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ABSTRACT

We describe an age-stage structured life history model that can be fit to historical escapement and Coded Wire Tag (CWT) data from Chinook Salmon stocks. The model uses a state space implementation of a statistical catch-at-age approach to estimate time-varying freshwater and marine natural mortality, maturation, and fishing mortality rates. A freshwater Ricker stock-recruitment model is used to predict egg-smolt mortality rate. This relationship is informed by escapement and CWT recovery data. Marine survival varies by age and over time and is predicted from mixed effect models which include factors such as harbour seal abundance and sea surface water temperature. The model also estimates age-specific vulnerability to fishing and time-varying age-specific maturation rates. The model relies on the same 'gorilla' assumption using in the management of Chinook Salmon by the Pacific Salmon Commission, that trends in marine mortality, maturation, and exploitation rates for hatchery indicator stocks are representative of natural stocks. This assumption allows prediction of marine mortality, maturation, and exploitation rates for naturally-produced smolts, thus informing estimates of freshwater Ricker stock-recruitment parameters and annual deviations.

The model provided excellent fits to escapement and CWT data from five Chinook Salmon stocks from the East Coast of Vancouver Island (Cowichan, Qualicum, Puntledge summer run, Puntledge fall run, and Quinsam). Annual mortality rate of age 1 fish was highly variable over the modelled 1980-2020 period. Estimates of the time-varying proportion of fish maturing by age showed an increase in age 2, age 3, and/or age4 proportions starting in the early 1990's for Cowichan, Puntledge fall, and Quinsam stocks Most parameters were well determined. There was a positive effect of sea lion and resident killer whale abundance on age 2 and older mortality rates. The direction of fixed effects on age 1 mortality appeared realistic; mortality rate increased with seal abundance and the total number of hatchery smolts released into the Strait of Georgia. Oceanographic effects on age 1 mortality, indexed by temperatures in the Strait of Georgia, were relatively weak compared to these other factors. These fixed effects on age 1 ocean mortality explained a substantive amount of interannual variation in mortality rates for the Cowichan River stock (0.66), but substantively less for other stocks (0.18-0.32). The unfished equilibrium escapement was poorly determined from the data and was largely driven by

the assumed prior distribution. Thus, the extent to which escapement will increase under improved survival conditions predicted by the model is highly uncertain.

After fitting to historical data, the model can be used to simulate future abundance patterns under alternative policy choices for freshwater habitat enhancement, hatchery production, exploitation, and management of marine mammal populations. The model advances our ability to evaluate potential causes of variation in stock productivity over time, and should be helpful for quantitative elements of Chinook Salmon Recovery Potential Assessments.

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We thank Steve Baillie for compiling the CWT data, and Kevin Pellet for providing key insights and estimates about life cycle mortality patterns. Wilf Luedke and Eric Rechisky identified the need to develop an improved model for Recovery Potential Assessments for Chinook Salmon.

1.0 Introduction

Recent analyses of chinook population dynamics data (Nelson et al. 2018, Weir et al. 2022, Doutaz et al. 2022) have attempted to use classic Ricker stock recruitment theory to assess changes in productivity and management reference points. This approach attempts to relate observed recruitments measured as catch plus escapement to the spawning abundances that produced those recruitments, as we would do for species like sockeye where both catches and escapements are measured directly. As noted by Cunningham et al. (2018), this approach can underestimate uncertainty in recruitment for chinook salmon because the fish are caught by ocean fisheries and mature (and are caught by terminal fisheries) at multiple ages with different sizes/fecundities. Typically, the classic VPA-approach is needed to estimate the catch component of total recruitment. The data we actually have to estimate recruitment for chinook salmon are observations of spawning stock (escapement) and recovery rates of known numbers of fish CWT-tagged as smolts in fishery catches and in the escapement. Ideally, stock-recruitment models should be fit directly to the available data to account for the uncertainty in recruitment, but also to take advantage of information on marine survival rates, exploitation rates, and maturation rates from the CWT data.

This report describes an age-stage structured life history model that can be fit to escapement and CWT data for Chinook Salmon stocks. The model follows the general statistical catch-at-age approach first applied to Chinook Salmon by Cunningham et al. (2018). It estimates changes in both freshwater and marine natural mortality rates, and fishing mortality rates over time. The model is fit to data using the same basic state space approaches used for fitting age-structured fish population models in general (Staton et al. 2017; Connors et al. 2020), and reference points can be calculated that explicitly account for effects of changing age composition (and hence mean fecundity) due to changes in fishing and other mortality factors (Ohlberger et al. 2018; Xu et al. 2020, Manishin et al. 2021). A key part of this approach is to express mortality rates as competing instantaneous rates for each stage-age, so as to avoid incorrect estimation of changes in total mortality rates when fish are simultaneously being killed by multiple mortality agents. Further, after fitting to historical data, the model can be used to predict future abundance patterns under alternative policy choices and possible patterns of future recruitment anomalies. This avoids using a two-step process where a stock-recruitment model is fit to data and parameter estimates from that model are then passed to an age-structured forward simulation model. Predictions from this two-step procedure might not in fact be consistent with the historical data if run as a retrospective simulation.

2.0 Model Description

2.1 Basic age-structure accounting

The basic stage-age structured model predicts numbers alive by age and year (late spring) for a single Chinook Salmon stock, along with catches and numbers of fish maturing and surviving to spawn at each age. For each year *t*, the number of naturally produced ocean-age 1 smolts (N[age=1, t]) is first predicted from the numbers of eggs laid the previous fall (E[t-1]),

(1) $$N[1,t])=E[t-1]\cdot\exp(-MES[t-1]) + \mathbf{HatchSmolt[t]}\cdot\mathbf{HatchSurv},$$

where MES[t-1] is the total natural egg-smolt mortality rate for fish spawning in year *t-1*, HatchSmolt is the total number of smolts from a hatchery that are released (regardless of whether they were given a Coded Wire Tag (CWT) or not), and HatchSurv is the survival rate those fish experience shortly after release (Table 1). In eqn. 1 and those that follow, bolded symbols denote model variables which are fixed at predefined values and not estimated (i.e., constants). Then for each ocean age 2…5, early summer abundance is predicted over time as,

2) $$N[a+1,t+1]=N[a,t]\cdot\exp(-v[a]\cdot F[t]-M[a,t])\cdot(1-mat[a,t]),$$

where v[a] is vulnerability of age *a* fish to total fishing mortality rate F[t], M[a,t] is annual natural mortality rate of age *a* fish in year *t*, and mat[a,t] is the proportion of fish maturing at age *a* in year *t* (Table 1). Age-specific vulnerabilities are assumed to be constant over time and are estimated in logit space based on uninformative normal priors with means defined in Table 1 and standard deviations set to twice the value of the means (i.e., CV=2, logit_vul[] in Table 2).

The annual instantaneous fishing rate F[t] is calculated from,

3) $$F[t] = Fbase\cdot\mathbf{RelRegF[t]}+wf[t],$$

where Fbase is the estimated base fishing mortality rate prior to the start of the modelled period which beings in 1980 (Table 2), RelRegF are assumed 0-1 scaling factors that determine how much Fbase varies over years (Table 3), and wf's are estimated annual random effects on fishing mortality that are drawn from a zero-centered normal distribution with estimated standard deviation wf_sd (Table 2). In data rich situations when annual CWT recoveries for the entire modelled time series are available, annual fishing mortality rates can be determined based on estimates of Fbase and wf only. However, in most cases there are large gaps in CWT time series, especially for early years of the estimation. Fishing mortality rate is not estimable for such portions of the time series, and hypotheses of changes in fishing mortality rate (Fbase·RelRegF) are needed. Note RelRegF can be well-defined using by smoothing annual exploitation rate estimates for southern BC index stocks available in annual Pacific Salmon Commission Technical Reports. In data rich situations with a sufficient CWT recovery time series, RelRegF can be set to one for all years so that estimates of F are not influenced by a regional fishing mortality rate trend. Note that the interpretation of wf's depend on how RelRegF is set. If all values of RelRegF are one, then wf's represent the annual deviations in F from a single mean estimate of the average fishing mortality rate defined by Fbase. Alternatively, if RelRegF varies over time, then wf's represent the annual deviations from the long-term trend defined by Fbase·RelRegF[t].

The instantaneous natural mortality rate in the ocean, M[a,t], varies by age and over time. Some chinook populations have shown evidence of progressive or persistent changes in these M's, at least for the first ocean year, and the net effect of such changes has been estimated either by treating the Ricker "a" parameter as slowly changing over time (e.g. Wor and Velez-Espino Appendix I in Doutar et al. 2021), or by explicitly modeling changes in mortality rates as functions of known mortality factors (e.g. seal predation by Nelson et al. 2019). We argue that species at risk recovery potential assessments this model is intended to support, should try to assess possible impacts of known stress factors that have changed over recent years, by modeling at least the first-order (linear) effects of such stressors. Suppose we have time series estimates of relative levels or values of a set s=1…n stressors, measured as "observed" values X[s, t]. This set might include known changes in sea-surface temperatures, and abundances of known marine mammal predators on chinooks (seals, sea lions, Northern resident killer whales). Given any such stressor time series set, we model changes in M[a,t] as,

4) $$M[a,t] = Mo[a] + \sum_{s=1}^{s=n} Mx[s] \cdot \mathbf{vs[s,a]} \cdot \mathbf{X[s,t]} + wo[t].$$

Here Mo[a] is an estimated age-specific baseline (average historical) mortality rate determined by factors that are not expected to change over time (Table 1). Two values for Mo are estimated, one for age 1 fish and another for ages 2 and older fish. Mx[s] is the estimated effect of a unit change in X[s,t] on mortality rate of age *a* fish that have relative vulnerability vs[s,a] to factor *s* (Table 2, with Mx referring to Mseal, Mtemp, Mhatch, and Mbig). We assume the relative vulnerabilities vs[s,a] to be known, and most often to be either 0 or 1 depending on whether age a stock is vulnerable to mortality agent *s*. Note that if the X[s,t] are scaled so as to have maximum value 1.0 (e.g. by dividing seal abundance by the historical maximum abundance), then estimate values of bo[s] represent the maximum increase in mortality rate over the modelled period caused by mortality factor *s*. The current model structure assumes seals, water temperature, and hatchery smolt abundance can effect age 1 mortality rates and predation by Steller sea lions and Northern resident killer whales can effect age 2 and older mortality (Scordino et al. 2022; Chasco et al. 2017). wo[t]'s are annual random effects on ocean mortality, which are only applied to age 1 fish. These effects are drawn from a zero-centered normal distribution with estimated standard deviation wo_sd (Table 2). The random effects allow variation in mortality rate over time due to factors other than the fixed additive effects Mx[s]·X[s,t].

Importantly, eqn. 4 is a "competing risks" model for mortality, where each mortality factor is assumed to independently kill age *a* animals. This basic assumption of additivity in mortality rate components may well be violated if risk factors interact in complex ways; for example Walters and Christensen (2019) show how increases in first ocean year chinook mortality that are apparently explained by increases in seal abundance could in fact be due at least partly to increases in temperature that make juvenile chinooks more vulnerable to seal predation (e.g. by increasing disease incidence rates or time spent foraging when metabolic rates increase with temperature).

Maturation rates (mat[a,t] in eqn. 2) are allowed to vary by age and over time. Time variation is required to model trends showing an increase in the proportion of younger ages in catch and escapement resulting from early maturation, perhaps due to changes in ocean conditions, impacts of hatchery breeding practices, or fishing. Annual age-specific base maturation rates in logit space are assumed to be random variables from normal distributions with estimated means matb[a] and estimated age-specific standard deviations mat_sd[a] (Table 2). We assume that fish do not mature at age one (thus mat[a=1,t]=0) and that all fish age 6 will mature (thus mat[a=6,t]=1).

Catches (C[a,t]) and spawner abundance (S[a,t]) are predicted based on the abundance in the ocean, fishing and natural mortality rates, and maturation rates from,

5a) $C[a,t] = N[a,t]\cdot(1-\exp(-v[a]\cdot F[t]))$, and

5b) $S[a,t] = N[a,t]\cdot\exp(-v[a]\cdot F[t]-\mathbf{Msum})\cdot m[a,t]$,

where Msum is the natural mortality rate from early summer to arrival at the spawning grounds (marine+upstream migration natural mortality components aggregated, Table 1). Egg production in year *t* is predicted from the sum product of age-specific spawning numbers (S[a,t]), the mean fecundities per spawner (fec[a], Table 1), and the proportion of spawners not taken for broodstock (pwsp[t]) from,

6) $E[t]= \sum_{a=1}^{a=6} S[a\ \ t] \cdot \mathbf{fec[a]} \cdot \mathbf{pwsp[t]}$.

2.2 Ricker egg-smolt stock-recruitment relationship

The model uses a Ricker stock-recruitment relationship to predict annual smolt production as a function of the number of eggs deposited one year earlier, and annual non-density dependent deviations in egg-smolt mortality rate. The Ricker stock-recruitment model R=S·exp(a-b·S) was derived by assuming that natural mortality rate from egg to recruitment (smolts) increases linearly with spawner abundance (log(smolt/spawner)=a+b·Spawner). Note the density independent term of total mortality represents ‘a’ in the Ricker model and the dependent component is ‘b·S’. If we assume as did Cunninham et al. (2018) that this density dependence is concentrated in the egg-smolt period (due to competition for good spawning sites and density-driven mortality of fry when they are crowded in limited juvenile nursery areas), we can write the Ricker model for egg-smolt mortality rate MES[t] for spawning in year *t* as,

7) $$\text{MES}[t] = \text{MESmin}+(\text{MESo}-\text{MESmin})\cdot \text{E}[t]/\mathbf{Eo} + \text{wfw}[t],$$

where MESmin is the minimum mortality rate that occurs when egg deposition (E[t]) is close to 0 (no density effects), and MESo is the average mortality rate for an unfished population that on average has total egg deposition Eo. Hilborn and Walters (2021) note that the decrease in natural mortality rate as stock size is reduced from its natural level (at egg deposition Eo) to near 0 (MESo-MESmin), is actually just the standard Ricker 'a' parameter (the log of the compensation ratio CR), and is typically around 0.2MESo. For the Cowichan River chinook stock, application of eqn.7 implies an egg-smolt survival rate of around 2.5% for the unfished population, increasing to around 13% at low population sizes given a Ricker 'a' near 2.0. The model also includes annual random effects on egg-smolt mortality rate (wfw[t]) that are assumed to be random variables drawn from a zero-centered normal distribution with estimated standard deviation wfw_sd (Table 2). Note these random effects are added to the density independent component of the model.

2.3 Initialization

MESo is calculated as -log(1/EPSo), where EPSo is the average annual number of eggs produced per smolt (recruit) for an unfished population at equilibrium. The one in numerator represents 1 smolt, so dividing one smolt by the number of eggs required to produce it is the egg-smolt mortality rate. EPSo is calculated from survivorship to age (L[a]), and base mortality and fecundity for each age,

8) $$\mathbf{EPSo} = \sum_{a=1}^{a=6} L[a] \cdot \mathbf{fec[a]} \cdot \text{Mo}[a] \cdot \exp\,(-\mathbf{Msum}),$$

where L[a] is unfished survivorship from smolts to age *a* prior to maturation calculated as,

9) $$\mathbf{L[1]}=1,\ \mathbf{L[a]} = \mathbf{L[a-1]}\cdot \exp(-\text{Mo}[a-1]\cdot[1-\text{matb}[a-1]) \text{ for } a>1.$$

Note in this calculation that survivorship to age L[a] is exactly the same as what Kevin Pellett (DFO, pers. comm.) has called the marine portion of his "survival curve" analyses of Cowichan chinook PIT tagging data, just scaled to start at 1 for smolts (L[1]=1) and including only baseline natural mortality rates; what the MESo calculation does is to "back up" from each 1 smolt to the number of eggs needed to produce that smolt in an unfished population with egg-smolt total mortality rate MESo.

The model estimates the log of the compensation ratio (cr) and the log of the unfished spawning stock size (log_so), and then transforms these values into the egg-smolt Ricker variables in eqn. 7. First, the unfished recruitment, ro (smolts at equilibrium) is calculated based on the ratio of the transformed estimated unfished spawning stock size (so) to the spawners per recruit at equilibrium (spro determined from eqn. 8 without the fecundity term). Unfished recruitment is then used to calculate the egg production at equilibrium Eo (Eo=recruits·eggs per recruit = ro·EPSo). The 'b' term in the ricker model, (MESo-MESmin)/Eo, is calculated from the cr to Eo ratio. Note that dividing cr by Eo puts the density dependent term (Ricker 'b') on the correct scale (the change in mortality per unit change in egg abundance). Finally, from eqn. 7, at equilibrium, egg deposition E[t]=Eo, thus E[t]/Eo=1. Under this condition MESmin + cr=MESo, and hence the 'a' term in the Ricker model (MESmin in eqn. 7) is calculated as MESmin=MESo-cr.

The state space model approach requires additional parameters that do not appear in standard stock-recruitment modeling, namely the initial numbers at age N[a,t=1] in the first model year. Not all of these parameters are estimable, so we need to make some simplifications. The simplest option is to assume that relative numbers at age were near equilibrium with respect to some historical average smolt abundance ro (N[a=1,t=1]) with numbers at older ages given by some assumed survivorship to age which includes an assumed average fishing mortality rate Fhist for five years prior to the first year of the estimation period (1980). The abundances by age in the first year are calculated using,

10a) N[1,t=1]=ro

10b) N[a+1,t=1]=N[a,t=1]·exp(-Mo[a-1]-v[a-1]·**Fhist**)·(1-matb[a-1])), a>1.

A "stronger" alternative would be to assume that ro (smolts produced at the unfished equilibrium) was also near equilibrium with respect to the historical average fishing mortality rate Fhis (Table 1). In that case we would set ro to the equilibrium smolt numbers predicted by the Ricker egg-smolt survival model,

11) ro=[ln(EPShist)-MESmin]/[EPShist*Mden]

where EPShist is the fished analog of EPSo above, but calculated with survivorships L(a) including fishing and maturation effects as in eqn. 10b and with density effect parameter Mden=(MESo-MESmin)/ Eo. However, this second alternative would ignore stochastic effects on abundance over the decade or so prior to *t*=1, a dangerous assumption. Thus, a third alternative would be to start the simulations with either of the above options, but 10-20 years before the first observations, e.g. starting at t=-10, then do multiple forward simulations with reasonable past recruitment anomalies wfw[t] and wo[t] so as to acknowledge considerable uncertainty about the N[a,1] values. And a fourth alternative would be to choose an ro value to exactly fit the first observed escapement (or average of the first few observations), while assuming the survivorship schedule implied by Fhis along with assumed vulnerability, maturation, and Msum values needed to predict spawners per smolt.

2.4 Model fitting approach

The model is fit to stock-specific data using a state space approach implemented in the Bayesian software package stan (Stan Development Team 2023). Model parameters are estimated by fitting to data from 1980 to 2020 (41 years). Projections can then be made for future years based on the estimated posterior distributions of parameter estimates, and alternate scenarios on fishing mortality and factors that potentially influence survival rates (see section 2.5). We fit the model separately to data from five Chinook Salmon stocks from the East Coast of Vancouver Island which include the Cowichan River (Cow), Qualicum River (Qual), Puntledge River Summer (Punt sum), Puntledge River Fall (Punt fal), and Quinsam River (Quin).

The model is fit to stock-specific data using three separate data likelihoods which include spawner abundance and CWT recoveries in catch and escapement. Observed spawner abundances for each year (obsS[t]) are compared to predicted spawner abundances S[t], which are simply the sum of the predicted spawner abundance by age (S[a,t] from eqn. 5b, Table 2).

We assume these observations have log-normally distributed observation error, with variances that depend on method of spawner estimation (fence counts, mark-recapture, visual survey). We estimate a single log spawner abundance observation error for the entire modelled period (lnS_sd) using a minimally informative prior (lnS_sd in Table 2). The spawner time series contain basic information on absolute stock scale (so) and also trends in total mortality rate, including information on unexplained egg-smolt mortality variation (wfw[t]).

The model is also fit to the estimated total CWT recoveries in catch and escapement in subsequent years. These recovery observations are assumed to be Poisson distributed, with predicted Poisson means dependent on the number of CWT-tagged smolts that are released an all the mortality, vulnerability, and maturation parameters used to predict numbers at age in the model (Table 2). Model predictions of CWT recoveries in catch and escapement are given by eqn.'s 5a and 5b, but with smolt numbers N[a=1,t] set to the number of CWT smolts released in year *t* after accounting for initial release mortality and other factors that lead to reduced survival rates of hatchery smolts (HatchSurv). The number of CWT recoveries provided by DFO were expanded values that accounted for different sampling rates among fisheries and in the escapement. Ideally, the CWT likelihoods would be based on unexpanded recoveries to properly account for the sampling error. To approximate the sampling error, model predictions of total CWT abundance in catch and escapement were reduced by an approximate aggregate sampling rate of 10% (Table 2). This adjustment leads to more realistic (higher) estimates of uncertainty and can have important effects on model fit and parameter uncertainty because it effects the eight given to the CWT likelihoods in the overall fitting process.

The model was run for 2000 iterations for each of three chains which was sufficient to achieve acceptable convergence, as assessed by the Gelman-Rubin convergence statistic (Gelman et. al., 2004, $\hat{r} < 1.05$). The model takes ~ 6 minutes to run per stock on a PC with an Intel i7 2.9 GHz processor. The short run time allows rapid evaluation of alternate data sets and parameter estimation assumptions.

We use Gelman and Pardoe's (2006) pseudo-R^2 statistic (pR^2) to evaluate the utility of the fixed effects for explaining interannual variation in age-1 ocean mortality. The statistic is calculated as one minus the ratio of variation in the mortality rate across all years due to random effects only, to the variation explained by both fixed and random effects (e.g., eqn. 4). If the fixed effects are a good predictor of mortality rate, the ratio will be lower and the pR^2 value will be higher. We also calculate Gelman and Pardoe's (2006) pooling statistic (λ) which quantifies the extent of statistical shrinkage (i.e., pooling) in random effects. If the data indicate that random effects on age-1 ocean mortality are well determined and highly variable across years, the extent of pooling will be low and λ will be low.

Source code for the estimation model (CHLM.stan) and supporting files (data preparation, setting up model, graphical R scripts to view predictions and data) are available at xx (https://www.dropbox.com/home/Ecometric%20Research%20Team%20Folder/CHLM). Details of the analysis used to develop the data and other input files and fixed parameters used by the mdoe are provided in Appendix A. Practical details for running the model are provided in appendix B.

2.5 Using the fitted model results for policy analysis

Projections of catch and escapement based on alternate future scenarios about fishing and natural mortality factors are based on posterior distributions of model parameters determined from the estimation model described above. The posterior distributions of model parameters are saved to stock-specific files .Rdata files at the end of the fitting process. The R script which does the projections reads in one of these stock-specific posterior distribution files. Code within the script allows users to adjust future conditions, such as a fixed harvest rate or the number of hatchery smolts released. Future scenarios can also be defined in .csv files (e.g., covariates.csv).The script then calculates future escapements and catches based on these user-defined scenarios and samples of parameter values drawn from the posterior distributions. Future projections therefore account for uncertainty in the estimated parameters.

In summary, the basic structure of the model is essentially the one used to project future Fraser River chinook abundances developed by Kendra Holt and Brooke Davis in Weir et al. (2022), i.e. a Ricker stock recruitment relationship linked to age structured survival and maturation equations. Our model can be used directly for projections without first doing a separate stock-recruitment fitting exercise, simply by propagating the equations over future years t under various assumptions about future fishing, recruitment anomalies, and possibly other management actions like reductions in marine mammal abundance. Also, by fitting then projecting from the end of the fits, we insure against inconsistencies in assumptions between separate analyses, i.e. we ensure that the Holt-Davis structure would fit the historical data if run in “retrospective” mode.

3.0 Results

The estimation model provided good fits to the data and realistic trends. Predicted escapements closely followed observed escapements and the predicted 95% credible interval almost always contained the observations (Fig. 1, upper panels). Egg-smolt stock recruitment models indicated relatively low productivity and modest density dependence (Fig. 1, lower panels). The prior on unfished escapement (log_so in Table 2) had a strong influence on this model parameter as there was little information in the data to inform it as is often the case in stock-recruit time series (Fig. 2). The model provided excellent fits to the expanded CWT recoveries in the catch and escapement (Fig. 3).

Annual mortality rate of age 1 fish was highly variable (Fig. 4, upper-right panel). Annual mortality anomalies for egg-smolt mortality (lower-left panel) and age 1 ocean mortality (lower-right panel) were also highly variable. Estimates of annual mortality anomalies were uncertain, but 95% credible intervals did not overlap during periods with very low or very high mortality. The range of egg-smolt annual mortality deviations were greater than those for age 1 ocean mortality, but note that the latter includes fixed effects (e.g., seal abundance, hatchery abundance), thus the annual deviations reflect factors that vary over years other than those caused by the fixed effects. Model-based estimates of time-varying proportion of fish maturing by age showed an increase in age 2, age 3, and/or age4 proportions starting in the early 1990’s for Cowichan, Puntledge fall, and Quinsam stocks (Fig. 5).

Posterior distributions of key model parameters were relatively smooth, potentially indicating they were well defined and that the model had converged (Fig. 6). The vast majority of estimated parameters and derived variables had acceptable convergence statistics (Table 4). There was a positive effect of sea lion and resident killer whale abundance on age 2 and older mortality rates (Mbigm, Fig. 6). The direction of fixed effects on age 1 mortality appeared realistic. Mortality rate increased with seal abundance (a positive mean for Mseal), and the total hatchery smolts released into the Strait of Georgia (Mhatch). Oceanographic effects on age 1 mortality, indexed by temperatures in the Strait of Georgia were relatively weak compared to these other factors, as seen by highly variable estimates of Mtemp and a mean close to 0. Fixed effects on age 1 ocean mortality explained a substantive amount of interannual variation in mortality rates for the Cowichan River stock (0.66), but substantively less for other stocks (0.18-0.32, Table 5). Given the generally limited effect of fixed effects on age 1 mortality for all stocks except Cowichan, the extent of pooling in random effects (wo[t]) was low (λ). There was more shrinkage (pooling) for the Cowichan stock because more of the interannual variation in age 1 mortality was explained by fixed effects.

Correlation in parameter effects for these fixed effects are partially determined by the trends in these covariates. For example, all stocks showed a negative correlation between Mseal and Mtemp effects on age 1 mortality. This occurred because there was a relatively strong positive correlation between seal abundance and water temperature over time (r=0.65), thus the model had some difficulty separating these effects. Estimates of standard deviations controlling the magnitude of annual random effects on freshwater mortality, age-1 ocean mortality, and fishing mortality were generally well-defined by the data and seen by the substantive differences between posterior and prior distributions (Fig. 7). This was not the case for the wfw_sd estimate for the Puntledge fall stock. Estimates of the standard deviation controlling the extent of observation error in escapement (lnS_sd) were well defined from the data. Posterior distributions for baseline ocean mortality (Mo for age 1 and 2+ fish) were well defined by the CWT data, as seen by the defined posterior distributions relative to the uninformative prior distributions (Fig. 8). In contrast, vulnerability to fishing for age 2 and 3 fish was not well-informed by the data so posterior and prior distributions were similar. We used a moderately informative prior distribution for these vulnerability terms where the standard deviation of the normal distribution was 50% of the assumed mean (logit_vul[] in Table 2). Using the less informative distribution used for mortality, where the standard deviation was twice the assumed mean (CV=2), led to high vulnerability for age 2 fish, which did not seem realistic. Mean maturation rates by age (logit_matb[a] in Table 2) well defined by the data (Fig. 8).

4.0 Conclusions and Future Directions

The age structured Chinook Salmon model we developed is an advancement for evaluating potential causes of variation in stock productivity over time, and for evaluating future management options. There are two relatively unique aspects of the model. The first is the use of a freshwater Ricker stock-recruitment model parameterized for egg-smolt mortality rate. This relationship is informed by escapement and CWT recovery data. The second is the approach to fitting the model to CWT recovery data to inform estimated trends in marine mortality, maturation, relative vulnerability, and annual exploitation rates. The model relies on the same 'gorilla' assumption using in the management of Chinook Salmon by the PSC, that trends in marine mortality, maturation, and exploitation rates for hatchery indicator stocks are representative of natural stocks. This critical assumption allows prediction of marine mortality, maturation, and exploitation rate for naturally-produced smolts, allowing the model to estimate the freshwater Ricker stock-recruitment parameters and annual deviations. The model should be helpful for quantitative elements of upcoming Chinook Salmon Recovery Potential Assessments.

There are a number of additional analyses and minor modifications to the model that could made in future analyses. These include:

1. **Covariate effects on freshwater mortality.** Currently, the model does not include fixed effects in the calculation of freshwater egg-smolt Ricker stock-recruitment parameters. Time series of covariates such as stream flow, water temperature, or measures of habitat quality or restoration effort could be developed and incorporated in the model as they are for ocean mortality. The simplest assumption is to assume these covariates are additive fixed effects on the productivity term of the stock-recruitment model in the model (log of cr, the compensation ratio). The forward simulation model allows users to adjust one or both Ricker terms to simulate the effects of changes in habitat quality or quantity.
2. **Coding structure for fixed effects on ocean mortality.** Currently, the coding approach for the fixed effects on ocean morality assume the covariate values for each term are in a specified order in the input file. In addition, the covariates used to predict age 1 and age 2+ ocean mortality are hardwired in the code, requiring users to modify the code to explore alternate models. Any changes to the estimation model also need to be made to the forward simulation model. The flexibility of the approach could be improved so users could specify which variables to include in the mortality calculations.
3. **Data input file structure.** Currently, the model requires a number of separate input files, some of which are stock-specific and some being more generic or regional (historical exploitation rates). A better input data structure would make it easier to apply the model to more stocks and avoid errors.

4. **Standardization of covariate data for fixed effects.** Currently the standardization methods for covariate values used in the model are slightly inconsistent. We recommend that DFO develop their own covariate files and consistent standardization methodology. As currently configured, the estimated base ocean mortality rates represent mortality in the absence of fixed effects such as seal abundance (i.e., seal abundance is very low during the initialization period). Our standardization approach assumes that covariate values are zero at levels assumed to be present during the historical period that the model is initialized to. An alternate and more robust scheme would be for users to define the covariate values for the initialization period.

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6.0 Tables and Figures

Table 1. Assumed constants used in the estimation component of the age-structured Chinook Salmon population model. Cow, Qual, Punt_sum, Punt_fall, and Quin refer to Cowichan, Qualicum, Puntledge summer, Puntledge fall, and Quinsam stocks. The model assumes age 1 fish do not mature (mato[1]=0) and that all age 6 fish will mature (mato[6]=1). The model assumes vulnerability of age 1 fish to fishing is zero (vulo[1]=0) and that age 4 and older fish are fully vulnerable (vul0[4:6]=1).

Variable	**Description**	**Value**				
HatchSurv	Survival rate of hatchery smolts shortly after release	0.5				
Msum	Mortality rate from early summer to spawning	0.51				
CWTexp	CWT catch and escapement sampling rate	0.1				
so_sd	Standard deviation in the log of unfished equilibrium escapement	0.5				
		Cow	**Qual**	**Punt_sum**	**Punt_fall**	**Quin**
Fhist	Average fishing mortalitiy rate 5 years prior to 1980	1.3	1.5	1.5	0.7	0.8
so_mu	Log of the mean unfished equilibrium escapement					
	log(3x max historical escapement/10000)	2.04	1.41	-0.04	1.63	1.41
so_min	Minmum unfished equilibrium escapement					
	log(2x max historical escapement/10000)	1.9	0.6	-2.3	1.1	0.6
fec	Fecundity (eggs per spawner) by age					
	a=1	0	0	0	0	0
	a=2	87	0	0	0	0
	a=3	1153	800	800	800	800
	a=4	2780	2000	2000	2000	2000
	a=5	2700	2500	2500	2500	2500
	a=6	3000	3000	3000	3000	3000
vulo	Mean of prior for relative vulnerability to fishing by age					
	a=2	0.08	0.05	0.08	0.08	0.04
	a=3	0.90	0.36	0.43	0.43	0.30
mo	Mean of prior for base natural mortality rate by age (no covariate effect)					
	a=1	3.00	3.00	3.00	3.00	2.81
	a=2+	0.30	0.30	0.30	0.30	0.30
mato	Mean of prior for base maturation rate by age					
	a=2	0.10	0.03	0.08	0.08	0.00
	a=3	0.40	0.20	0.26	0.26	0.04
	a=4	0.95	0.72	0.67	0.67	0.35
	a=5	0.99	0.94	0.95	0.95	0.91

Table 2. Description of estimated model parameters, their prior distributions, and data likelihoods used to fit the model. Values in bold denote constants that are not estimated (see Table 1 for their definitions).

Parameter	Description	Assumed Distribution
Basic parameters		
Fbase	Base fishing mortality rate	uniform(**0, 10**)
Mo[1]	Age-2+ natural mortality without time varying effects (initialization period)	normal(**mo[1]**, 2***mo[1]**)
Mo[2]	Age-1 natural mortality without time varying effects (initialization period)	normal(**mo[2]**, 2***mo[2]**)
Mseal	Coefficient for effect of seal abundance on age 1 mortality rate	uniform(0, 10)
Mtemp	Coefficient for SOG water temperatureeffect of seal abundance on age 1 mortalit	uniform(-10, 10)
Mhatch	Coefficient for SOG hatchery releases on age 1 mortality rate	uniform(0, 10)
Mbigm	Coefficient for effect of large mammal predation on age 2+ mortality rate	uniform(0, 10)
wfw[t]	Annual egg-smolt mortality rate anomalies	norma(0, wfw_sd)
wo[t]	Annual age 1 natural ocean morality rate anomalies	normal(0, wo_sd)
wf[t]	Annual fishing mortality rate anomalies	norma(0, wf_sd)
bo[s]	Coefficients for fators impacting natural ocean mortality	uniform (-10, 10)
logit_matb]a]	Logit of mean maturation rates by age over years	normal(logit(**mato[a]**), 2*abs(logit(**mato[a]**)))
logit_matt[a,t]	Logit of maturation rates by age and year	normal(logit_matb[a], mat_sd[a])
logit_vul[a]	Logit of vulnerability to fishing for ages 2 and 3	normal(logit(**vulo[a]**), 0.5*abs(logit(**vulo[a]**)))
cr	Log of egg-smolt stock-recruitment compenstion ratio	uniform(1, 10)
log_so	Log of unfished spawning stock size for stock-recruitment model	normal(**so_mu**, **so_sd**)[**so_min**,]
hyper-distribution variance terms		
wfw_sd	Standard deviation in egg-smolt mortality rate annual anomalies	gamma(2, 5)
wo_sd	Standard deviation in age 1 ocean mortality rate annual anomalies	gamma(2, 5)
wf_sd	Standard deviation in annual fishing mortality rate anomalies	gamma(2, 5)
mat_sd[a]	Standard deviation for annual variation in maturation rate by age	gamma(2, 5)
lnS_sd	Standard deviation in log of observed annual escapements (observation error)	gamma(2, 5)
Data Likelihoods		
log(obsS[t])	Escapement	normal(log(S[t]), lnS_sd)
obscwtcat[a,t]***CWTexp**	CWT recoveries in catch	poisson (predcwtcat[a,t]***CWTexp**)
obscwtesc[a,t]***CWTexp**	CWT recoveries in escapement	poisson (predcwtesc[a,t]***CWTexp**)

Table 3. The relative trend in annual exploitation rate used in the model. A value of 1 indicates that the annual fishing mortality rate would be equal to the estimated base fishing mortality rate representing conditions prior to the first modelled year of 1980 (Fbase, Table 1). RelRegF was calculated by smoothing annual exploitation rate estimates for southern BC index stocks available in annual Pacific Salmon Commission Technical Reports (see Appendix A).

Year	RelRegF		Year	RelRegF
1980	1		2001	0.5
1981	1		2002	0.5
1982	1		2003	0.5
1983	1		2004	0.5
1984	1		2005	0.5
1985	1		2006	0.5
1986	1		2007	0.5
1987	1		2008	0.5
1988	1		2009	0.5
1989	1		2010	0.5
1990	1		2011	0.5
1991	1		2012	0.5
1992	1		2013	0.5
1993	1		2014	0.4375
1994	0.875		2015	0.375
1995	0.75		2016	0.375
1996	0.6875		2017	0.375
1997	0.625		2018	0.25
1998	0.5625		2019	0.25
1999	0.5		2020	0.25
2000	0.5			

Table 4. The number of estimated parameters and derived variables (1508 per stock over 41-year modelled time period) that exceeded Gelman and Rubin's (2004) rhat convergence criteria of 1.05. Parameters that exceeded this criteria and their rhat statisitcs are shown in the rightmost column. See Table 2 for parameter definitions.

Stock	# of Variables	Variables and rhat for those with rhat>1.05
Cowichan	2	sd_matt[a=4]=1.07;sd_matt[a=5]=1.14
Qualicum	2	logit_mattb[5]=1.06, N[t=11,a=6]=1.06
Punledge summer	7	mat[ ]=1.06-1.09; wfw_sd=1.05
Puntledge fall	3	sd_matt[a=4]=1.08; sd_matt[a=5]=1.09; wfw_sd=1.06
Quinsom	0	

Table 5. Statistics describing the utility of fixed effects (combined effects of seal abundance, SOG hatchery production, and water temperature) for predicting interannual variation in age-1 ocean mortality (see eqn. 4). pR^2 (pseudo R^2) is the proportion of interannual variation in mortality explained by fixed effects (remainder explained by random effects). λ is the extent of pooling (statistical shrinkage) in annual random effects on age-1 ocean mortality (wo[t]). Higher λ's indicate more pooling.

Stock	pR^2	λ
Cowichan	0.66	0.31
Qualicum	0.20	0.15
Punledge summer	0.23	0.30
Puntledge fall	0.18	0.18
Quinsom	0.32	0.15

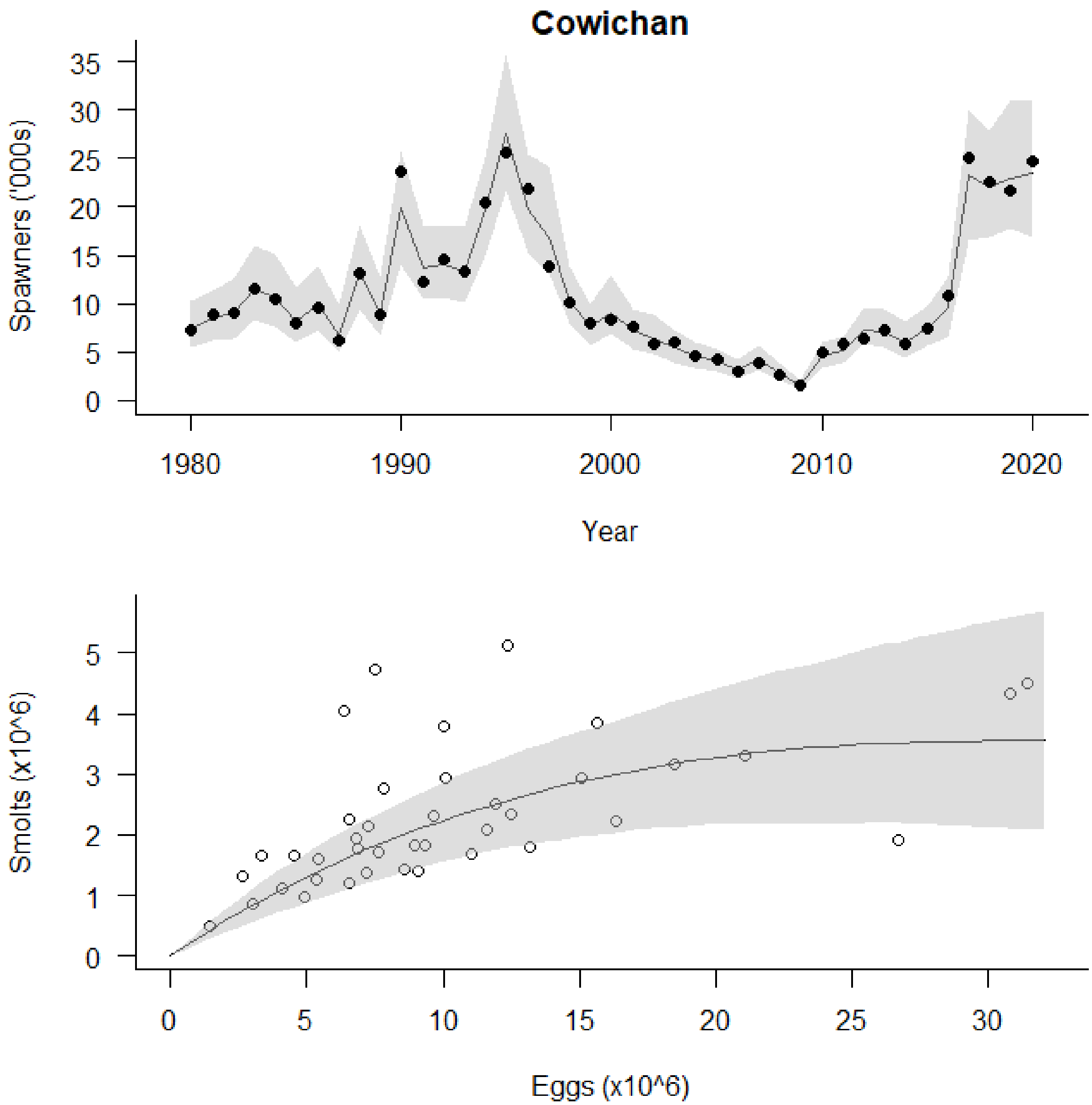
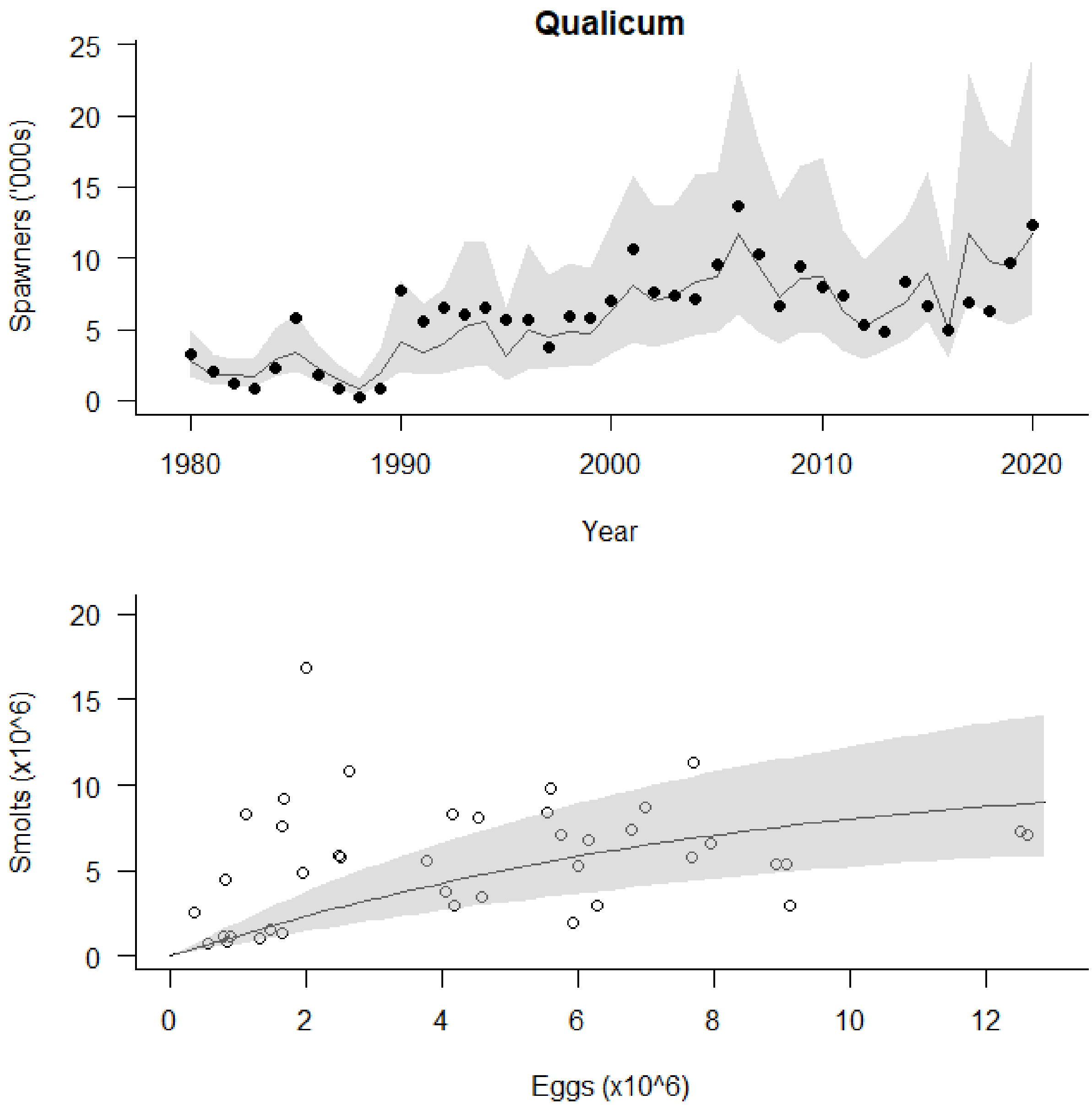


Figure 1. Comparison of estimated mean escapement (line) by year and 95% credible intervals (shaded area) to observations (points, top panel), and estimated egg-smolt stock recruitment relationship (bottom panel). The line and shaded area in the bottom panel represent the mean and 95% credible interval of the estimated relationship. The open points represent the mean estimated smolt abundance for each year given the egg deposition, the estimated stock-recruitment relationship and the random density-independent year effects on egg-smolt mortality (wfw[t]).



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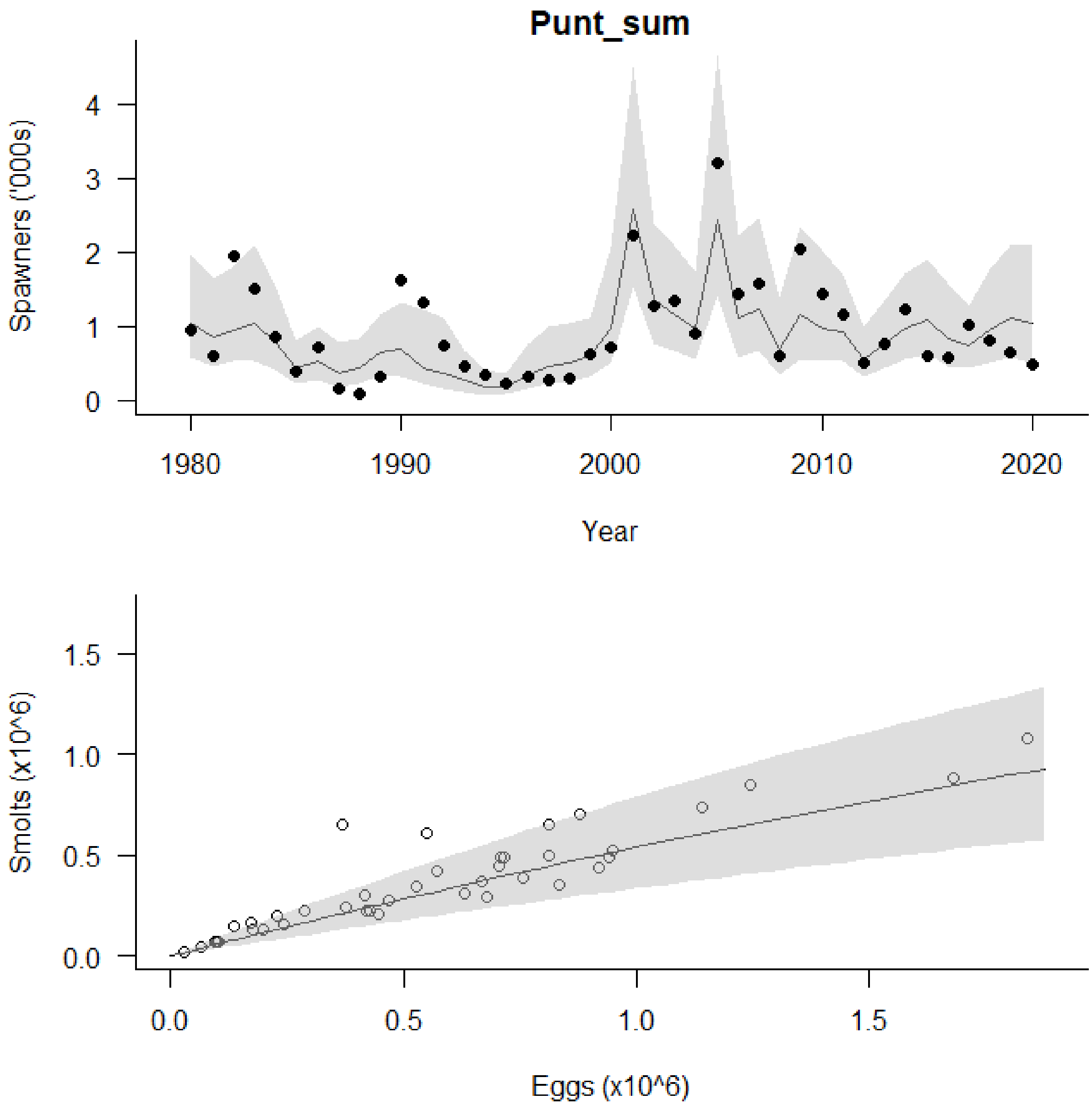

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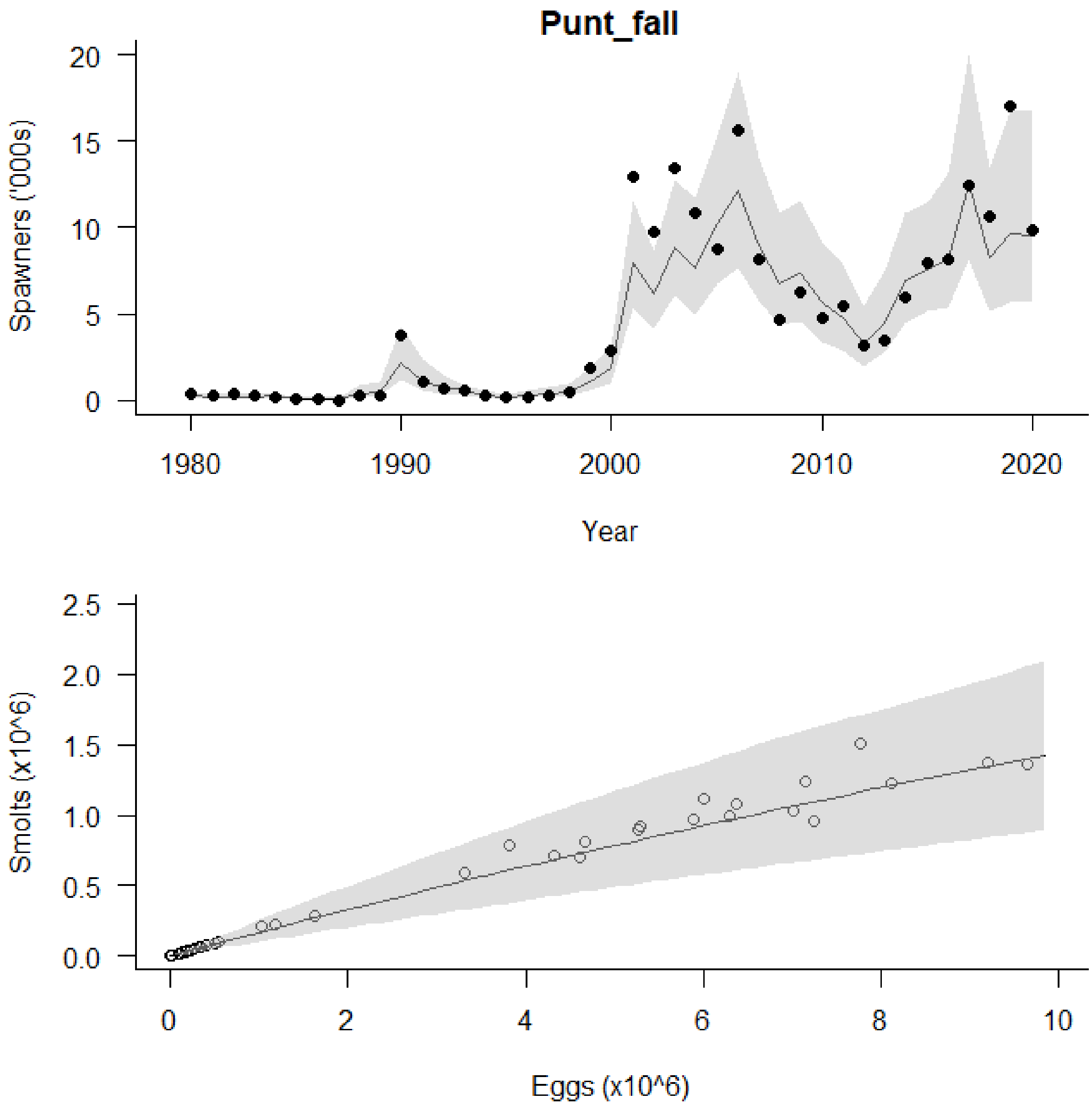

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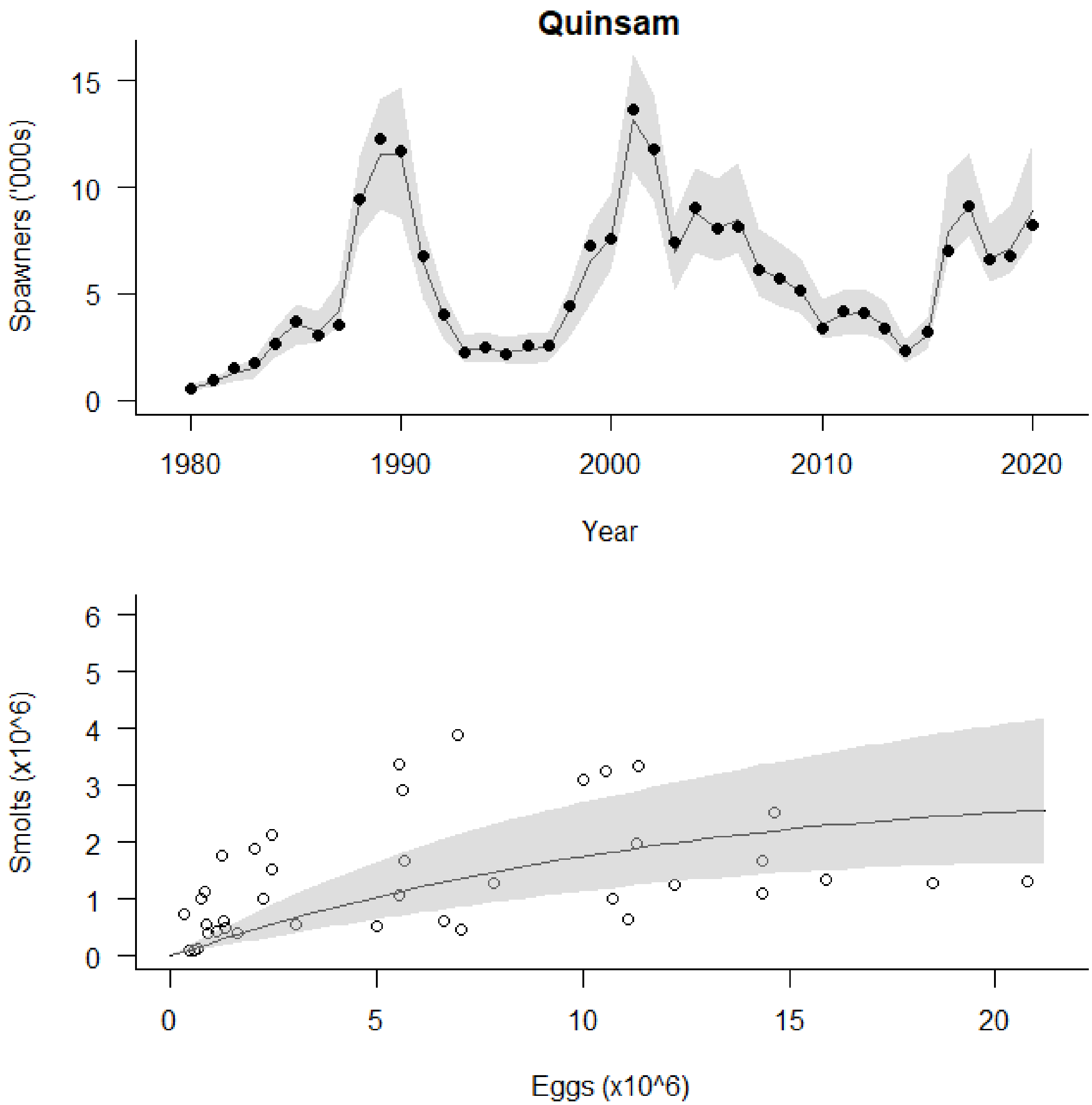

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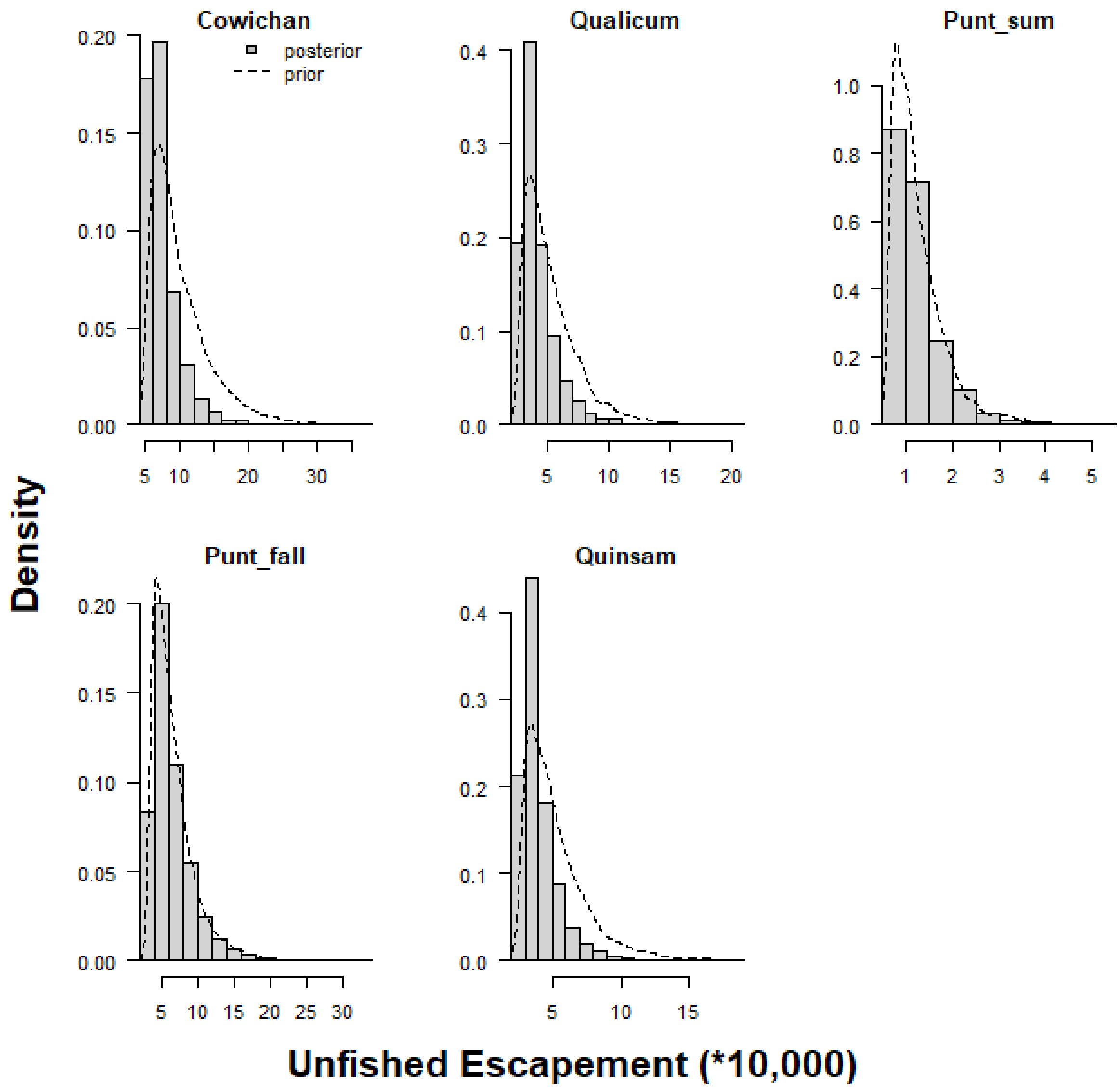


Figure 2. Comparison of posterior and prior distributions for the equilibrium unfished escapement by stock (transformed values of log_so in Table 2).

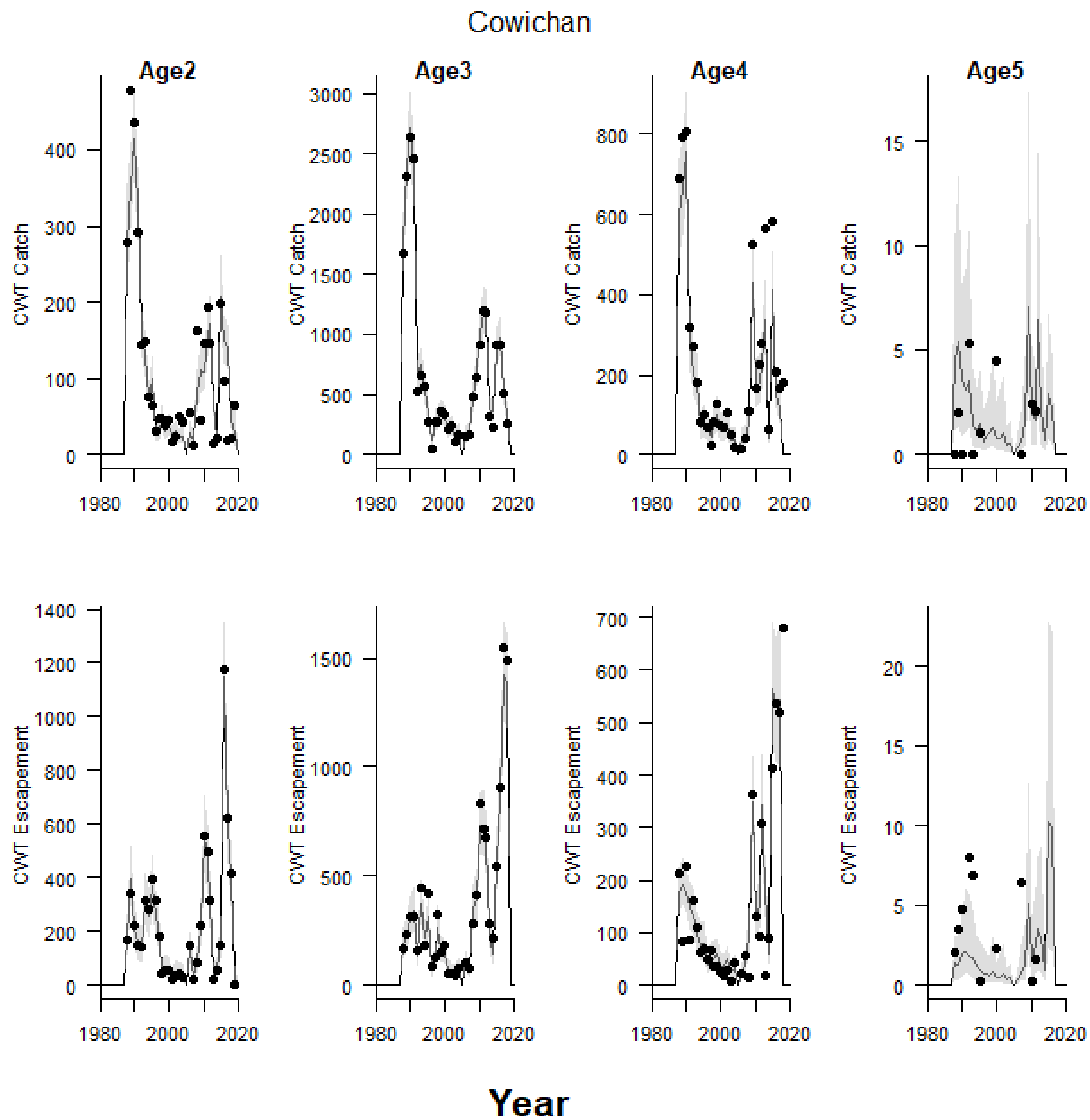
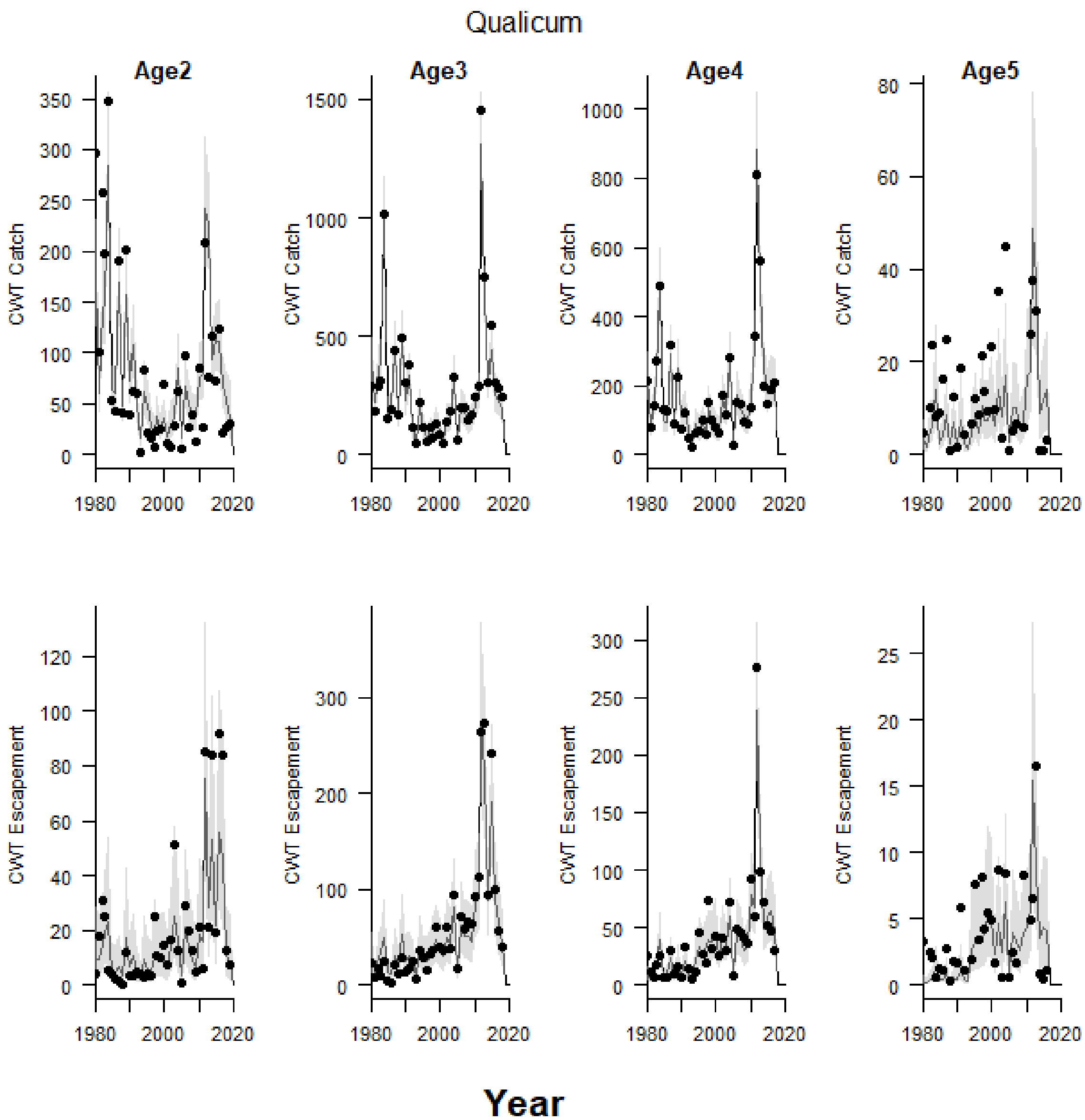


Figure 3. Comparison of observed (solid points) and predicted (lines represent means, shaded area represents 95% credible intervals) expanded CWT recoveries in the catch and the escapement.



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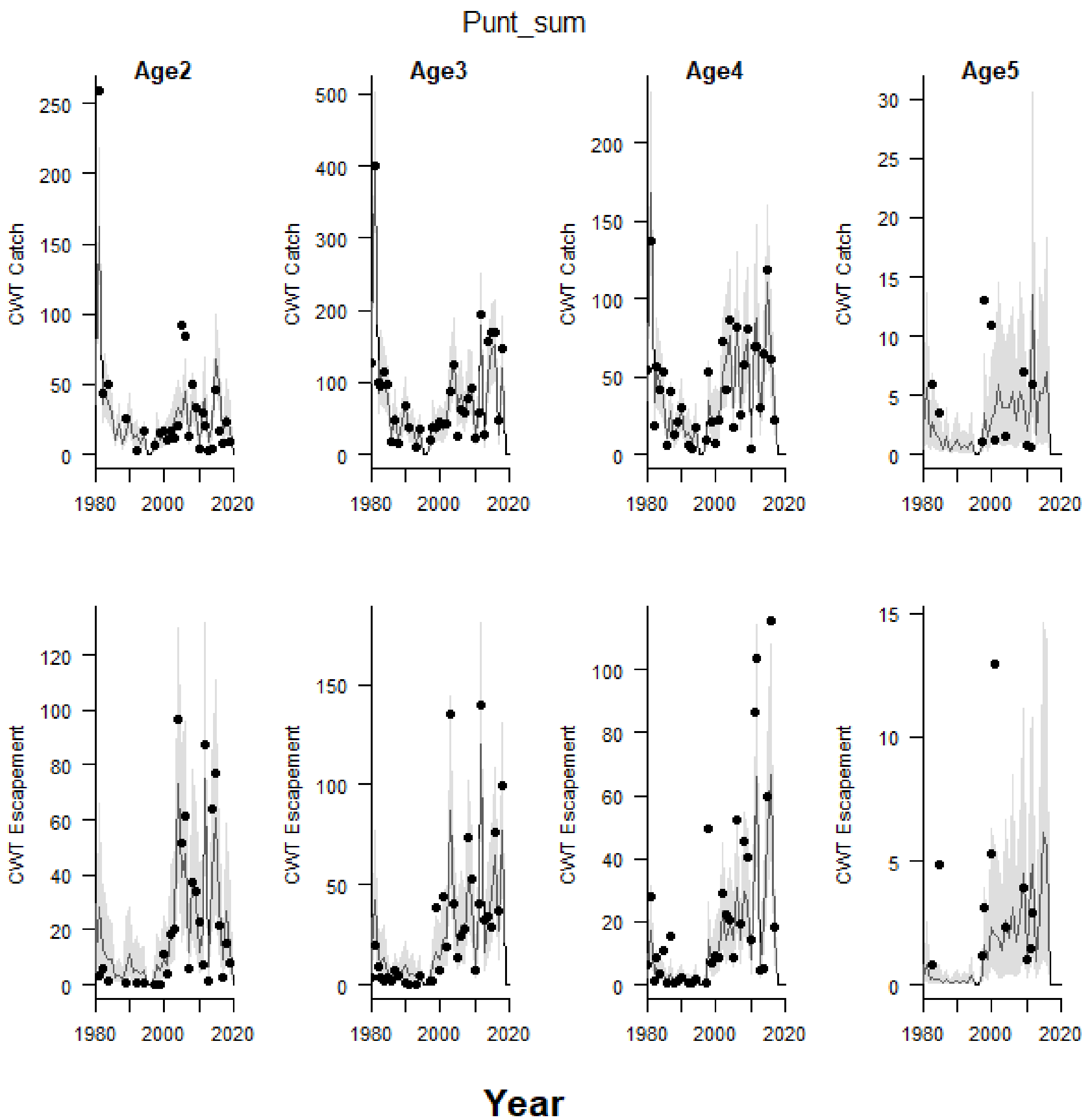

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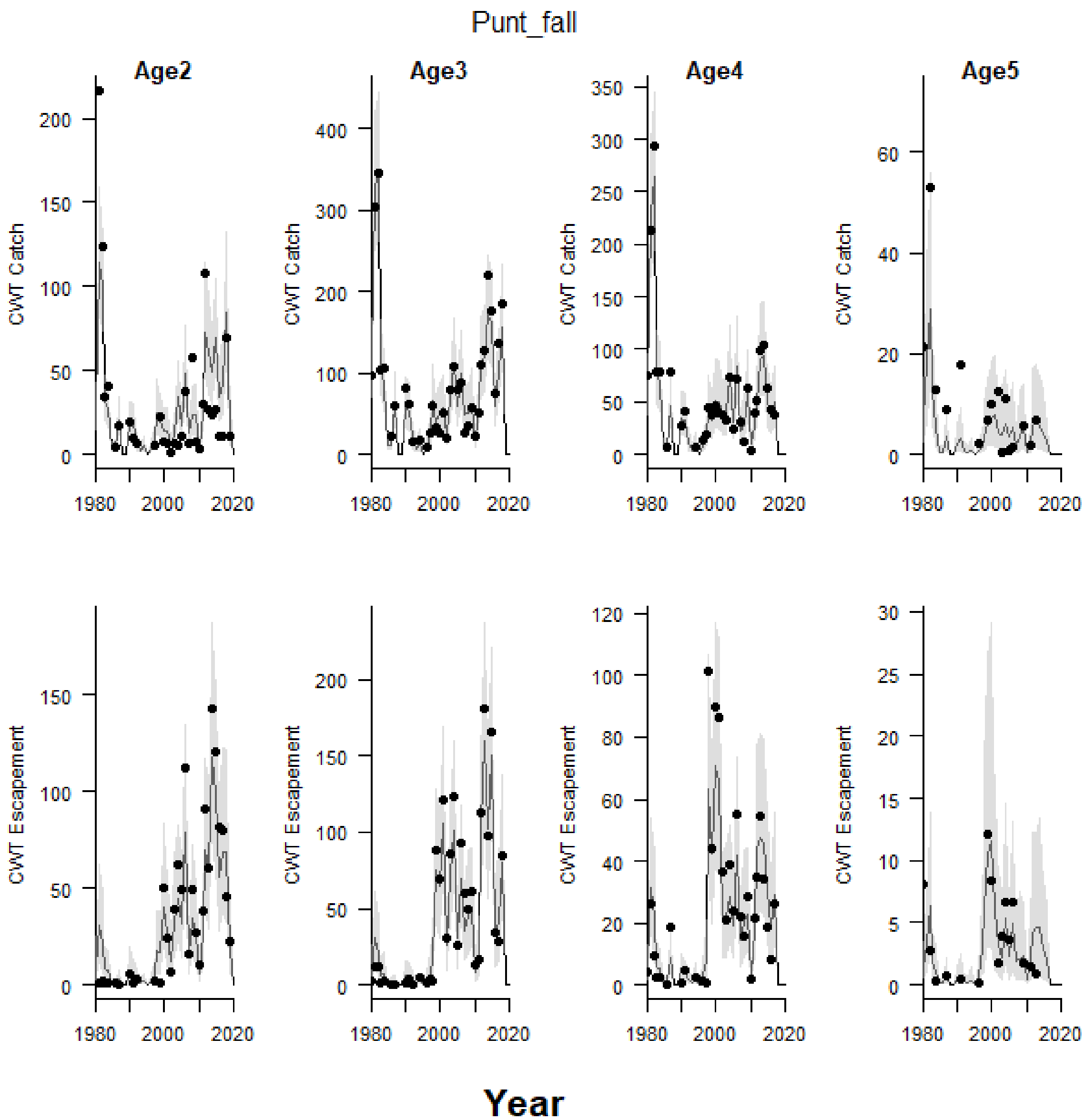

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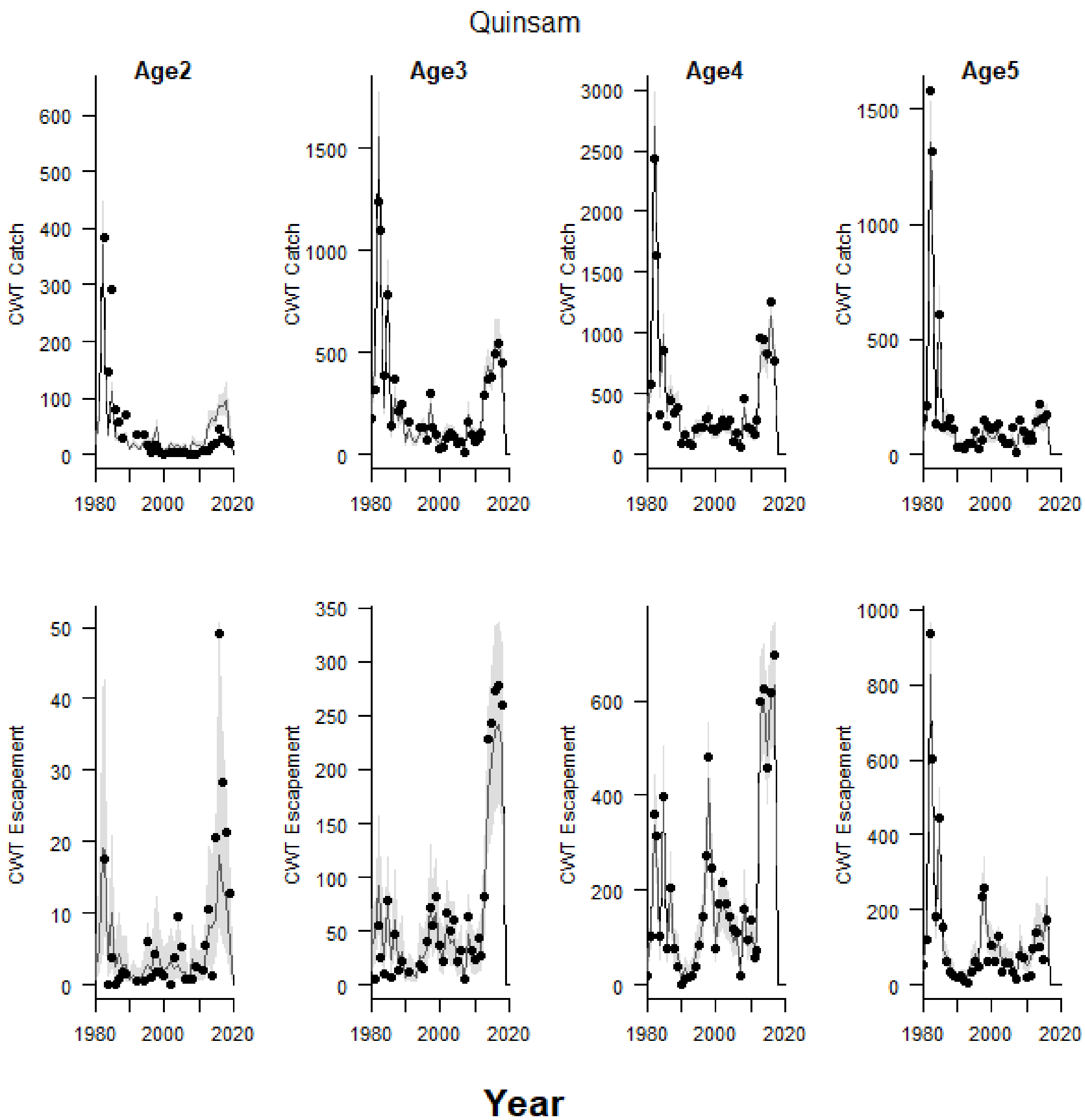

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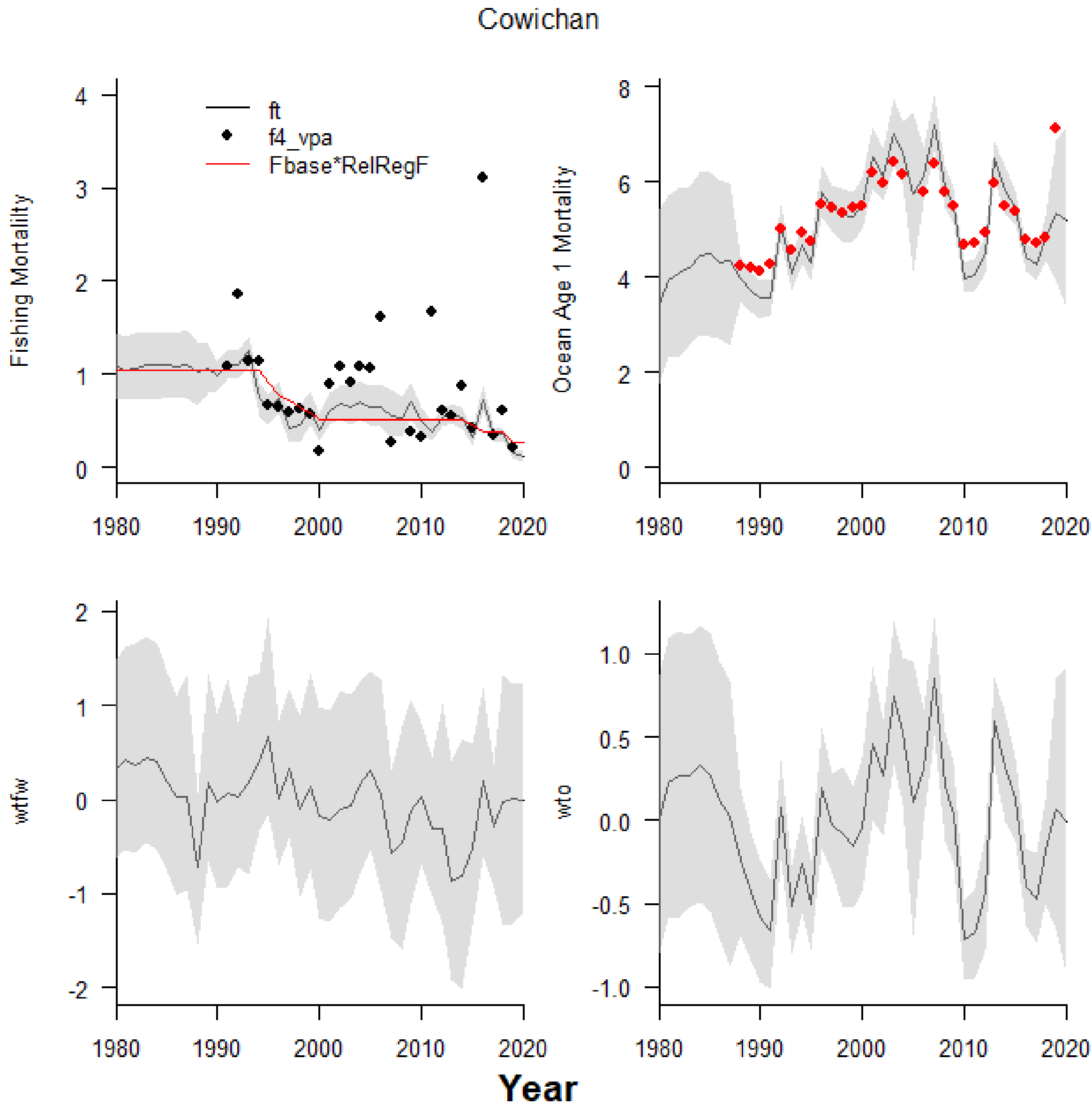
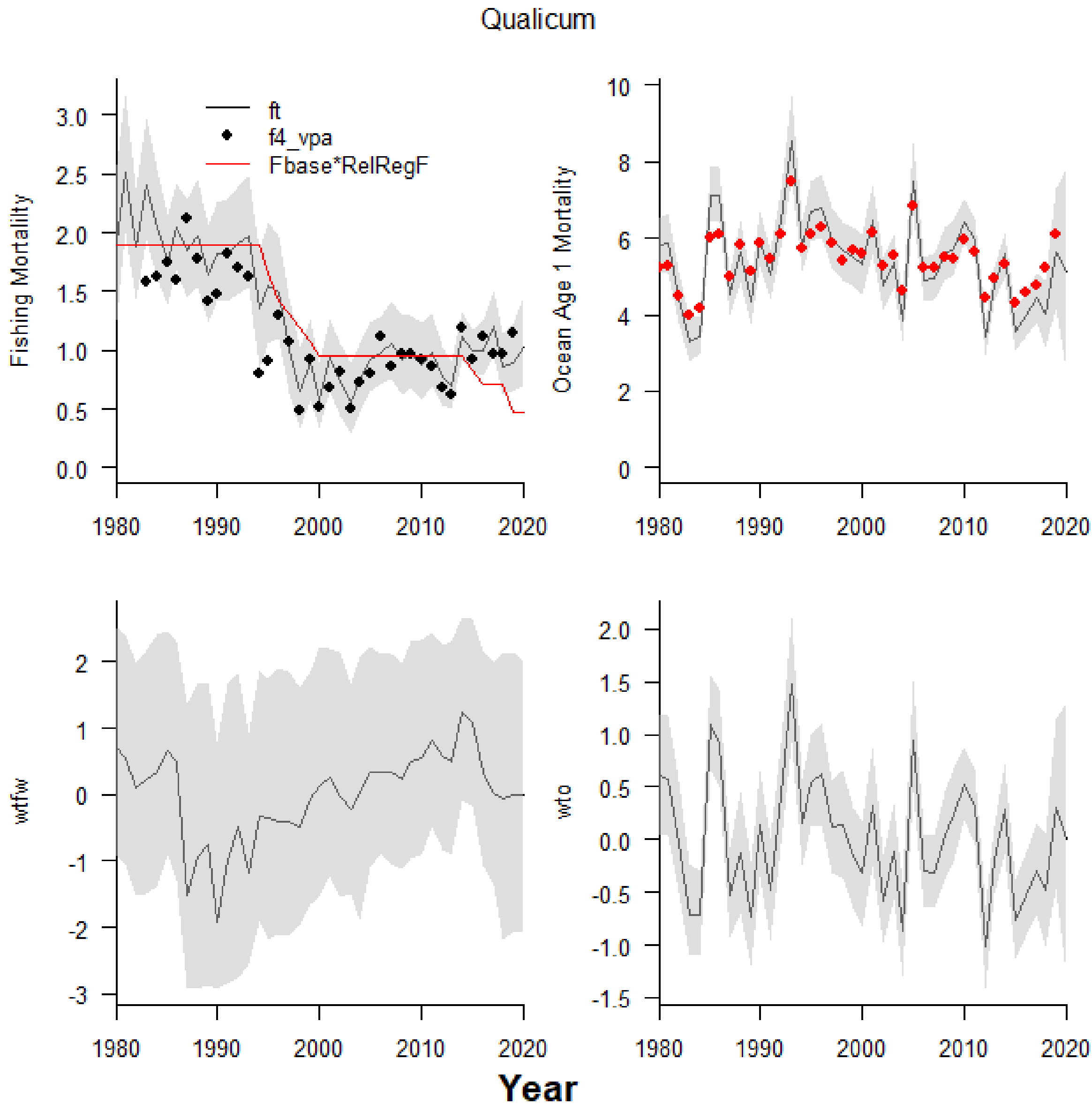


Figure 4. Model estimates of annual parameters. The upper-left panel shows the estimated annual fishing mortality rates (f[t], solid line shows the annual means, shaded area shows the 95% credible interval of annual means) in comparison to estimates of fishing mortality from VPA (virtual population analysis), and the average regional exploitation rate (Fbase·RelRegF[t]). The upper right panel shows age 1 mortality rates estimated by the model (lines and shaded area) in comparison to estimates from a VPA model (red points). The latter depend on model-based estimates of natural mortality and the expanded age 1 CWT recoveries. The bottom panels show means (lines) and 95% credible intervals (shaded area) of estimated annual random effects on egg-smolt mortality (bottom left panel) and age 1 ocean mortality (bottom right panel).



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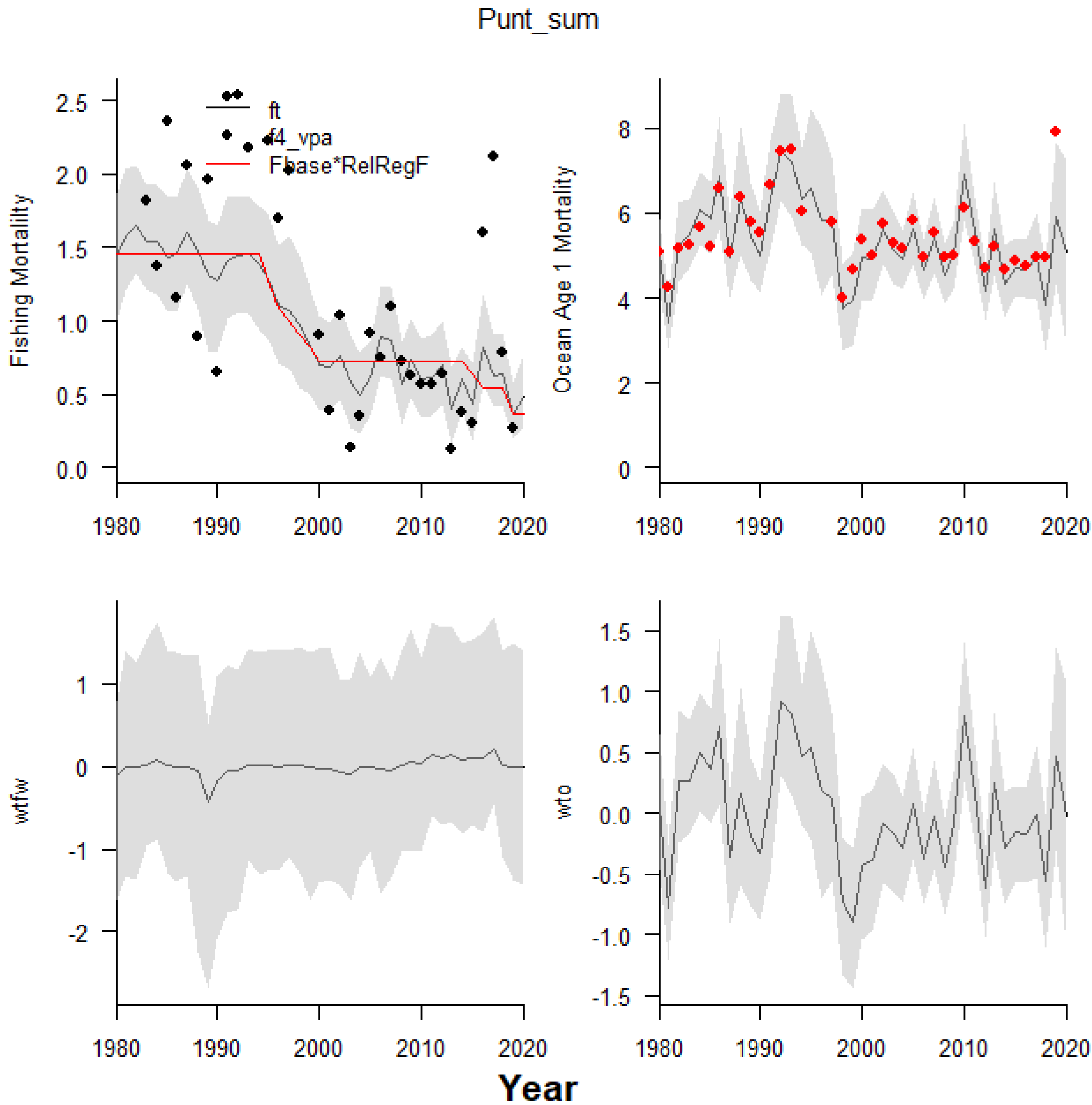

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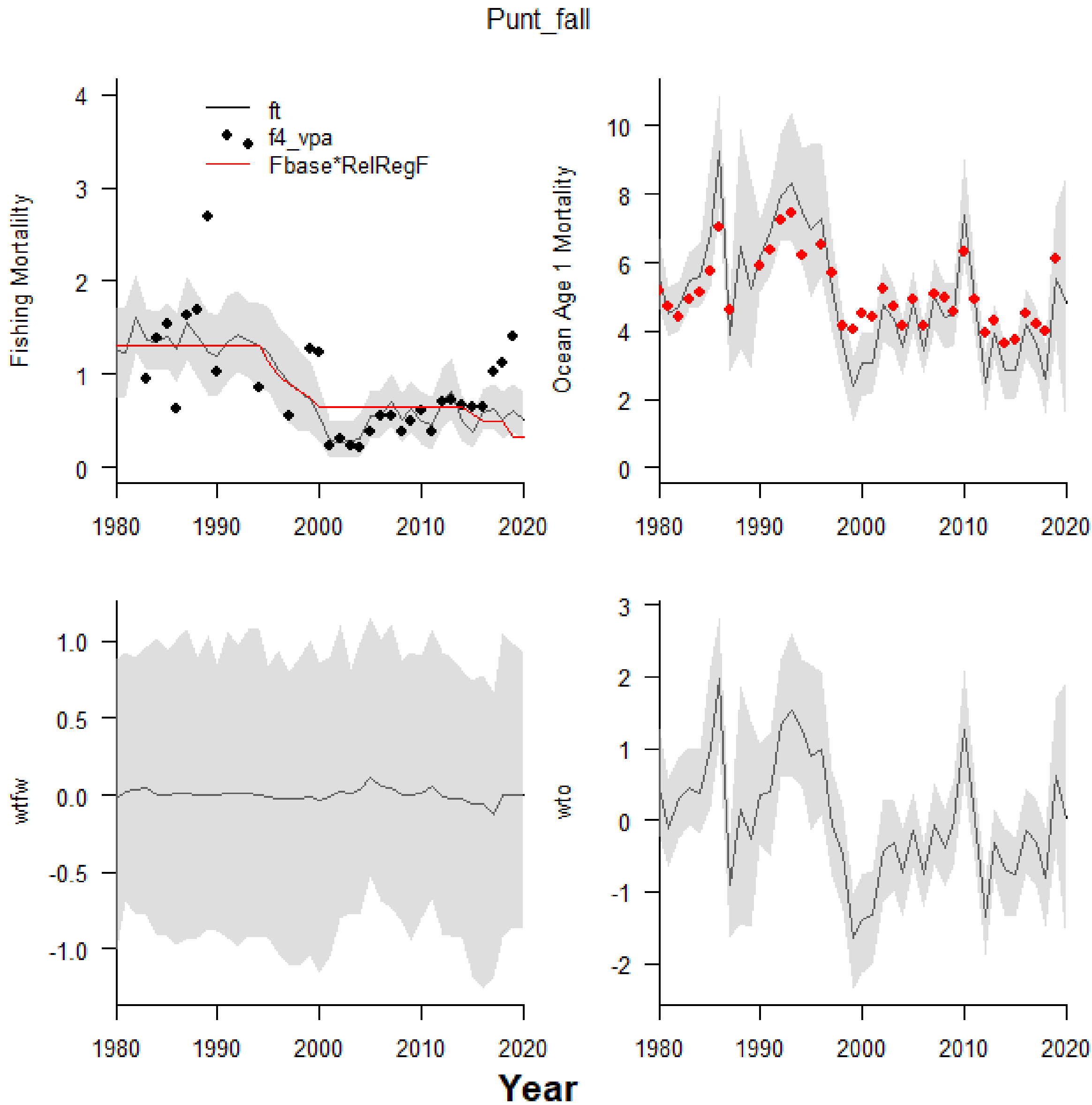

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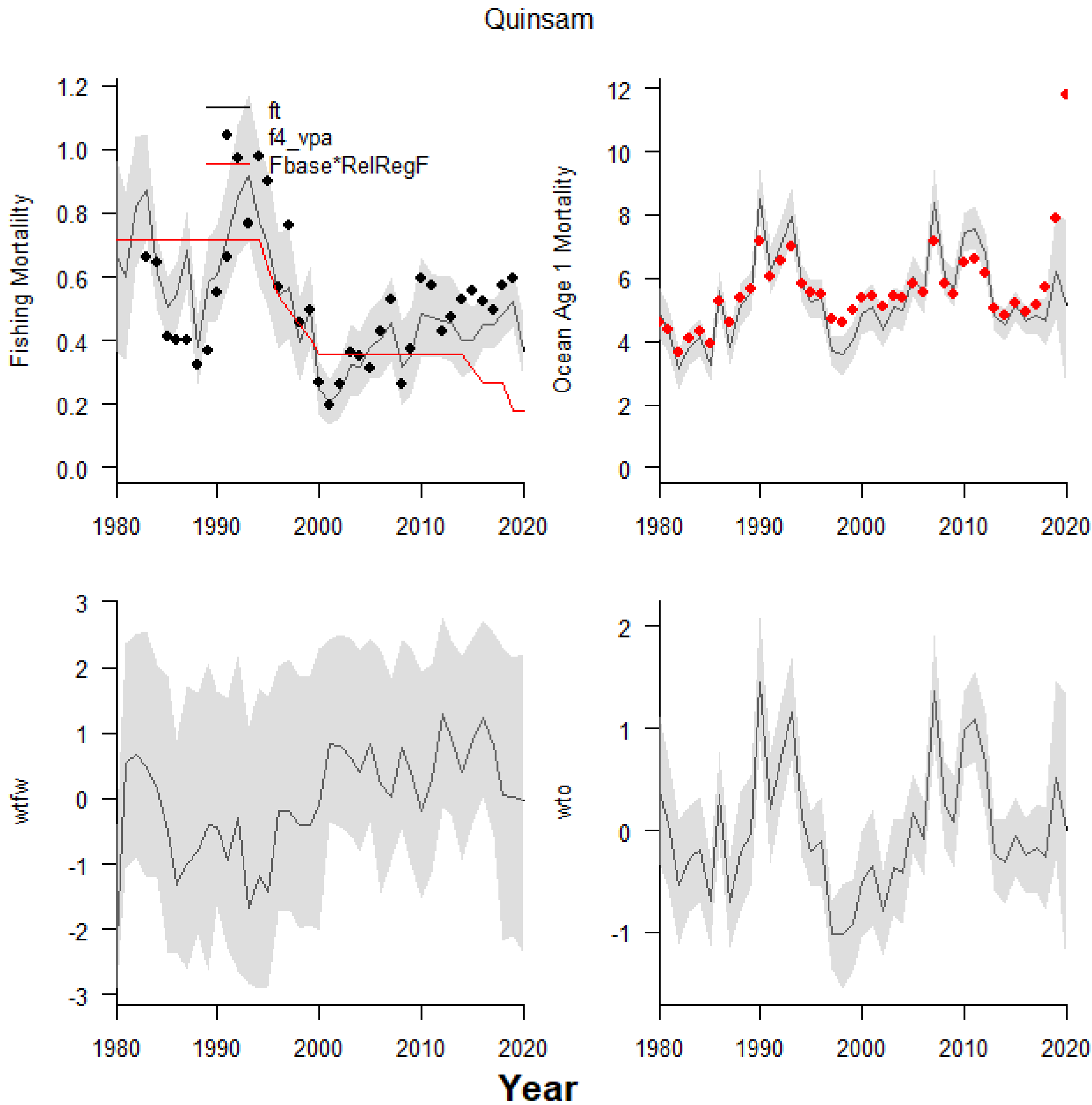

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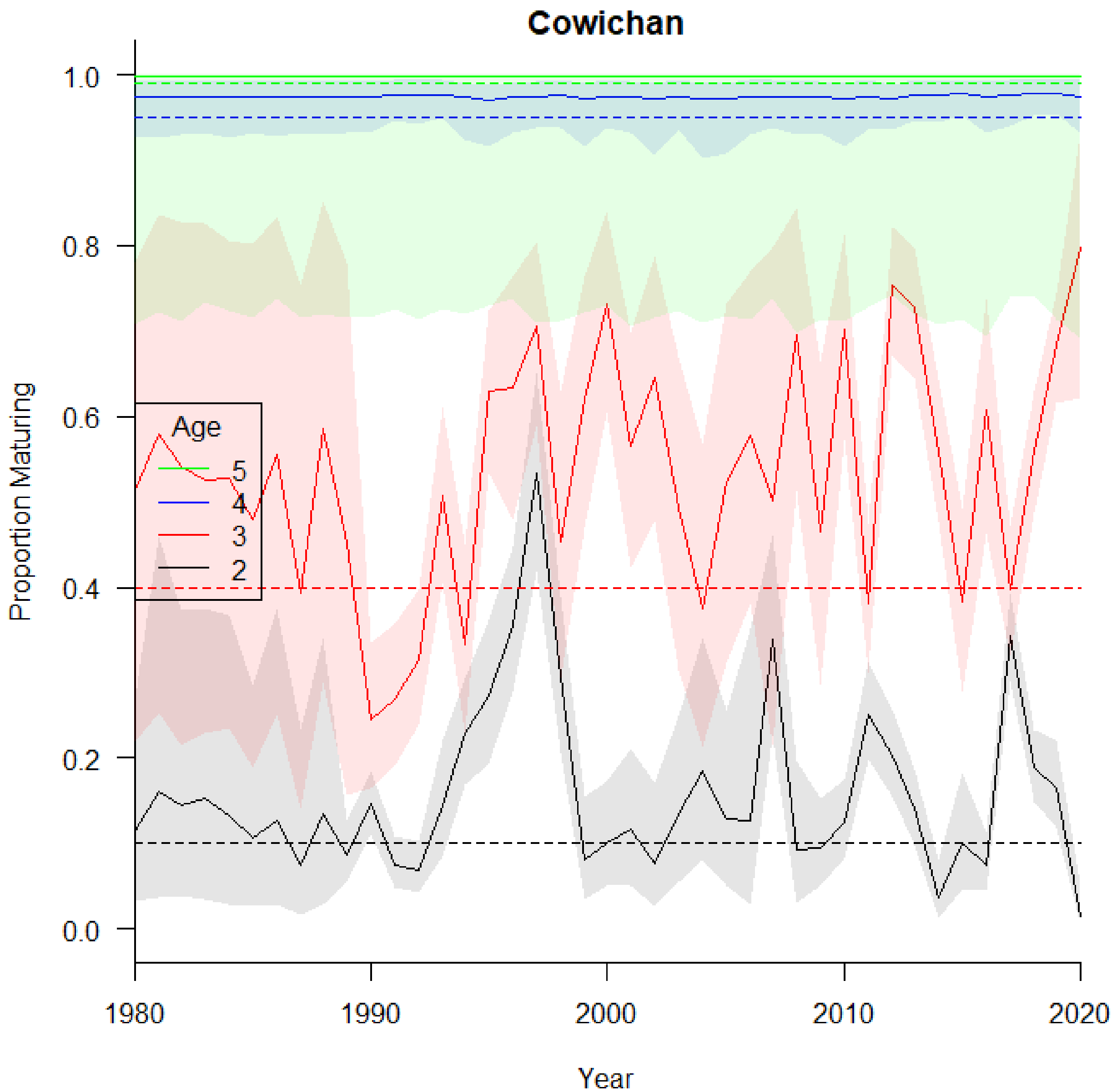
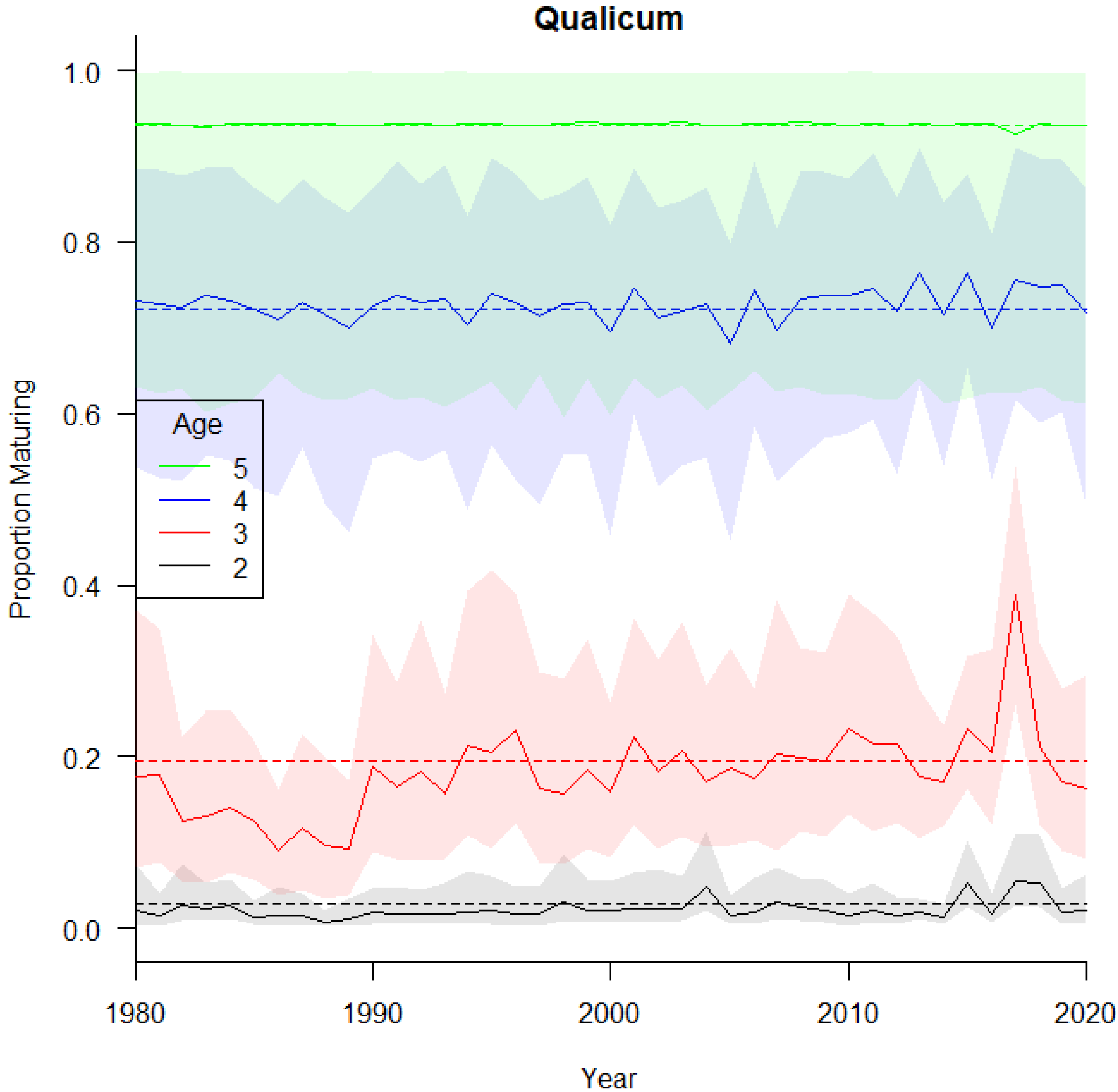


Figure 5. Annual estimates of the proportion of fish maturing at ages 2 to 5. Lines represent posterior means and shaded areas represent 95% credible intervals.



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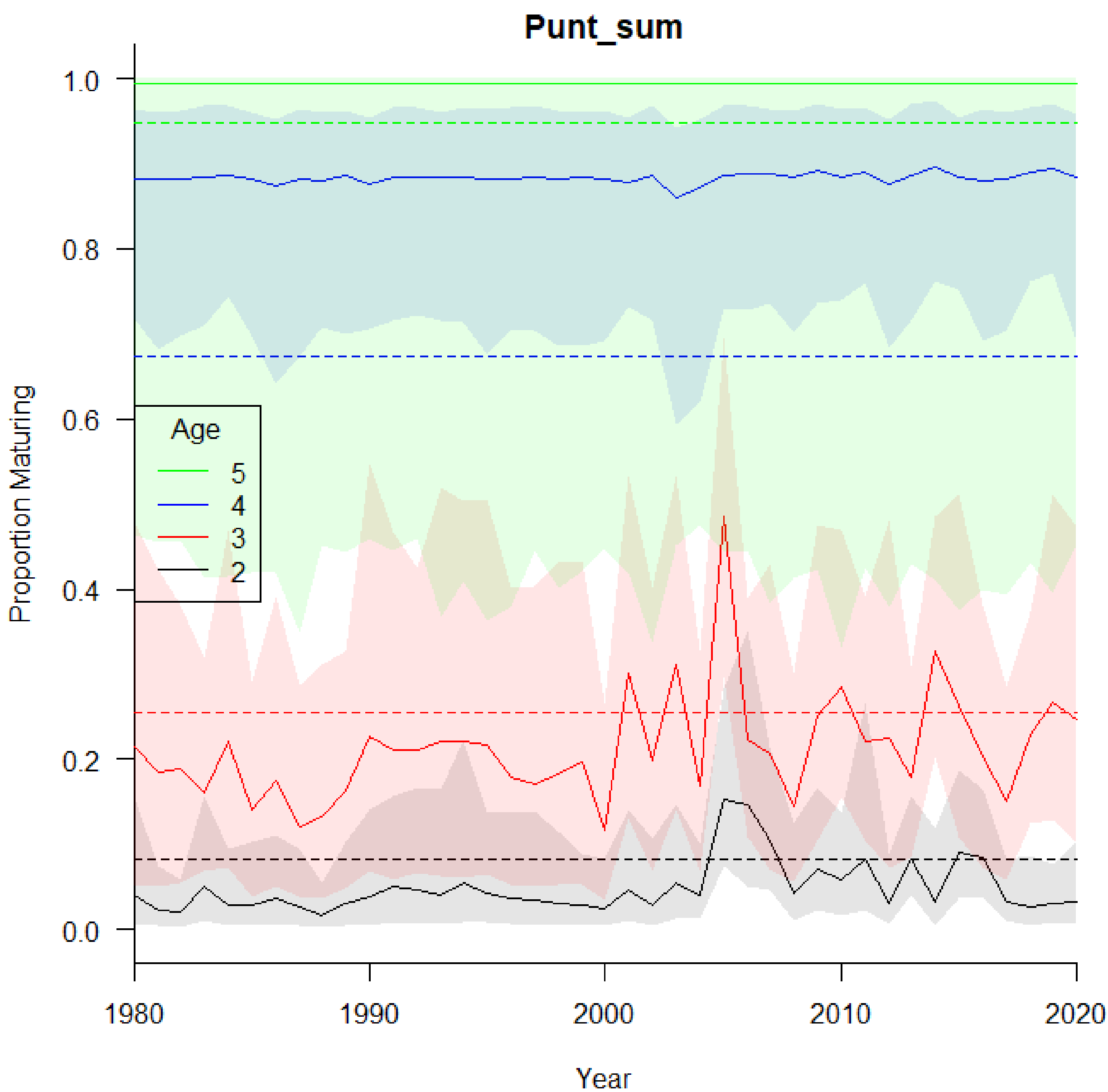

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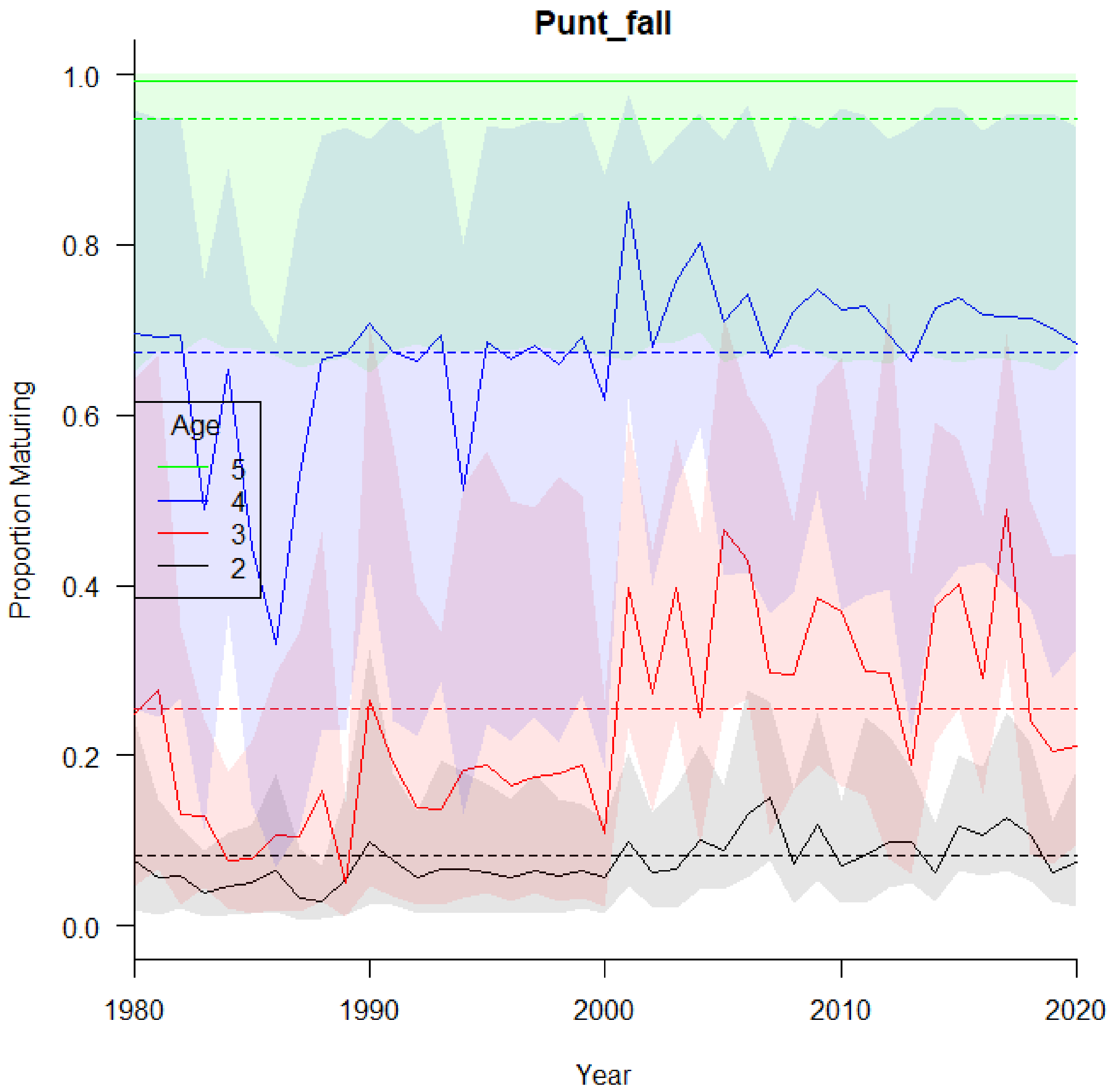

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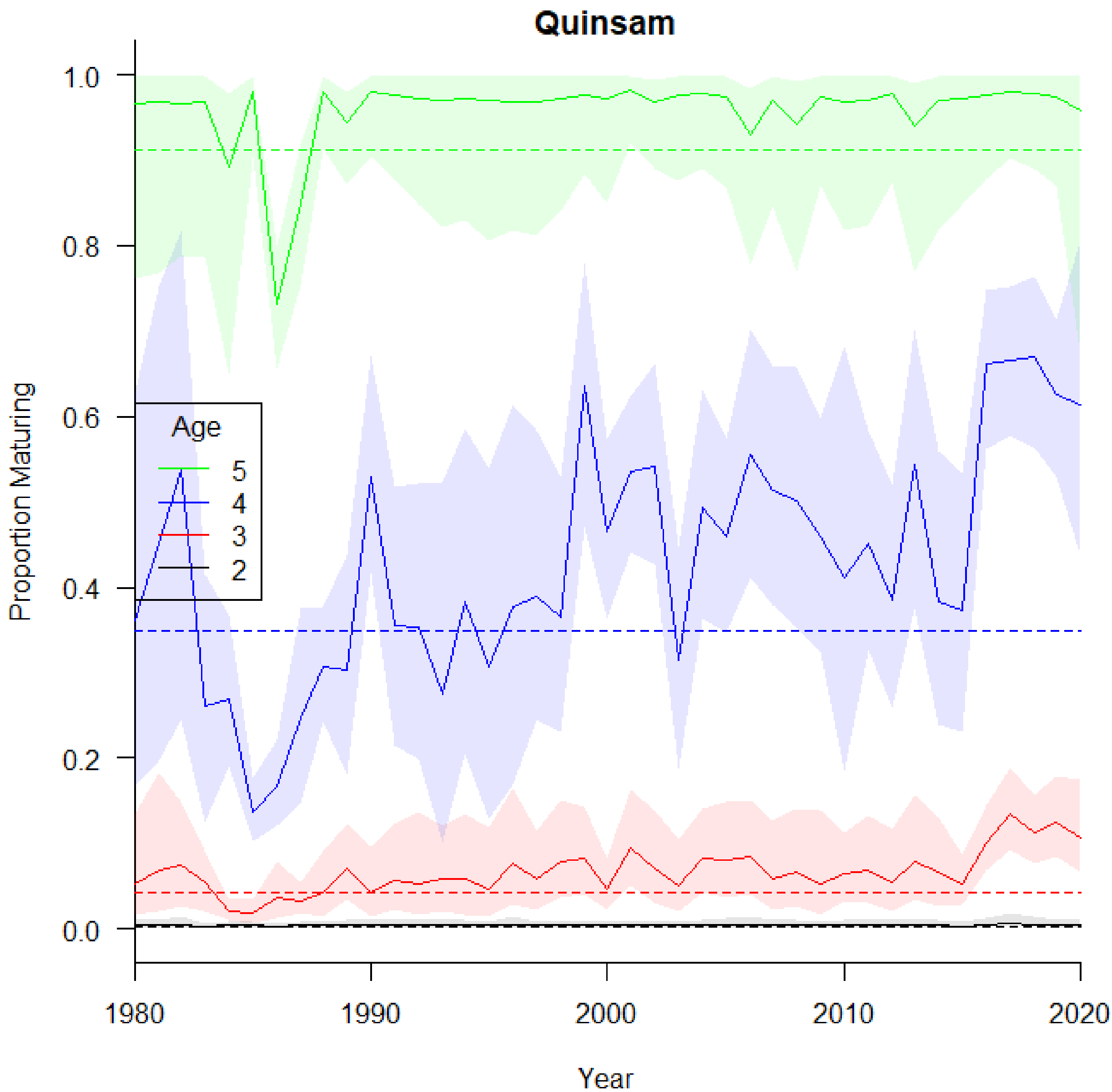

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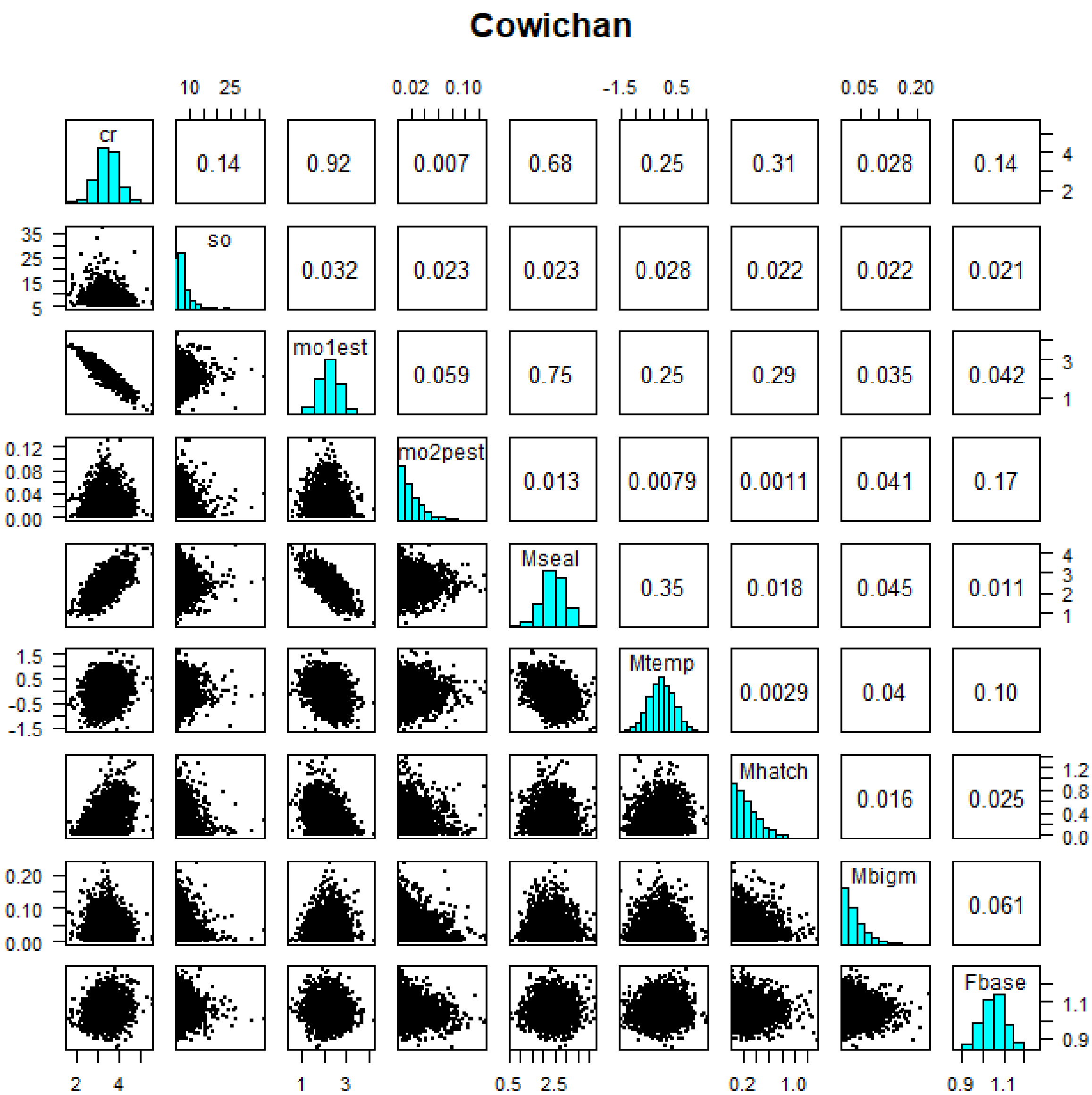
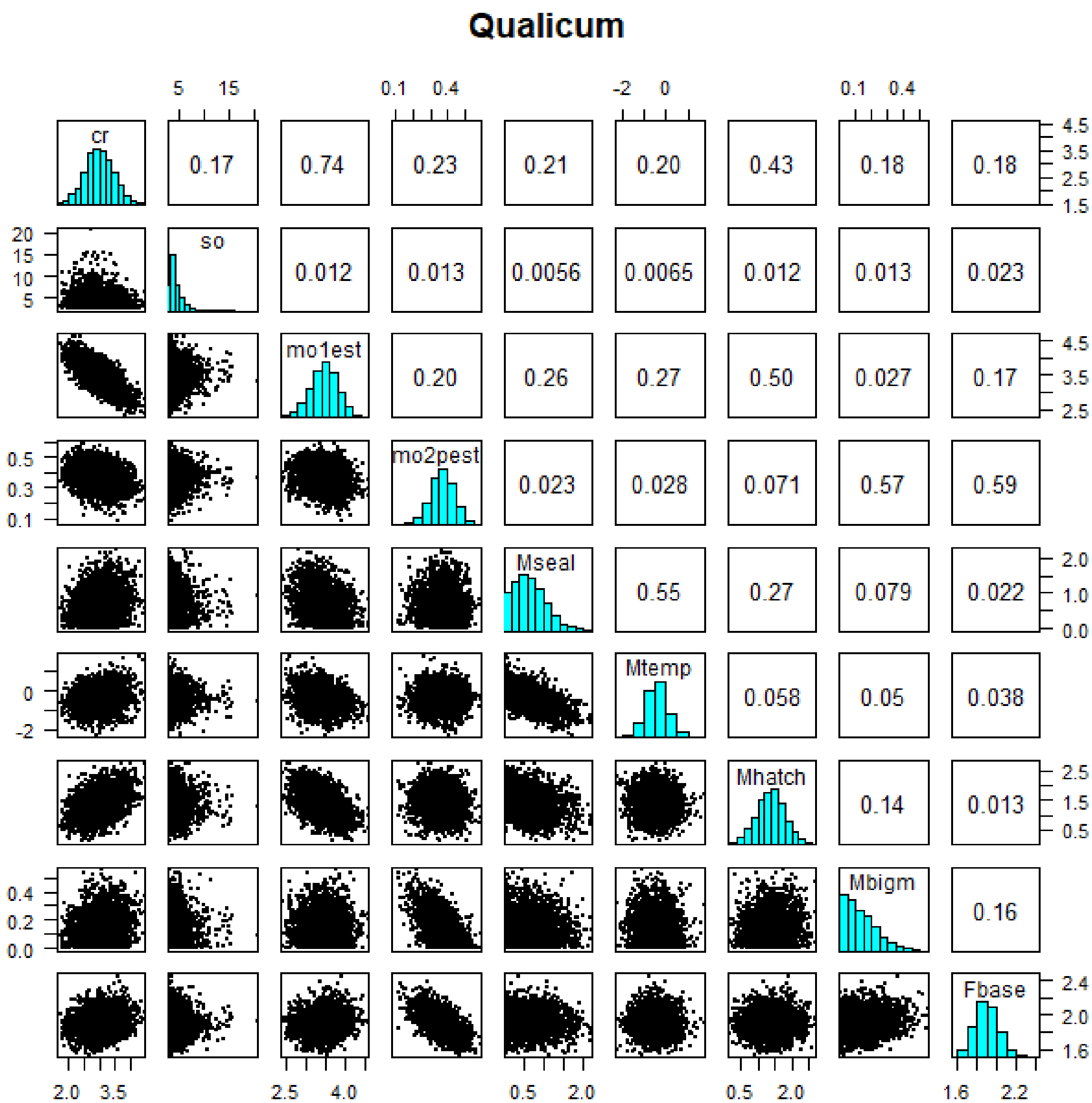


Figure 6. Pairs plot showing the estimated posterior distributions of critical parameters (diagonal blue histograms), and the correlation among parameter values across the posterior samples. The lower panels show the relationship among posterior samples, and the upper panels show the Pearson correlation coefficients. Mo1est and mo2pest represent Mo[1] and Mo[2:6]. Respectively. The other M's represent covariate effects of seal, water temperature, hatchery production, and large marine mammals.



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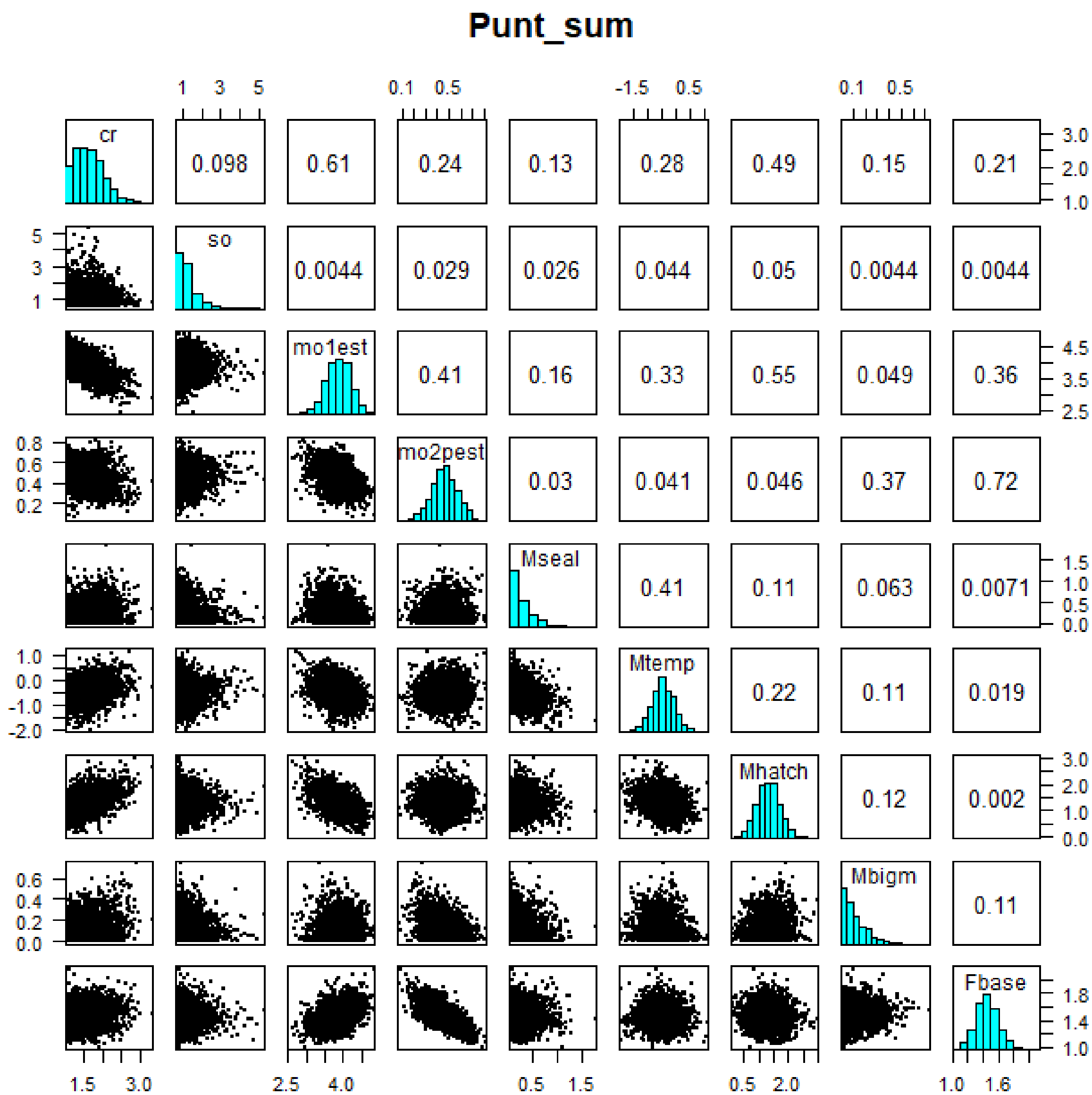

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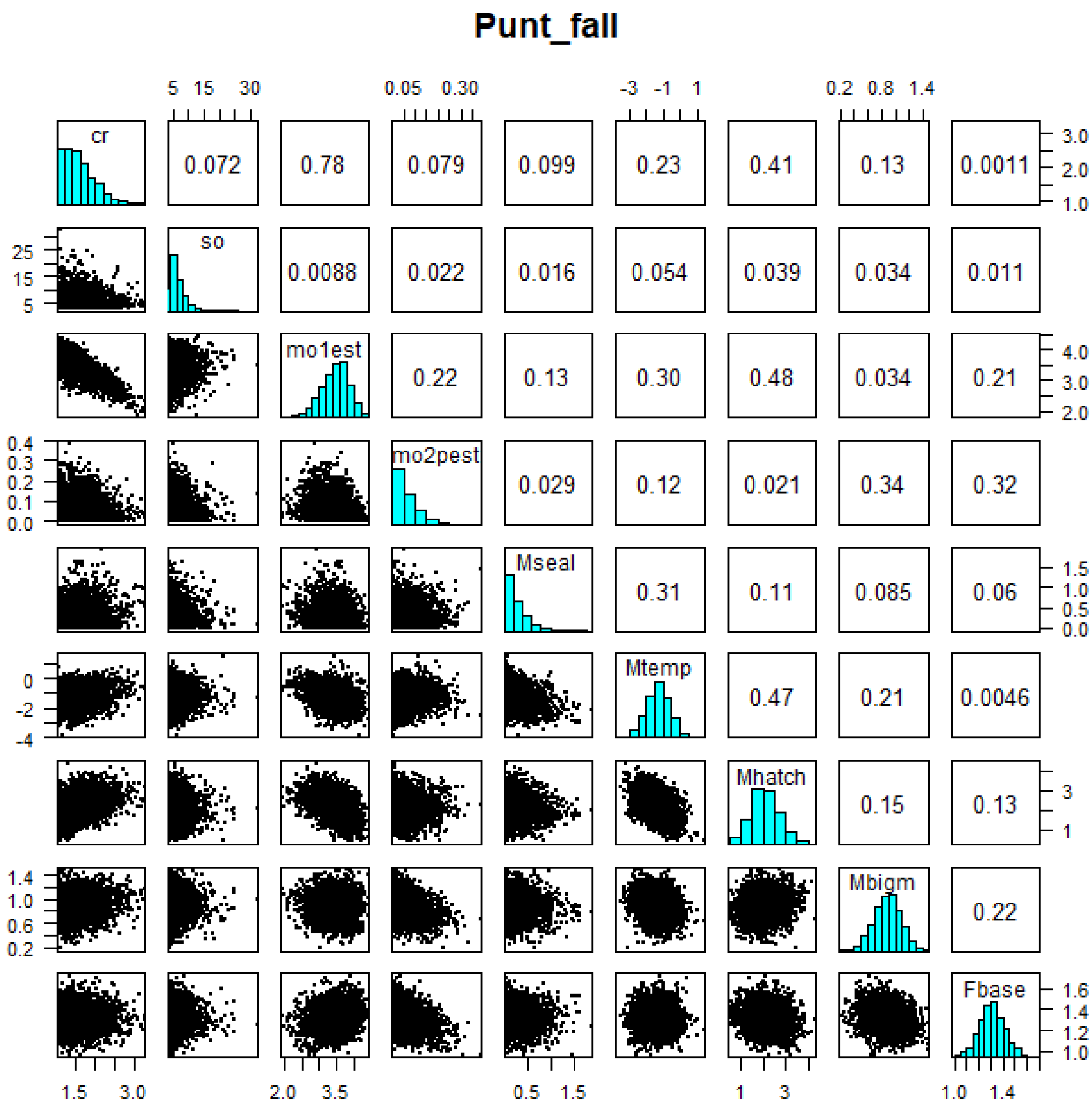

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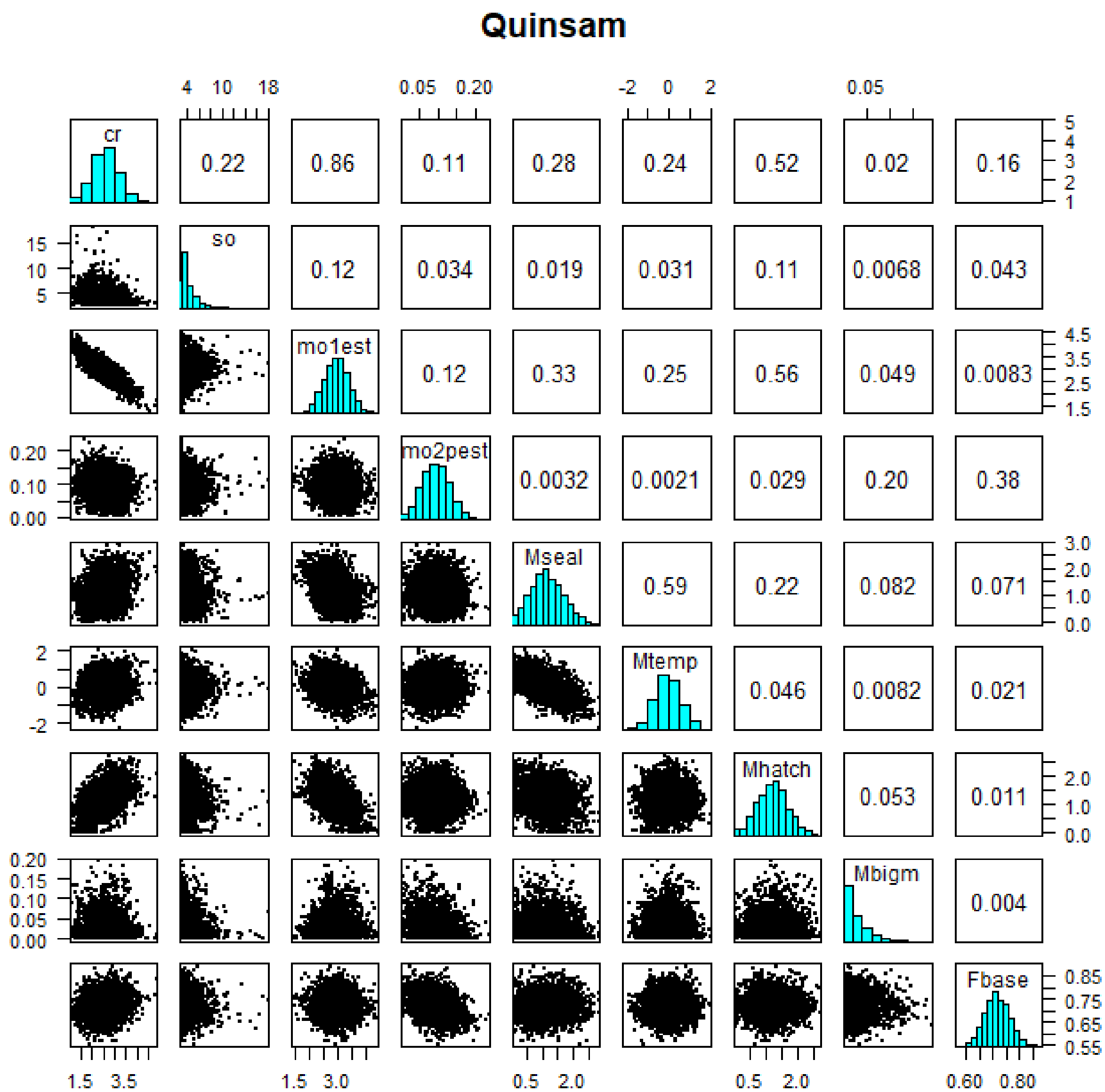

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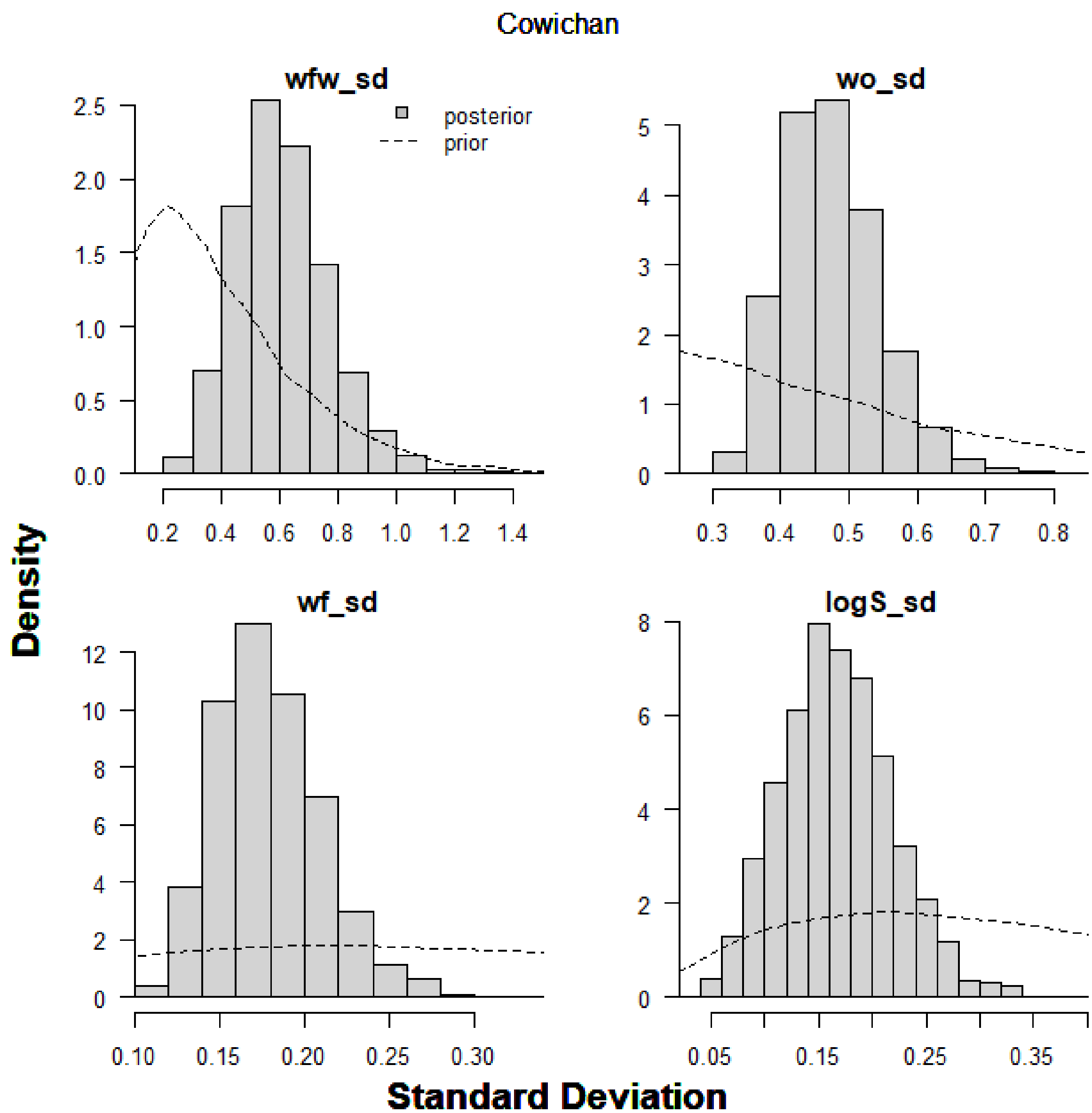
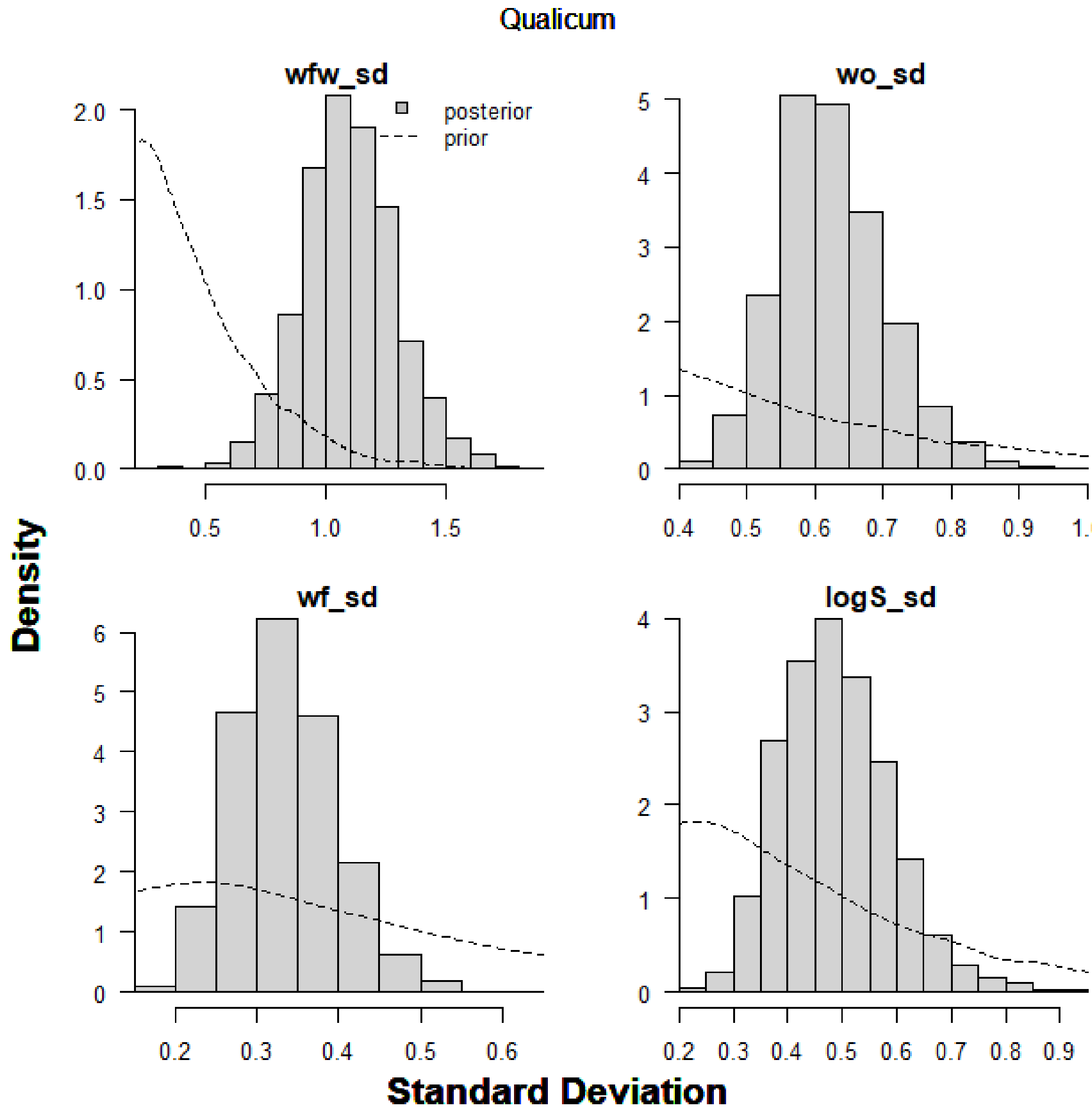


Figure 7. Comparison of posterior and prior distributions for standard deviations for random effects (wf_sd, wo_sd, wf_sd) and the observation error in the log of observed escapement (lnS_sd). See Table 2 for parameter definitions.



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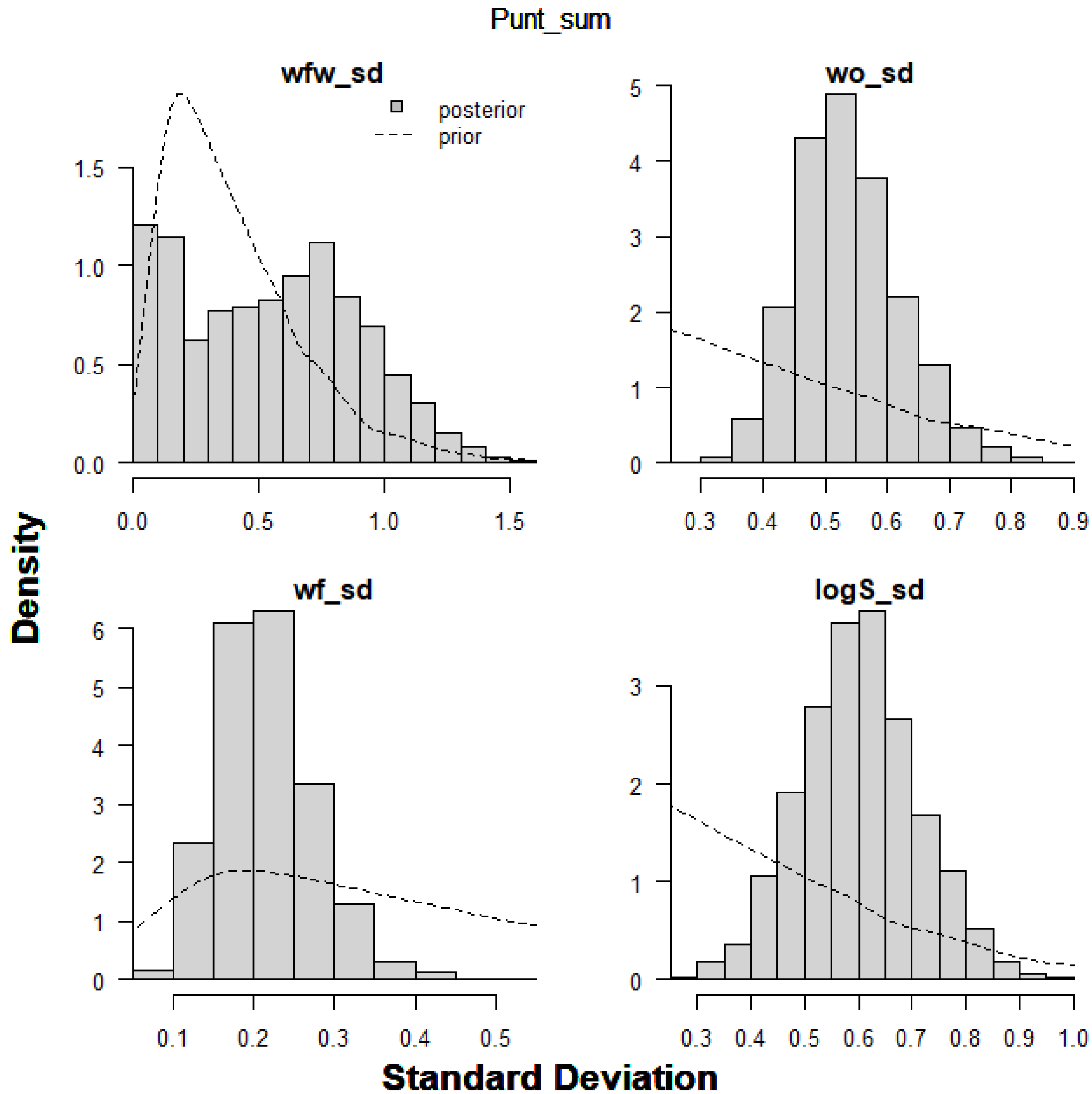

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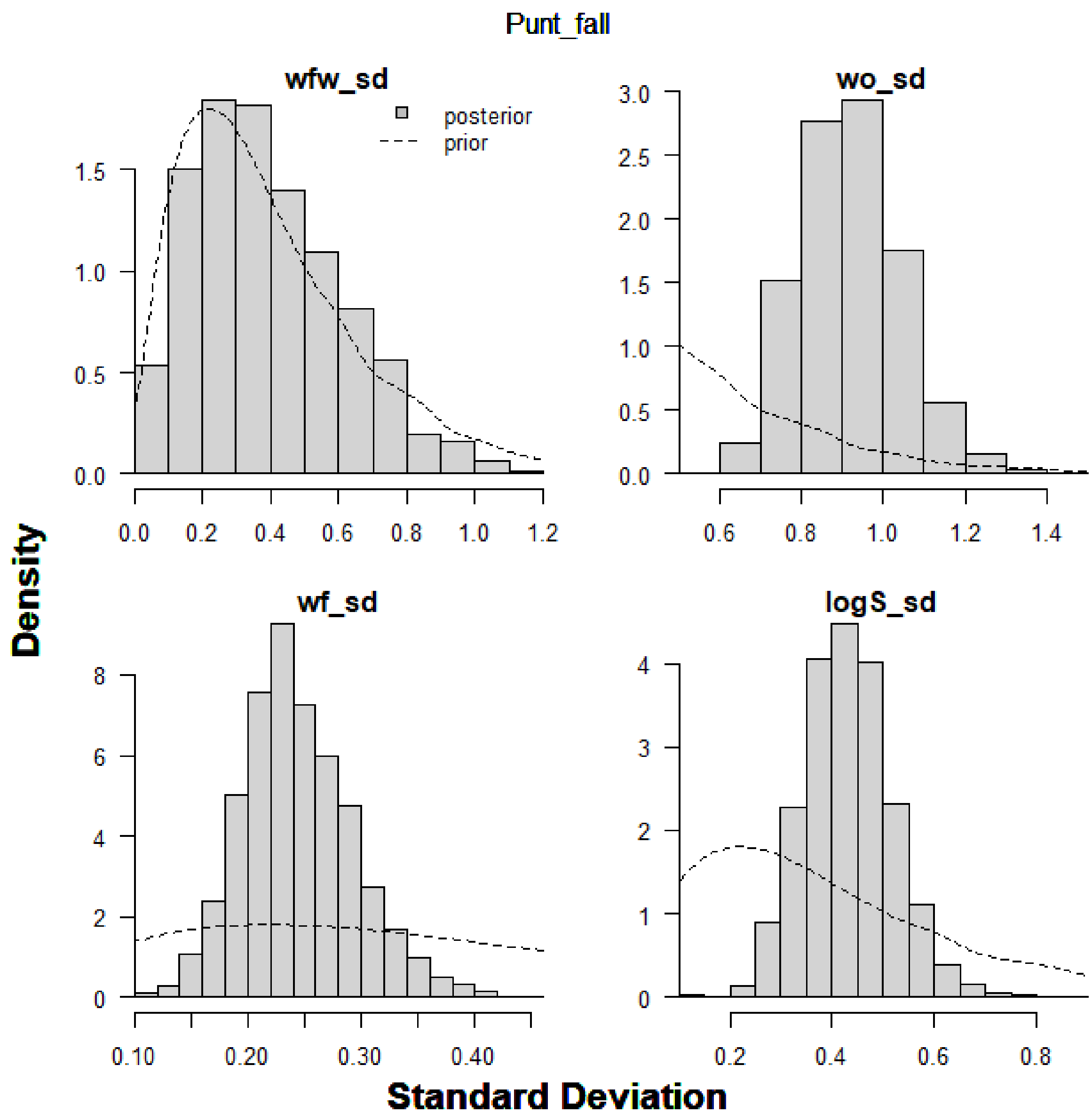

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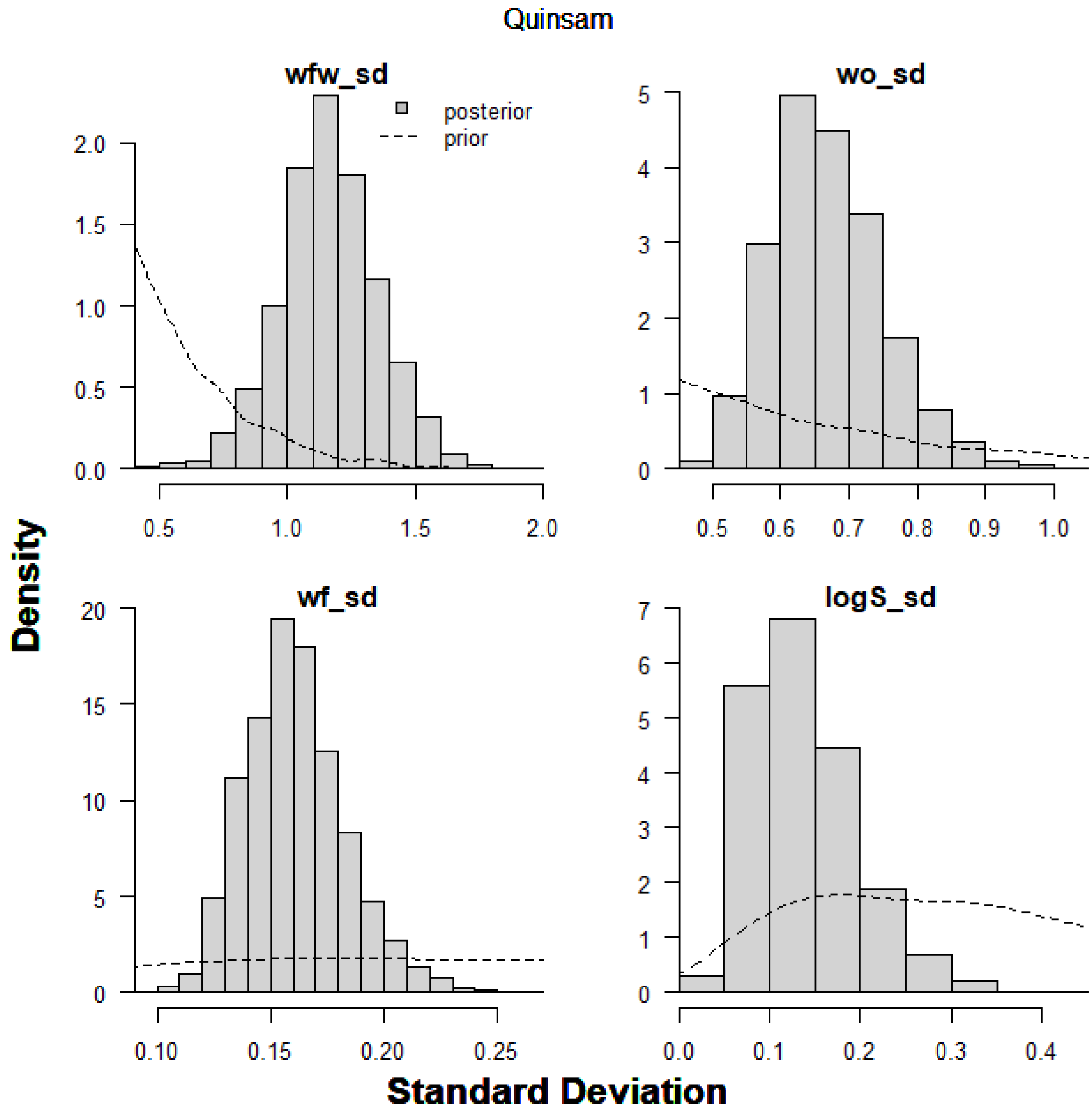

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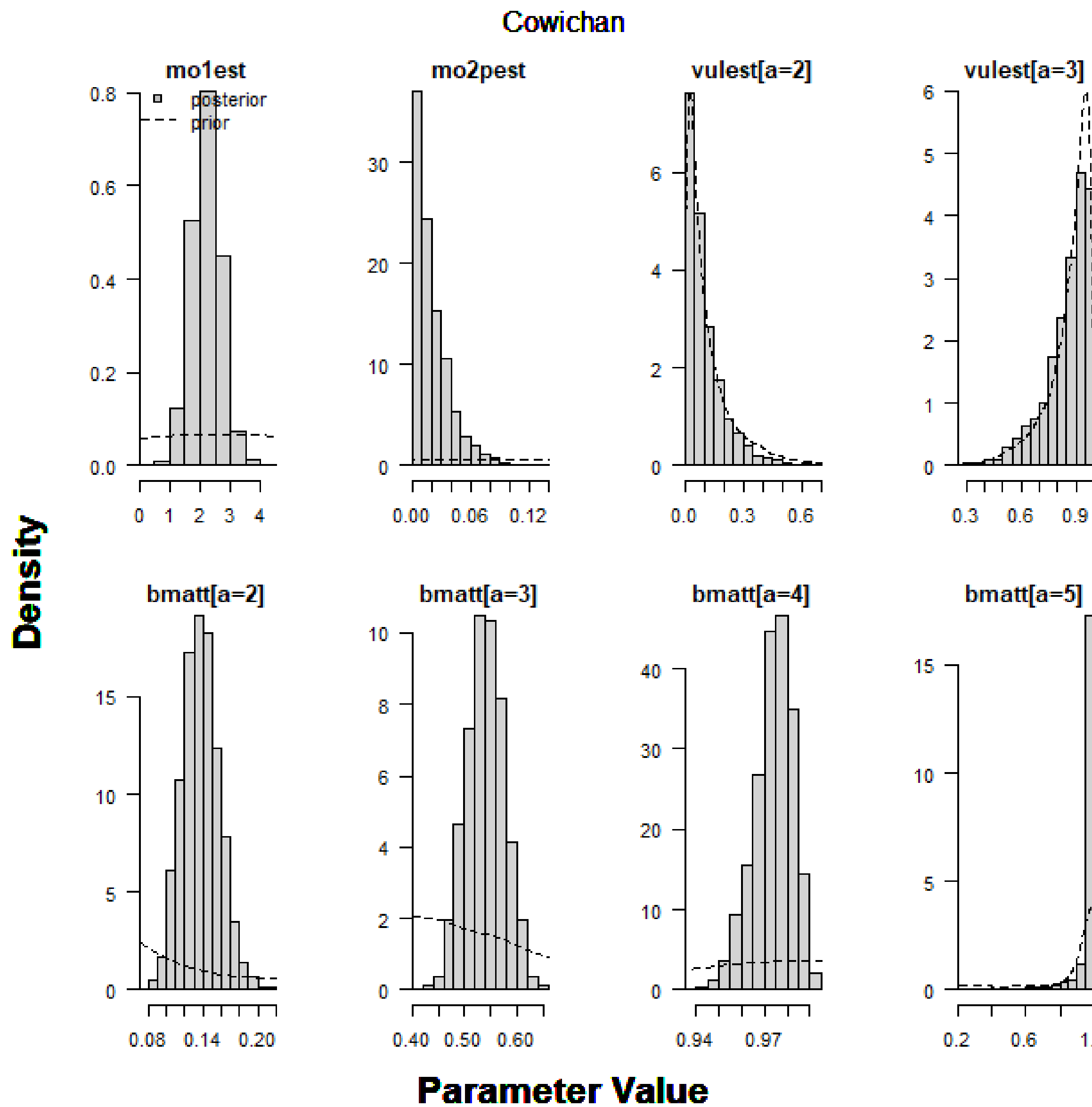
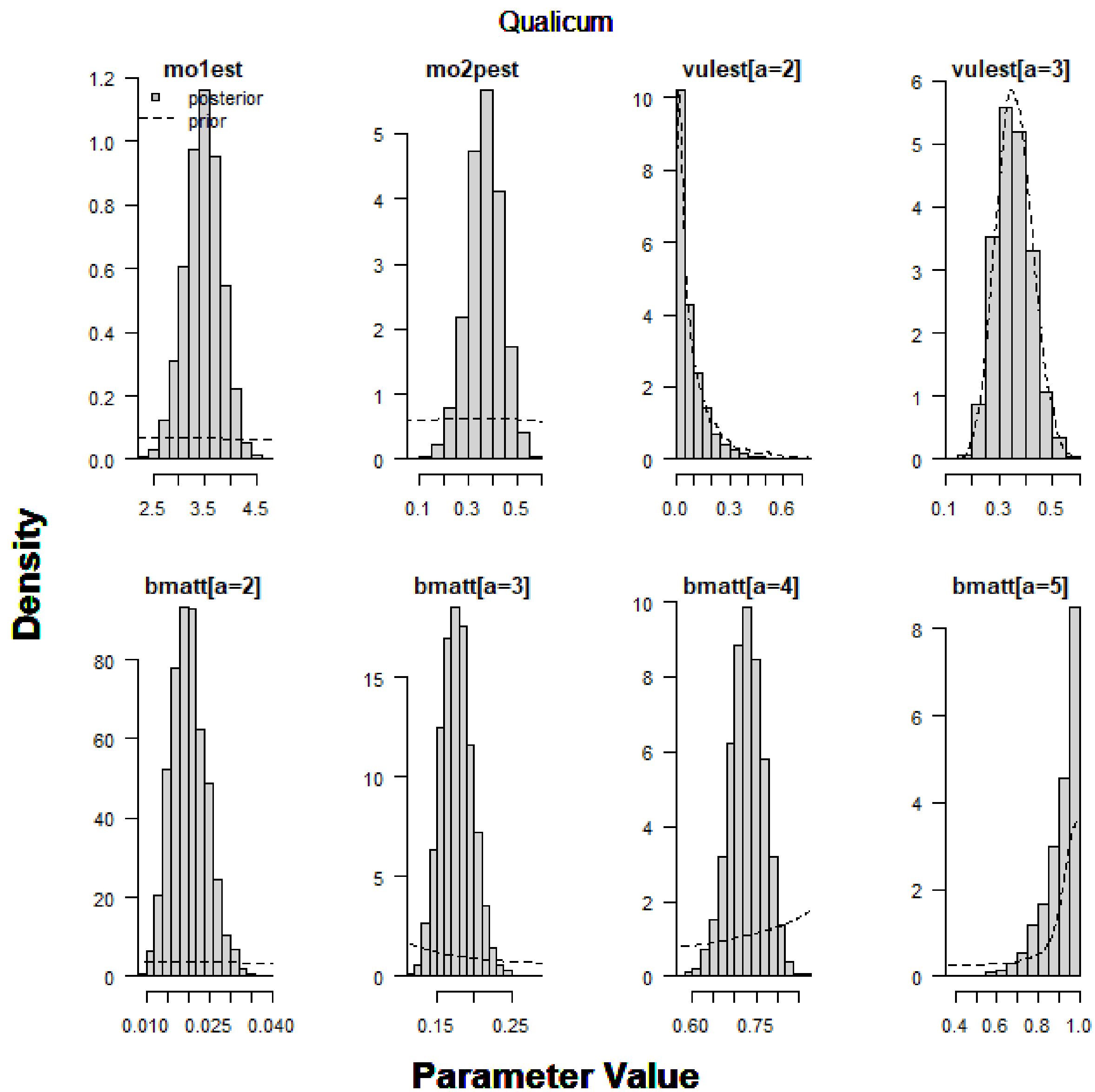


Figure 8. Comparison of posterior and prior distributions for parameters that depend on CWT data. mo1est and mo2pest represent Mo[1] and Mo[2] in Table 2. vulest[]'s represent transformed values of logit_vul in Table 2. bmatt[]'s represent transformed values of logit_mat[] from Table 2).



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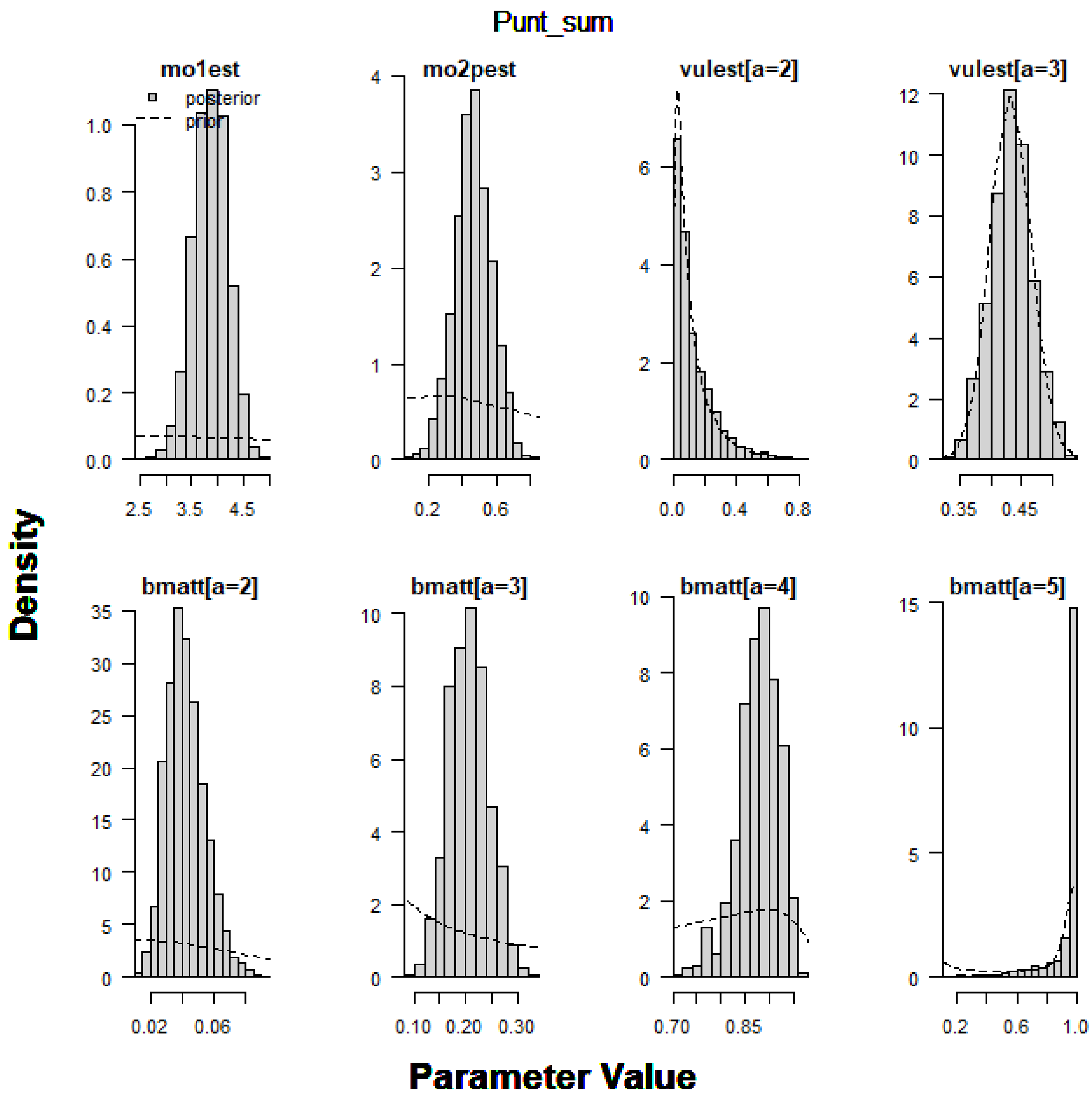

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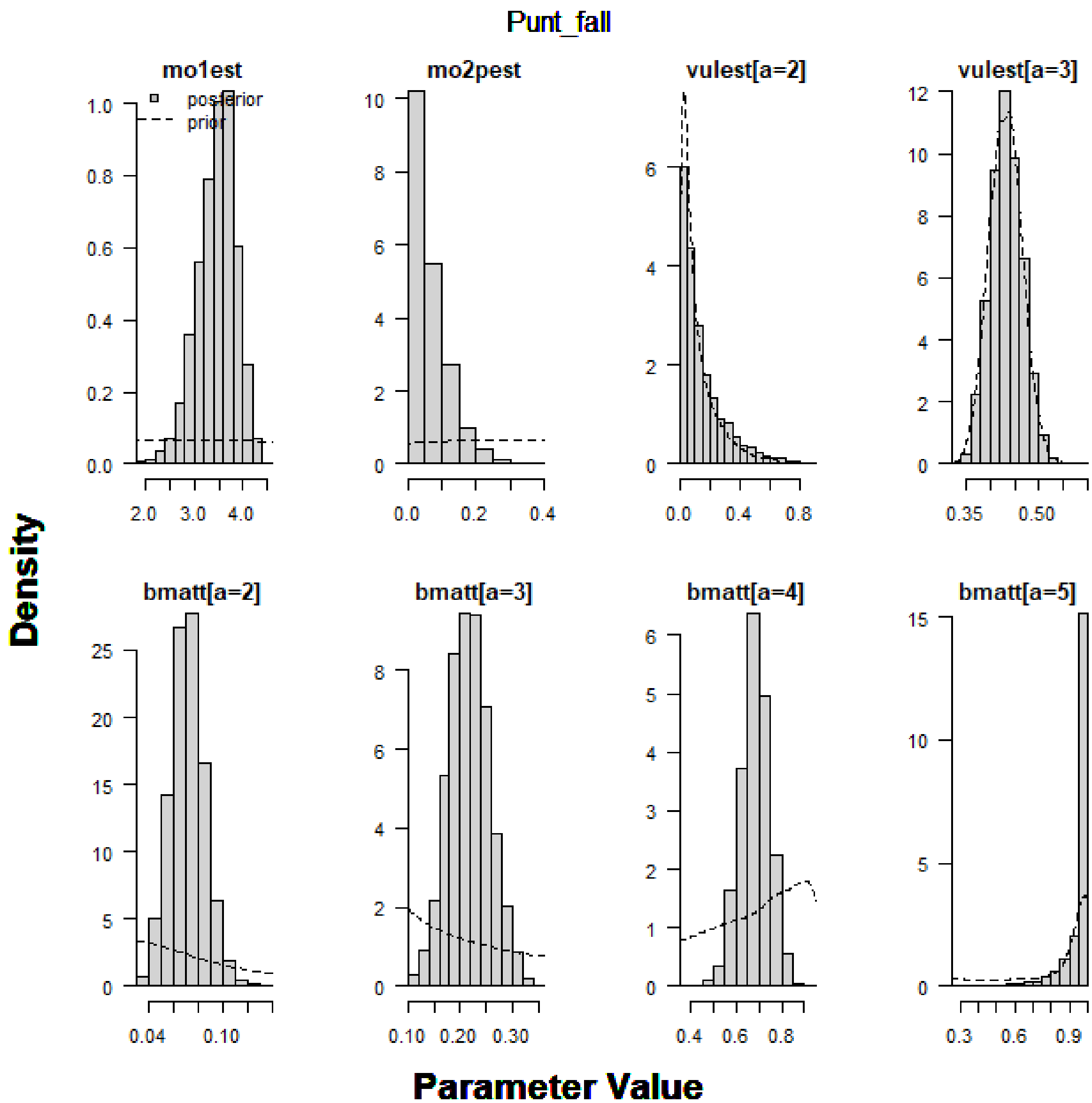

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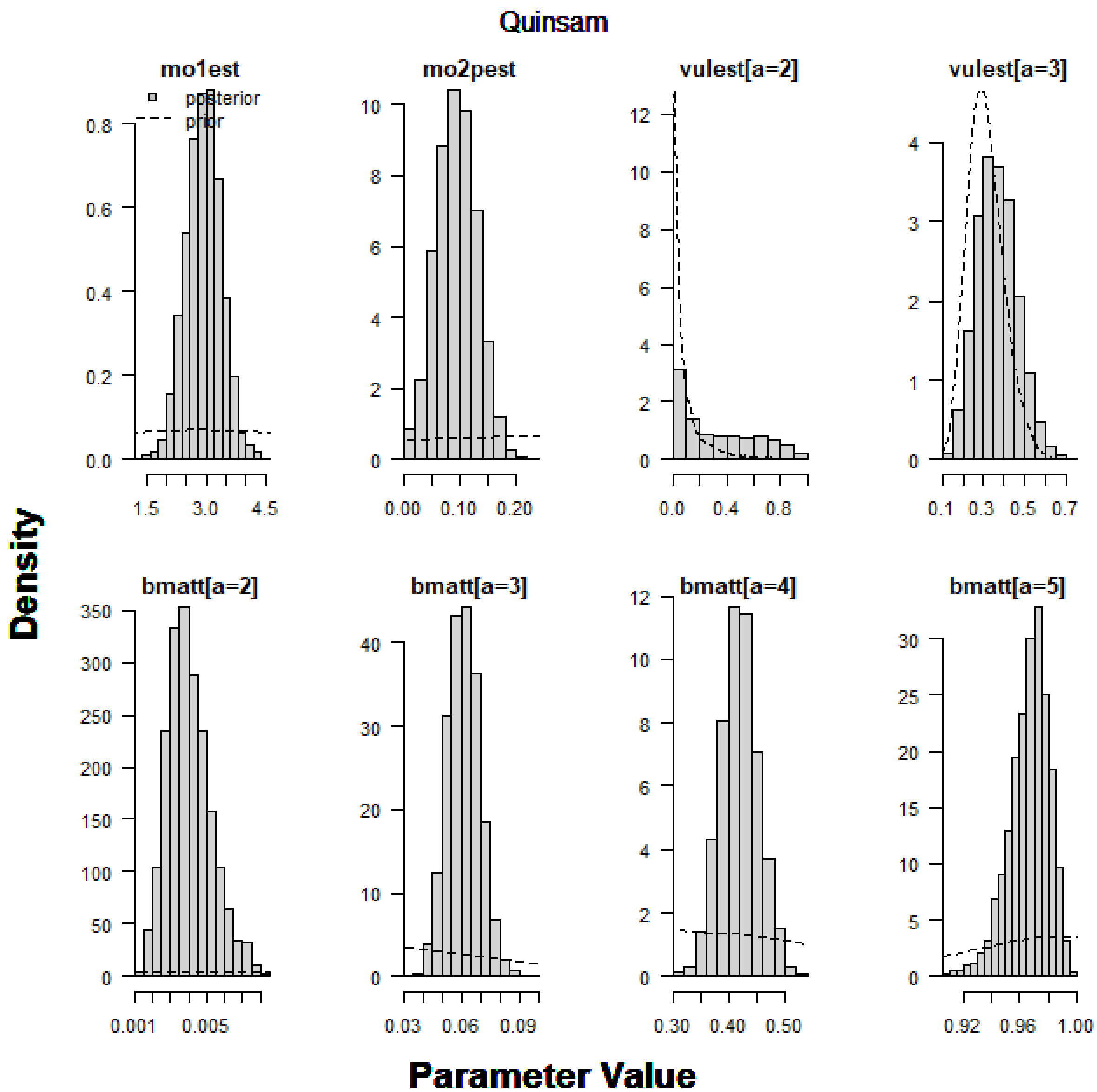

Figure 8. Con't.

Appendix A. Assumptions, Data, and Models used to Define Fixed Model Parameters and Construct Time Series to Estimate Time Variation in Marine Mortality Rates

This appendix briefly describes the approaches used to assign values for constants used I the estimation model and the approaches used to create covariate and historical fishing mortality time series.

HatchSurv: This fixed constant, survival rate of hatchery smolts shortly after release, was based on CWT observations for hatchery Coho Salmon which indicated that mortality rates of ~0.5 during downstream migration and early ocean rearing.

Msum: This constant, the mortality rate of mature fish from early summer through spawning, was provided by Kevin Pellett, DFO based on his experience with survival rate observations.

mo: These fixed constants are priors on estimated base mortality rates for age 1 and 2+ fish. They represent the base natural mortality rates by age when covariate values impacting ocean mortality are near zero. mo[a=1] is based on an average from ECVI stocks in the 1970s determined using CWT recovery rates (see MSR and Data sheets in *StGeo chinook release and catch data.xlsx*). mo[a=2+] values were those estimated by the Pacific Salmon Commision during the 1970s.

Seal N: This annual covariate of Harbour Seal abundance to predict variation in age 1 ocean mortality is based on a model of the trend in the Salish Sea seal abundance developed by Murdoch McAllister for other work (*murdoch's seal abundance in Georgia Strait Pinnipeds_inside_v2.xlsx*). Each annual abundance estimated is divided by the maximum estimate over the 1980-2020 time series. This time series could be improved/updated based on the most recent population estimates from DFO.

SOG hatch: This annual covariate to predict variation in age 1 ocean mortality is the annual number of total hatchery chinook Salmon smolt released in the Strait of Georgia. Each annual abundance estimated is divided by the maximum estimate over the 1980-2020 time series.

Temperature: This annual covariate to predict variation in age 1 ocean mortality is the annual average summer sea surface temperature at Entrance and Chrome Island stations. Annual values were standardized by subtracting the minimum over the 1980-2020 time series from each annual value, and then dividing this difference by the difference between maximum and minimum values over the times series (X[t]-min(X[]))/(max(X[])-min(X[])). The calculations for this covariate can be found in *chinook model temperatures.xlsx* and raw data can be found in *SOG_Temperature_PDO_chinook marine survival rates from CWT data.xlsx*.

Large Predator Abundance: This annual covariate to predict variation in age 2+ ocean mortality is an annual index large predator consumption of Chinook Salmon. The value for each year is the sum of estimated Chinook Salmon eaten per year by a Steller Sea Lion (SSL, per capita consumption) multiplied by ethe abundance of this species in Queen Charlotte sound. The index also includes the consumption of Chinook Salmon by Northern resident killer whales (NRKW), also calculated as the product of per capita consumption and abundance. The two per-capita consumption rates are calculated from average daily food consumption rates (60kg for NRKW, 17 kg for SSL and reported average proportions of chinook in their diets (60% for NRKW, 2% for SSL). The calculations for this covariate can be found in *SSL and NRKW abundance trends and potential Ms on chinook.xlsx*.

VPA Initialization: Model constants used as priors for relative vulnerability (vulo), mean maturation rates (mato), and the regional fishing mortality rate (RelRegF) were based on Virtual Population analysis in *StGeo chinook release and catch data.xlsx*.

Appendix B. Workflow for Chinook Salmon Age Structured Estimation and Forward Simulation Models

This appendix provides a brief description of the workflow required to run the estimation and forward simulation model. The estimation model estimates posterior distributions of model parameters and derived values (Fig. B1). The R script GetData.R reads in model input files (Excel or csv files). assigns some of the data model variable names, and calculates some constants needed by the model. The R script then calls Call_Model.R to put these variables in a list that can be read in by the stan model. This script also specifies initial values for some model parameters, and defines which output from the model that will be saved to an Rdata file. The stan model (CHLM.stan) is then called and output is saved in a subdirectory with a filename set to the fit_???.Rdata, where ??? is the abbreviation for the stock that was run (e.g., fit_Cow.Rdata for the output for the Cowichan model). A series of R scripts can then be called to examine model output and convergence. The R script MultiRun.R can be used to run the estimation model in a loop across stocks.

A forward simulation model is used to determine how escapement and survival rates vary under a range of potential futures (exploitation rates, hatchery production, trends in covariates assumed to impact marine survival). The simulation model reads in the posterior distribution of model parameters created when the estimation model was run. The forward simulation model also reads in the same data files used in the estimation. These data are generally only used to compare model predictions with data for the historical portion of the time series (1980- 2020). However, some files, such as covariates.csv also include potential future values.

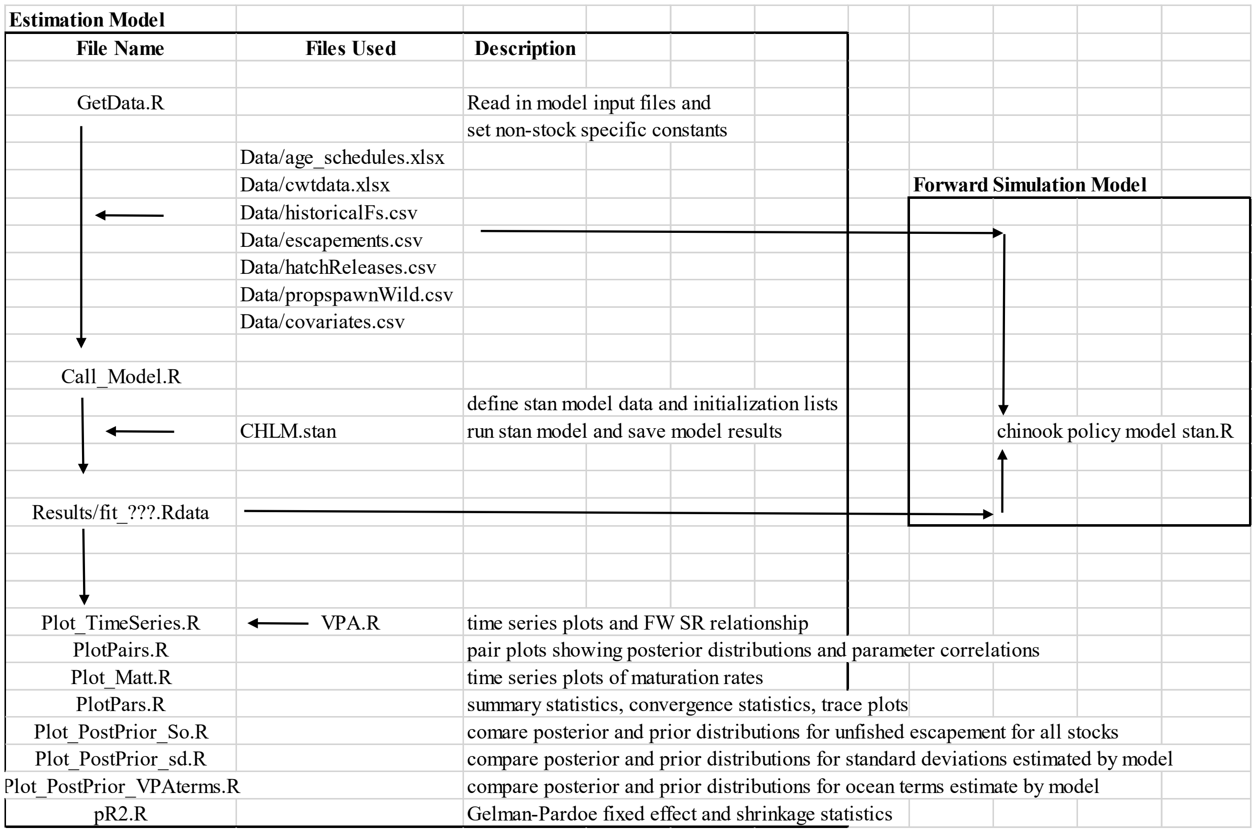

Figure B.1. Workflow diagram showing the inputs and scripts used to run the estimation (CHLM.stan), and forward simulation model (chinook policy model stan.R).