events extreme enough to cause effect may also not be present in our timeseries.

The lack of environmental influence on the productivity parameter may be due to the absence of contrast or extreme instances, in magnitude, frequency, or both, within our covariate datasets (e.g., Johnston et al., 2007). For instance, we planned to investigate the influence of brook trout (*Salvelinus fontinalis*) on recruitment productivity, as brook trout are known to negatively influence bull trout (Rieman et al., 2006; Warnock & Rasmussen, 2013); however, only three bull trout populations included in this study live in sympatry with brook trout, all in the same subbasin (Swan Lake). Therefore, we did not have enough contrast among subbasins to understand whether an influence of brook trout existed. One environmental covariate did exceed clear thresholds that have been shown to negatively influence bull trout, such as fine sediment (Shepard, Leathe, et al., 1984; Weaver & Fraley, 1991). However underlying geology of the area generally produces relatively low fine sediment levels compared to other geologies (Sugden & Woods, 2007), which was reflected in the fine sediment timeseries. However, many environmental drivers do not have a specific threshold at which bull trout may be affected.

The lack of environmental influence on bull trout productivity was unexpected; however, absence of environment-recruitment relationships is a common phenomenon (Gross & Hoenig, 2025; Matte et al., 2024). For example, "poor recruitment paradigm" suggests that outside the extreme range of a variable (i.e., lethal; Gross et al., 2022) that environmental variables may have little influence on recruitment. Additionally, shifting climate regimes cause some variables (e.g., temperature, hydrology) to reach extreme values that have rarely been observed (Chandrapavan et al., 2019; Oliver et al., 2021; Plumlee et al., 2024) or prevent data from being collected during the extremes (Briggs et al., 2024). Instances of extreme environmental events have been shown to influence recruitment of cold-water fishes when present multiple times within a dataset (Glassic & Gaeta, 2019, 2020), but the frequency and magnitude of extreme events within our dataset was low (Figs. S3-S6). Not having an environmental influence on recruitment productivity could be benefit resource managers because current tools cannot address these environmental covariates, and bull trout are a threatened species in need of conservation with clear recovery goals (US Fish and Wildlife Service, 2015).

Biological reference points

Biological reference points from spawner-recruitment models have largely been adopted for optimizing harvest (i.e., maximum sustainable yield; Hilborn & Walters, 1992) or as a precautionary approach to fisheries management (Serchuk et al., 1999). Here, we derived biological reference points from the spawner-recruitment model that could be used as recovery objectives instead of harvest objectives, which is generally uncommon in fisheries conservation (but refer to Pine III et al., 2013; Walters & Martell, 2004) and a novel approach for the conservation of bull trout. The simple reference points of S_{MAX} and S_{CAU} for these populations provide a framework to support bull trout conservation policy with an emphasis on biological relationships in addition to objectives relating to historical dynamics (Brewin, 2004; U.S. Fish and Wildlife Service, 2008). With these reference points, declines or recovery of bull trout can be better anticipated, and the cost and effect of management actions on meeting recovery goals can be evaluated (e.g., Glassic et al., 2024; Koel et al., 2019). The implementation of bull trout reference points derived here can be used to establish the baseline amount of effort needed to suppress lake trout *Salvelinus namaycush* in Swan Lake, Montana, U.S.A. (Cox et al., 2013; Fredenberg & Rosenthal, 2018; Rosenthal & Fredenberg, 2017; Scott, 2024) and could subsequently be used to understand the efficacy of that program in meeting bull trout recovery goals. Furthermore, as additional years of data are collected, refinement of the benchmarks can result in more efficiency and cost efficacy in the recovery of the species.

Data availability statement: At the time of publication, data were not publicly available from Montana Fish, Wildlife & Parks.

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Supplementary material

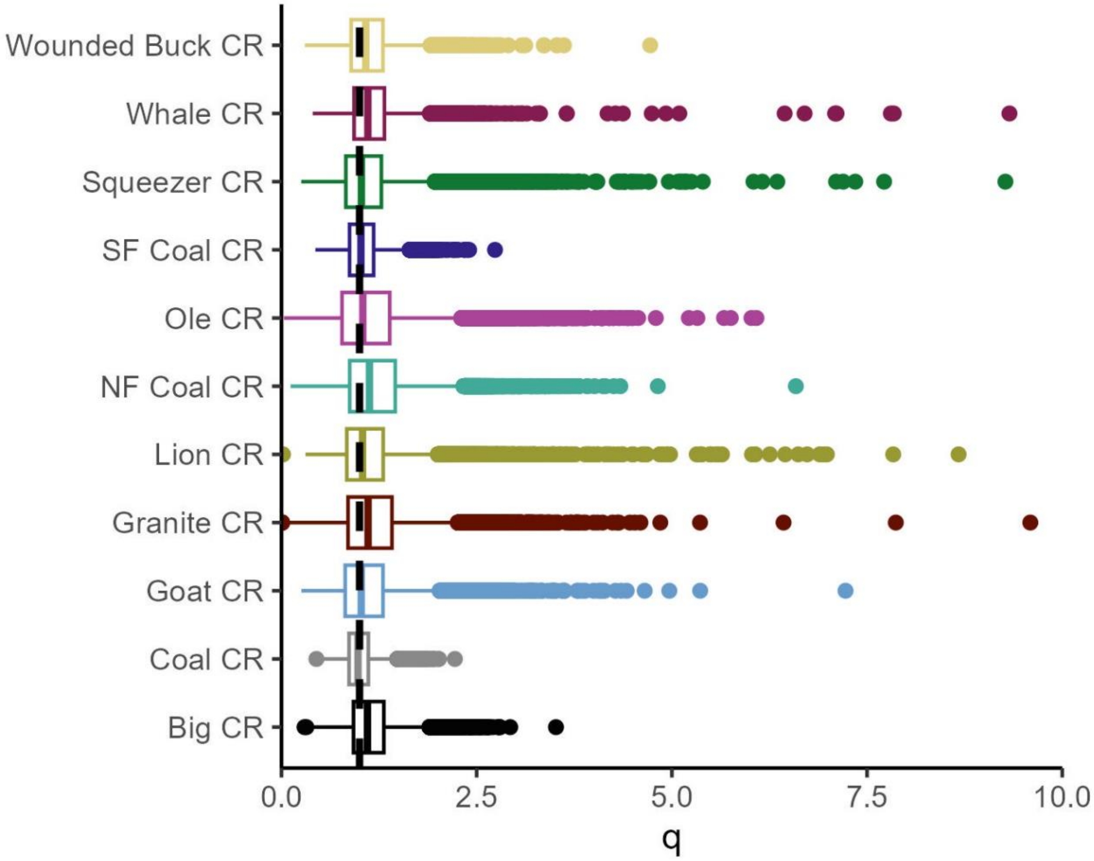

Figure S1. Beverton-Holt model parameter value, *q*, which determines the depensation tendencies (depensation at $q < 1$) of spawner-recruitment relationships for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations/populations in the Flathead River drainage of northwestern Montana, U.S.A. Black dashed line represents $q=1$. SF= South Fork, NF= north fork, CR = Creek. Box represents interquartile range, line is median, whiskers are 1st and 3rd quartile * 1.5, points are outliers.

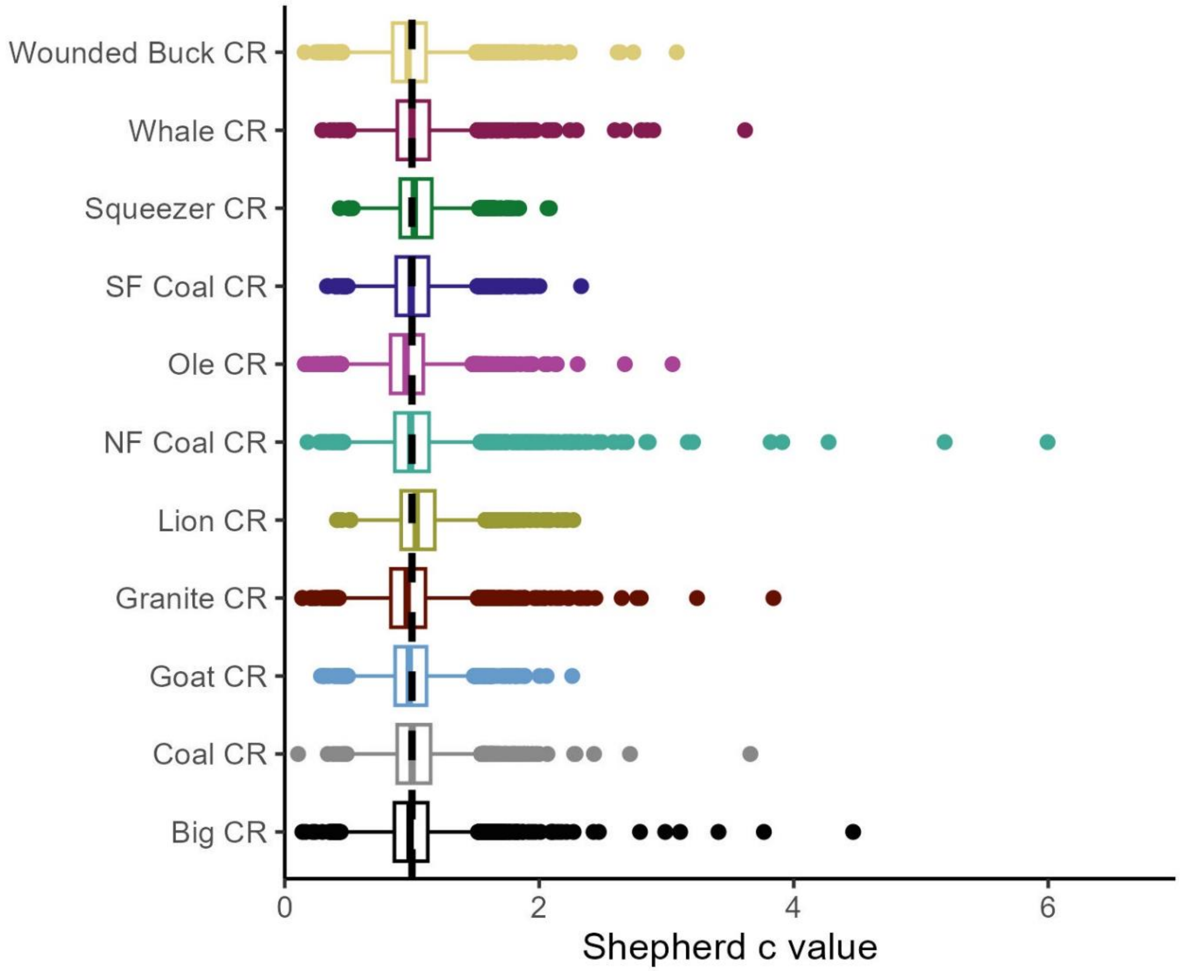

Figure S2. Shepherd model parameter value, c, which determines the overcompensatory tendencies of spawner-recruitment relationships for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations/populations in the Flathead River drainage of northwestern Montana, U.S.A. SF= South Fork, NF= north fork, CR=creek. The dashed line represents c = 1. Box represents interquartile range, line is median, whiskers are 1st and 3rd quartile * 1.5, points are outliers.

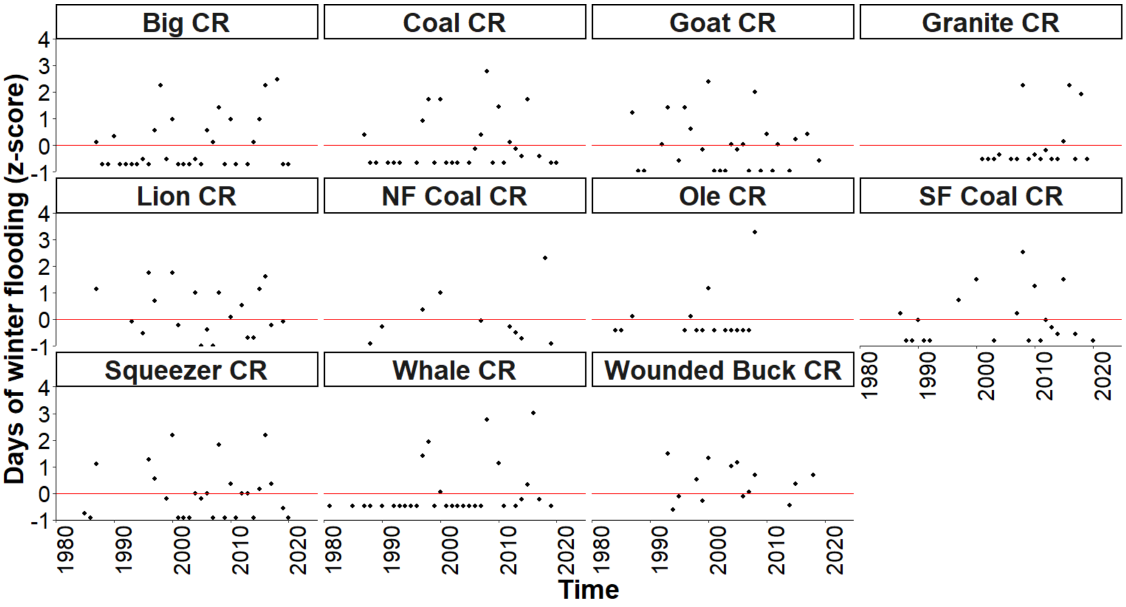

Figure S3. Z-scored days of winter flooding (the number of days that exceeded the 95th percentile days of annual streamflow DOY > 305 | DOY < 91) for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations in the Flathead River drainage of northwestern Montana, U.S.A. Each point is an observation and the red line = z-score of 0. SF= South Fork, NF= north fork, CR=creek. Streamflow data were modeled by Hoylman et al. (2025).

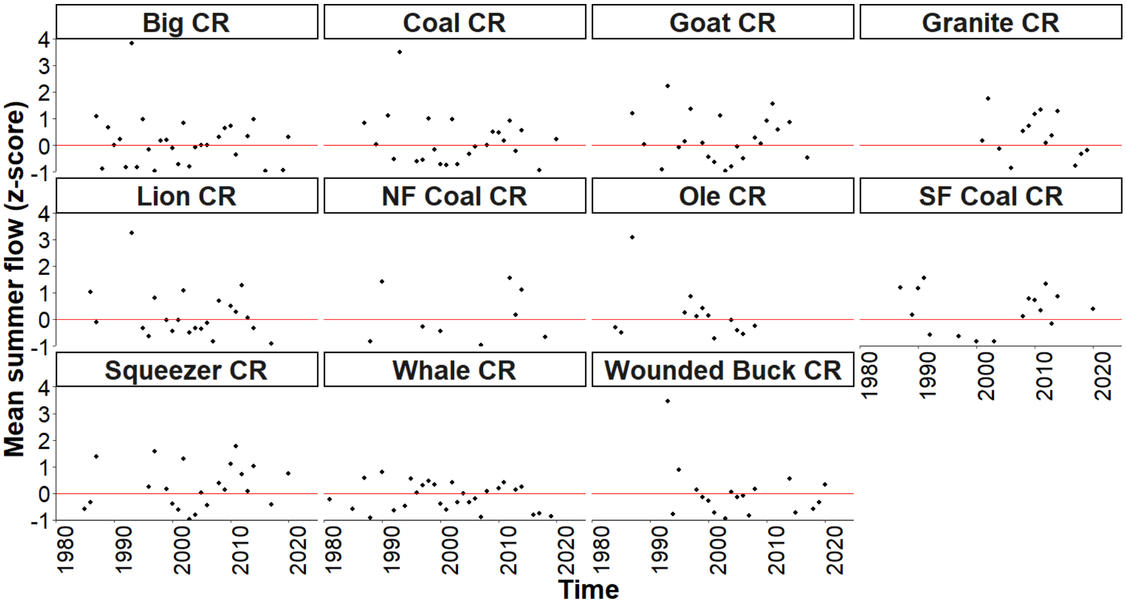

Figure S4. Z-scored days of annual mean summer streamflow (DOY=day of year; DOY > 196, DOY < 245) for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations in the Flathead River drainage of northwestern Montana, U.S.A. Each point is an observation and the red line = z-score of 0. SF= South Fork, NF= north fork, CR = creek. Streamflow data were modeled by Hoylman et al. (2025).

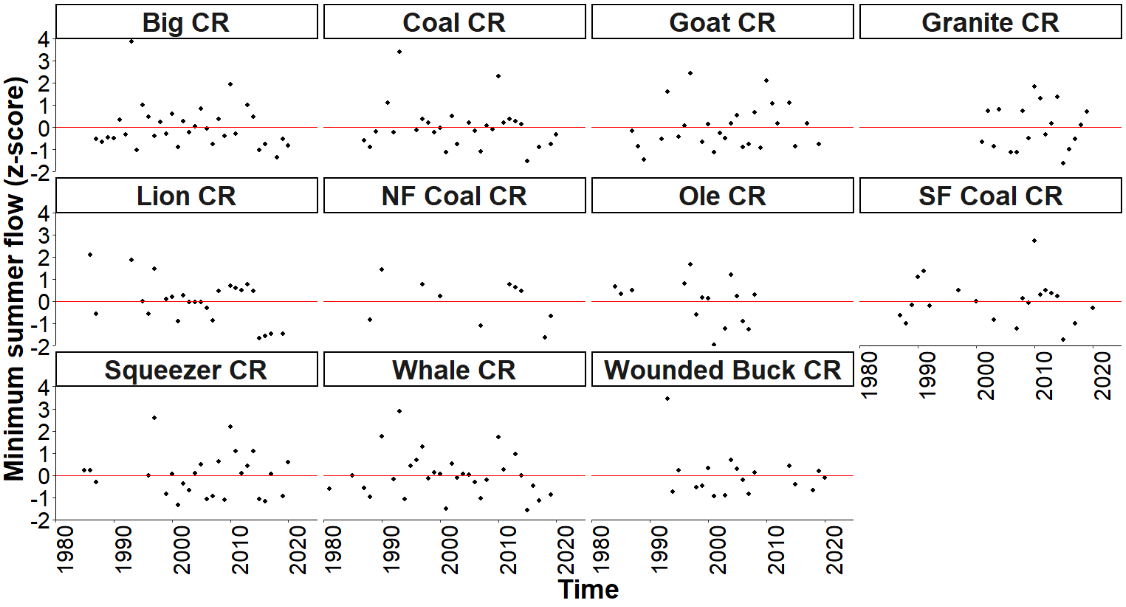

Figure S5. Z-scored days of annual minimum summer streamflow (DOY=day of year; DOY > 196, DOY < 245) for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations in the Flathead River drainage of northwestern Montana, U.S.A. Each point is an observation and the red line = z-score of 0. SF= South Fork, NF= north fork, CR = Creek. Streamflow data were modeled by Hoylman et al. (2025).

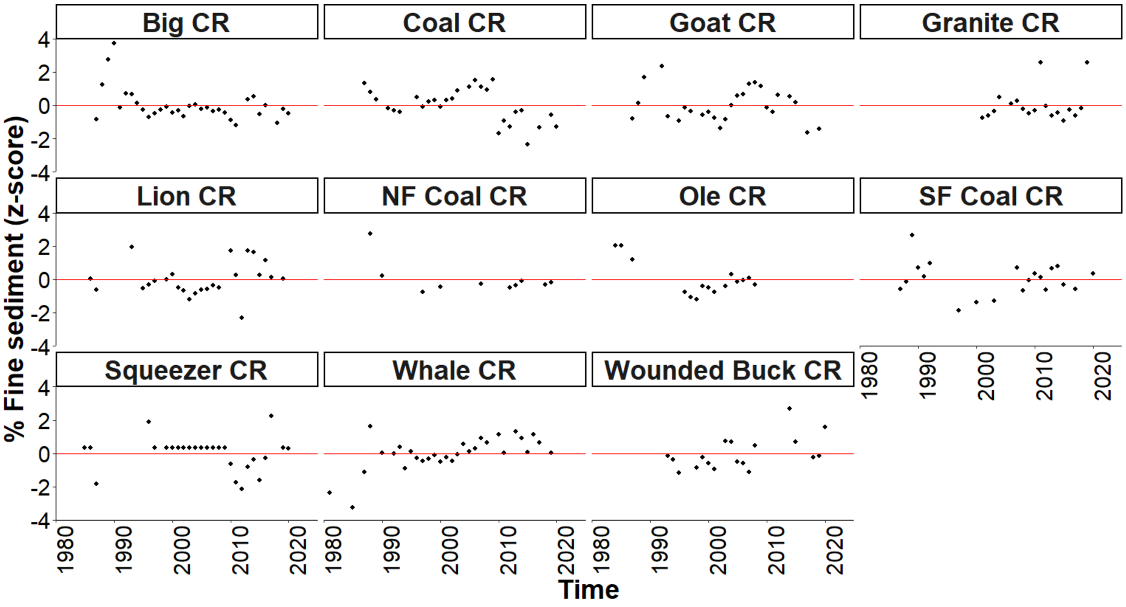

Figure S6. Z-scored % of fine sediment (<6.35 mm) from sampled sediment cores at bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations in the Flathead River drainage of northwestern Montana, U.S.A. Each point is an observation and the red line = z-score of 0. SF= South Fork, NF= north fork, CR = Creek. Fine sediment data were collected by Montana Fish, Wildlife & Parks.

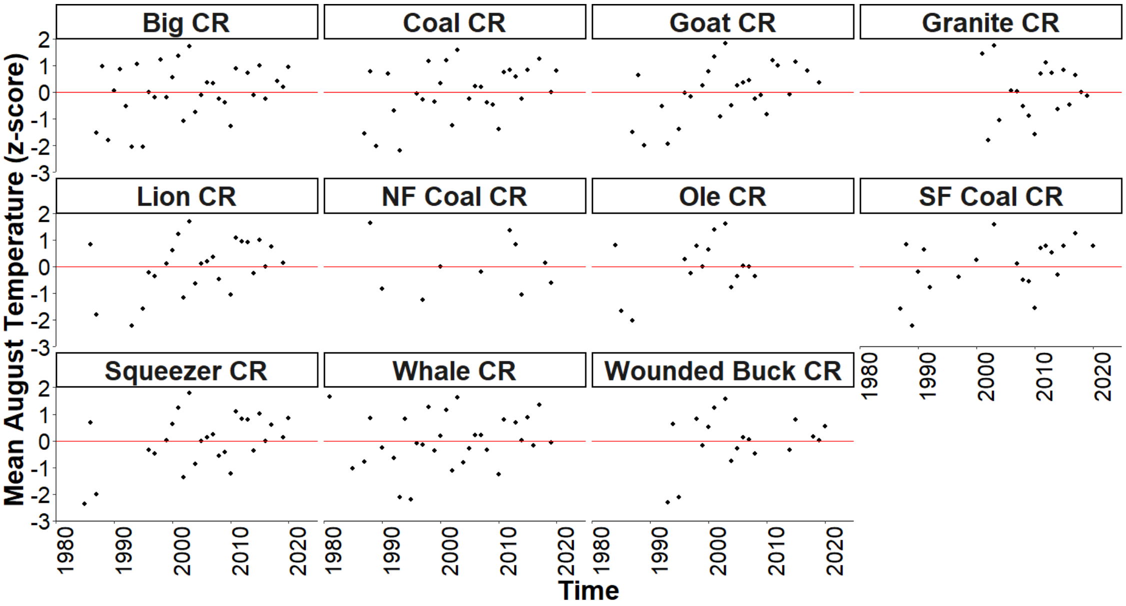

Figure S7. Z-scored days of annual mean August temperature for bull trout (*Salvelinus confluentus*) redd and age-1 sampling locations in the Flathead River drainage of northwestern Montana, U.S.A. Each point is an observation and the red line = z-score of 0. SF= South Fork, NF= north fork, CR = Creek. Temperature data from Daymet (Thornton et al., 2016).

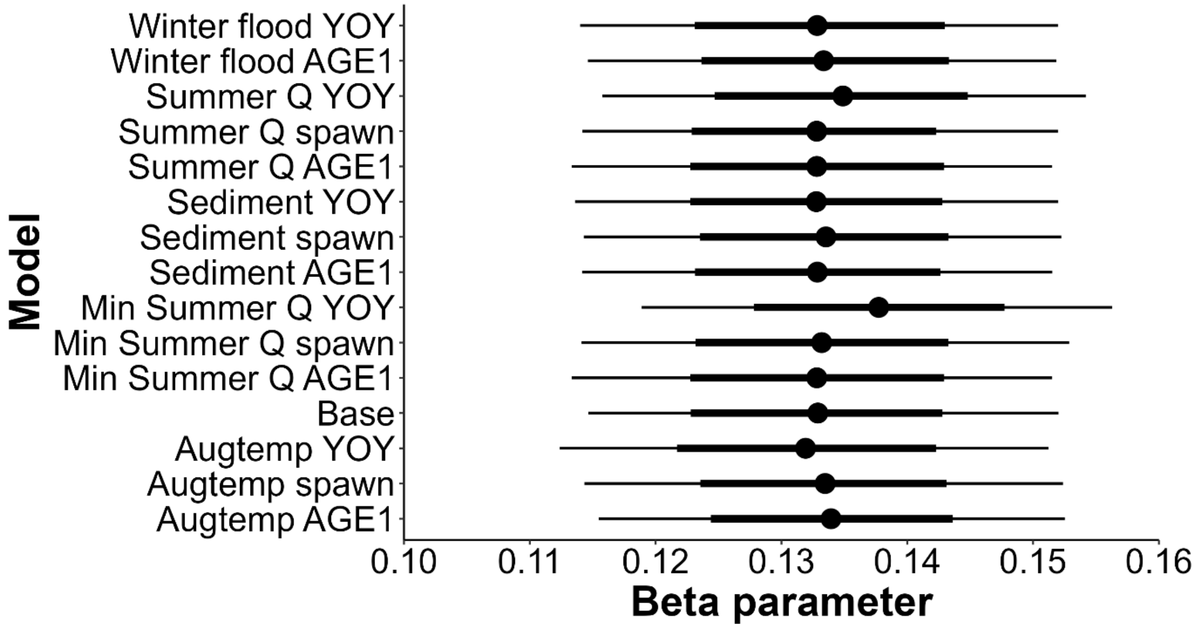

Figure S8. Comparison of the complete overcompensatory parameter estimate (β) for bull trout (*Salvelinus confluentus*) spawner-recruitment models in the Flathead River drainage, Montana, U.S.A. Point is mean, thick line is 50% credible interval, thin line is 80% credible interval. YOY = young-of-year. AGE1 = age-1 year. Spawn = spawn year. Q = streamflow. Summer Q = average summer streamflow (DOY=day of year; DOY > 196, DOY < 245). Winter flood = frequency of high winter flow events; the number of days that exceeded the 95th percentile days of annual streamflow DOY > 305 | DOY < 91. Sediment = median percentage of material smaller than 6.35 mm in each set of core substrate samples (n=12). Base = base model without any covariates. Augtemp = mean August temperature.

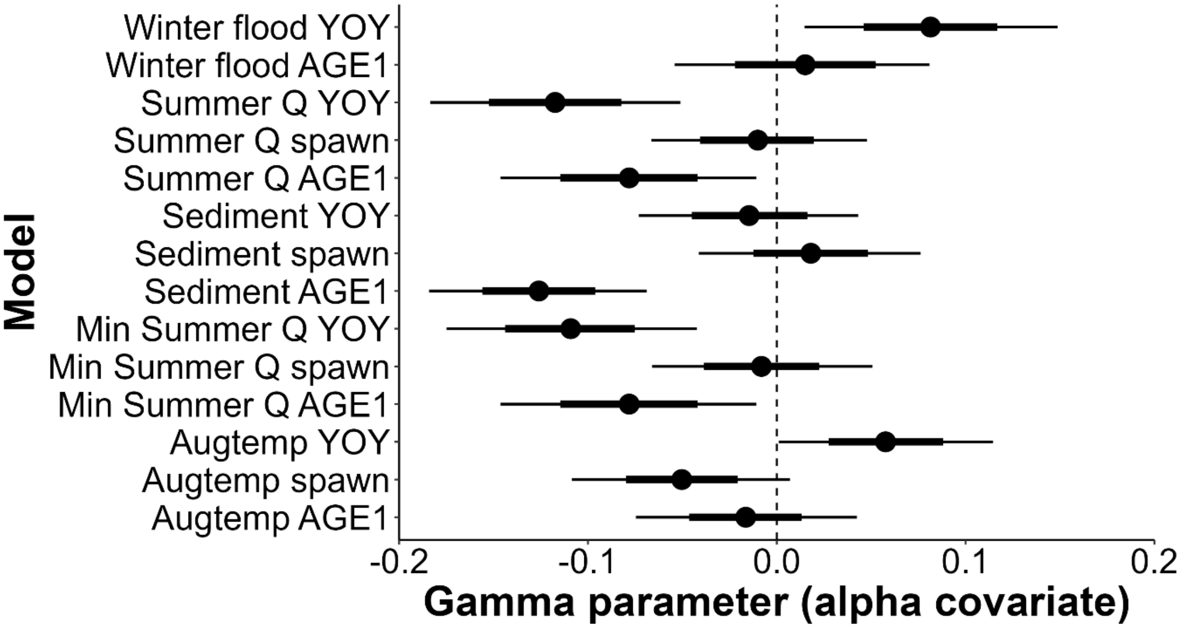

Figure S9. Comparison of the covariate effect (Gamma, γ) on the productivity parameter (alpha) bull trout (*Salvelinus confluentus*) spawner-recruitment models in the Flathead River drainage, Montana, U.S.A. Point is mean, thick line is 50% credible interval, thin line is 80% credible interval. YOY = young-of-year. AGE1 = age-1 year. Spawn = spawn year. Q = streamflow. Summer Q = average summer streamflow (DOY=day of year; DOY > 196, DOY < 245). Winter flood = frequency of high winter flow events; the number of days that exceeded the 95th percentile days of annual streamflow DOY > 305 | DOY < 91. Sediment = median percentage of material smaller than 6.35 mm in each set of core substrate samples (n=12). Base = base model without any covariates. Augtemp = mean August temperature.

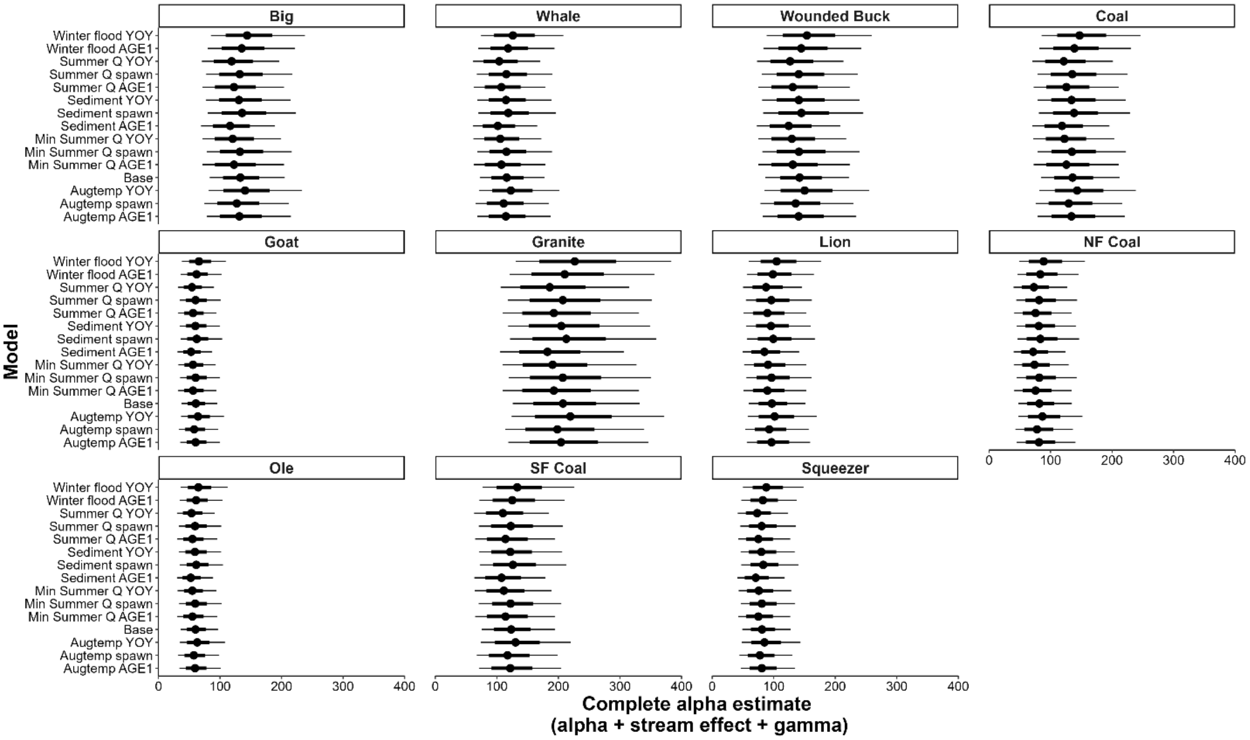

Figure S10. Comparison of the complete productivity parameter estimate (α) for different bull trout (*Salvelinus confluentus*) spawner-recruitment models, where each panel represents a different survey area/population in the Flathead River drainage, Montana, U.S.A. Gamma is the covariate effect on the productivity parameter. Stream effect represents variability across different survey areas. Point is mean, thick line is 50% credible interval, thin line is 80% credible interval. YOY = young-of-year. AGE1 = age-1 year. Spawn = spawn year. Q = streamflow. Summer Q = average summer streamflow (DOY=day of year; DOY > 196, DOY < 245). Winter flood = frequency of high winter flow events; the number of days that exceeded the 95th percentile days of annual streamflow DOY > 305 | DOY < 91. Sediment = median percentage of material smaller than 6.35 mm in each set of core substrate samples (n=12). Base = base model without any covariates. Augtemp = mean August temperature. Estimate is shown when the gamma effect is +3 standard deviations above the mean for each environmental influence modelled. SF= South Fork, NF= north fork.