# Population Viability of Willamette River Winter Steelhead 

An assessment of the effect of sea lions at Willamette Falls

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This document describes methods used to assess the effects of sea lions at Willamette Falls on the viability of four populations of wild winter steelhead. Several data sets were compiled, manipulated, statistically modeled, and ultimately used to project population dynamics through time. An accompanying webpage provides all the data and MATLAB computer code to replicate results: http://people.oregonstate.edu/~falcym/WillametteSteelhead.html

## Contents

$\qquad$
Overview of Method ..... 3
Abundance of Willamette Winter Steelhead ..... 4
Mortality from Sea Lions ..... 7
Age Composition of Spawners ..... 10
Angling Mortality ..... 10
Proportion of Hatchery-Origin Spawners. ..... 10
Spawner-Recruit Analysis ..... 11
PVA. ..... 13
References ..... 17

## PVA Results

The results of the PVA indicate that sea lions have a large negative effect on the viability of winter steelhead (Table 1). The remainder of this document elaborates how these results were obtained.

Table 1. Probabilities of quasi-extinction over a 100 year period in four populations of Willamette River winter steelhead under four different scenarios. Scenarios with sea lions assume that the predation mortality estimated during that year will continue indefinitely. The lowest predation rate was observed in 2015 and the highest predation rate was observed in 2017.

|  | Population |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
| $\quad$ Scenario | N. Santiam | S. Santiam | Calapooia | Molalla |
| No Sea Lions | 0.015 | 0.048 | 0.993 | 0.000 |
| 2015 Sea Lions | 0.079 | 0.158 | 0.998 | 0.001 |
| 2016 Sea Lions | 0.274 | 0.335 | 0.999 | 0.021 |
| 2017 Sea Lions* | 0.644 | 0.599 | 0.999 | 0.209 |
|  |  |  |  |  |

## Population

Viability Analysis

Population viability analysis (PVA) can be broadly defined as the use of quantitative methods to predict the future status of populations under defined conditions or scenarios. Here, a PVA is used to determine the probability of quasiextinction over a 100 year period. The PVA scenarios perpetuate observed effects of sea lions at Willamette Falls.

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## Overview of Method

Sea lions feed on adult salmonids attempting to find passage over Willamette Falls. Mortality of adults during their spawning run is considered to have a density independent effect on subsequent survival rates. This is analogous to harvest mortality. Thus we can usefully employ common fisheries stock assessment models to capture population dynamics.

With a time series of spawner abundance, spawner age compositions, and mortality due to fishing and sea lions, it is possible to compute the adult recruits (progeny) associated with each year's spawner abundance. Density-dependence in these data can be modeled with Ricker or Beverton-Holt type stock-recruitment functions.

Bayesian analysis uniquely permits probabilistic interpretation of parameter estimates, and the Markov chain Monte Carlo methods used to fit Bayesian models conveniently preserves the covariance structure among parameters. Bayesian methods were therefore used to probabilistically describe parameter uncertainty a stock recruitment relationship.

The estimated stock-recruitment relationship with parameter uncertainty and residual autocorrelation is combined with age composition and adult mortality data. This is sufficient information to project population dynamics through time. The PVA program takes 1000 random draws from the parameter posterior distribution of the best stock recruitment model, and then replicates a 100-year time series 100 times. The total number of simulations where spawner abundance falls below a critical threshold across 4 consecutive year is divided by the total number of simulations $(100,000)$. The result of this computation is the probability of quasiextinction.

Density
Dependence

Density dependence
occurs when
demographic parameters (e.g. birth rate or death rate) depend on the density of individuals in the population. For example, as the density (number) of fish increases, competition can cause survival rate to decrease. The form and magnitude of density dependence is a critical component of population dynamics, extinction risk, and optimal
harvest rate.

## Abundance of Willamette Winter Steelhead

The North Santiam, South Santiam, Calapooia, and Mollala river systems are used to delineate "populations" of winter steelhead. This delineation is consistent with previous conservation and planning efforts (ODFW 2008). Several sources of information were used to construct time series of spawner abundances in these focal populations.

A counting station on the fishway at Willamette Falls has produced a time series of annual abundances of winter steelhead dating back to 1946. Since Willamette Falls is below the focal populations, additional information is needed to apportion annual counts at the falls into each population.

A radiotelemetry study conducted in 2013 found that 106 out of 170 tagged fish ( $62 \%$ ) reached their maximum migration point within one of the four focal populations (Jepson et al. 2014). This is assumed to reflect spawning distribution because fish were rarely observed to wander among river systems (Jepson 2017 personal communication). Thus we conclude that $38 \%$ of the winter steelhead that pass Willamette Falls are not members of the focal populations.

Fish are enumerated at the Minto fish facility in the upper North Santiam and at Foster Dam in the upper South Santiam. These "known fate" individuals were therefore subtracted out of the Willamette Falls count $\left(N_{w f}\right)$ to obtain the number of fish whose spawning distribution needs to be determined $N_{t b d}$ :

$$
N_{t b d}=N_{w f} * 0.62-N_{m i n t o}-N_{\text {foster }}
$$

The quantity $N_{t b d}$ is apportioned to the focal populations based on miles of spawning habitat within each population $\left(L_{p}\right)$ multiplied by the observed redd density $\left(D_{t, p}\right)$. Note that $L_{p}$ is temporally static quantity (no time subscript), whereas $D_{t, p}$ varies in time and across populations. In the North Santiam and South Santiam populations, only spawning habitat mileage below the counting facilities is used because there is already a known number of fish that go above the facility. Let $D_{t, p=N S}$ be the density of redds in year $t$ within the North Santiam ( $N S$ ) population. The population abundance that year is

$$
N_{t, N S}=N_{t b d, t}\left(\frac{D_{t, N S^{*} L_{N S}}}{\sum_{p}^{4}\left(D_{t, p} * L_{p}\right)}\right)+\text { Minto Count } .
$$

Observations of redd density have been made at multiple sites within each population since 1985. However, weather conditions and staff workload can prevent observation of redd density at some sites and years. If a given site generally has a high density of redds, then neglecting the site on a given year could give a false appearance of low redd density within the population relative to the years when observation are made at the site. Across all four populations, there are 30 redd survey sites. The date when most surveys began is 1985. There are 30 sites X32 years $=960$ potential observations of redd
densities in the redd density data set. However there are 478 actual observations. The extent of missing values is therefore an issue that needs to be resolved so that all available data can be used while also minimizing biases associated with missing values from above average or below average sites.

A multiple imputation technique was developed to infer missing redd densities. Redd survey data from all four populations was combined with the Willamette Falls counts, Minto counts and Foster counts, yielding a matrix with 32 years (rows) and 33 locations (columns). Beginning with the first location, the first year with a missing value was identified. All existing redd densities in that location (across years) were linearly regressed on the redd densities in the next location. A prediction for the missing value was generated, and the $\log$ likelihood of the associated statistical model was recorded. A new linear regression was established from the next location, and the model prediction and log likelihood were once again recorded. This repeats across all locations, yielding 32 regressions for a single missing value. A final, model averaged prediction for the missing value was obtained as

$$
\widehat{D}_{t, p}=\frac{\sum_{i}^{l} \hat{y}_{*}^{*} w_{i}}{\sum_{i}^{l} w_{i}}
$$

where $\hat{y}_{i}$ is the model prediction from location $i$ and $w_{i}$ are individual model weights. The $w_{i}$ are calculated

$$
w_{i}=\frac{e^{-0.5 B I C_{i}}}{\sum_{i}^{I} e^{-0.5 B I C_{i}^{\prime}}}
$$

where $B I C_{i}$ is the Bayesian information criterion of regression $i$,

$$
B I C_{i}=2 * n l l+k * \log (n),
$$

$n l l$ is the negative $\log$ likelihood, $k$ is the number of estimated parameters (3) and $n$ is the sample size used in the regression.

Imputed values are not used to impute other values. Imputation of data can be problematic because methods such as the one employed here will artificially reduce the variance of the data. However, this is

## Likelihood

Likelihoods have provided a major theoretical foundation for scientific inference since the work of Ronald Fisher in 1922.
Given a probability distribution function, one can find parameter values that maximize the likelihood of observed data. Such
parameters are called maximum likelihood estimates, and the
likelihood of the observed data given these parameter estimates is a relative measure of the adequacy of the model.
not a problem in this particular application because the purpose is to merely avoid biasing an average across sites when a particular site has a missing value.

The result of the foregoing methods to apportion Willamette Falls counts of winter steelhead into time series of abundances in the four focal populations is presented in Figure 1.


Figure 1. Estimated abundances of wild winter steelhead since 1985. Prior to 1985, it is not possible to apportion Willamette Falls counts because few or zero redd surveys were conducted within each population.

## Mortality from Sea Lions

Sea lion predation on salmonids has been rigorously monitored by Wright et al. (2016) since 2014. The estimated number of winter steelhead killed by sea lions in 2014, 2015, and 2016 is 780, 557, and 915 respectively. Wright et al. (2016) note that the 2016 estimate applied to just the "falls strata" whereas monitoring in 2014 and 2015 included the fall and a "river" stratum just below the falls. Using information from years when both strata were monitored, Wright et al. (2016) find that the mortality in the river stratum is 0.385 of the falls plus river. The 2016 winter steelhead estimate in the falls stratum was expanded to a number reflecting mortality in the falls and river strata: 915/(1-0.385) = 1488.

However, as noted in the previous section, $38 \%$ of winter steelhead at Willamette Falls are not members of the four focal populations. Thus only $62 \%$ of the estimated mortality is on fish that pertain to the focal populations:

$$
\left[\begin{array}{c}
780 \\
557 \\
1488
\end{array}\right] *[0.62]=\left[\begin{array}{l}
486 \\
347 \\
927
\end{array}\right]
$$

An additional adjustment is needed because the mortality estimates pertain only to the time of the monitoring project, yet $23 \%, 30 \%$ and $22 \%$ of winter steelhead runs of 2014,2015 , and 2016, respectively, pass through the monitoring area before mortality monitoring begins (Figure 2). A loess quadradic polynomial local regression with span 0.4 was used to smooth daily counts of California sea lions (Figure 3, green). An "interaction index" was computed as the sum of the daily products between the loess smooth of California sea lions (CSL) and counts of winter steelhead (StW) at Willamette Falls:

$$
\text { Interaction Index }=\sum_{d a y=F e b 2}^{\text {June } 1} \text { CSLsmooth }_{\text {day }} * S t W_{\text {day }}
$$

The leftmost point of the loess smooth was then extended further to the left (Figure 3, black), reflecting the assumption that California sea lions are present at low densities before the monitoring project began. The interaction index was then recomputed beginning November 1. The ratio between these interaction indices is a factor for expanding sea lion mortality to the entire run of winter steelhead. These factors were computed three times, once for each winter steelhead abundance time series in given in Figure 2. Each factor used the 2016 sea lion information.


Figure 2. Vertical red bars give the initiation of the California sea lion (CSL) monitoring study relative to the run timing of winter steelhead (StW) at Willamette Falls.


Figure 3. Maximum daily counts of California sea lion (CSL) are identical to Figure 2c.

The factor values are 1.10, 1.14, and 1.09. Even though $23 \%, 30 \%$ and $22 \%$ of the steelhead runs went unmonitored for sea lion mortality, expanding for the unmonitored component of the runs adds just $10 \%, 14 \%$ and $9 \%$ because California sea lion abundance is relatively low during this time. The final morality estimates for year 2014, 2015, and 2016 are: $486^{*} 1.10=531,347^{*} 1.14=395$, and $927^{*} 1.09=1016$, respectively.

Wright et al. (2014) note that predation losses of salmonids were generally a few hundred or less at the Falls from the late 1990s through 2003. Starting with 150 salmonid mortalities, we made the same adjustments described above (expand for river stratum, deflate for proportion spawning outside the focal populations, expand by mean of three factors used to correct for early run timing) and then deflated the number again by the mean proportion of all the salmonid mortality during 2014, 2015, and 2016 that are winter steelhead ( $15 \%$ ). This computation results in 33 winter steelhead. This amount of mortality was assumed to occur from 1995 through 2003, with linear increase in mortality until the study of 2014, and zero mortality prior to 1995. This time series of mortality is then apportioned to each of the four populations by the relative abundance of fish in each population, as calculated in the previous section. Mortality by California sea lions was $15 \%, 13 \%$ and $24 \%$ of the winter steelhead runs in 2014, 2015, and 2016, respectively.

In the spwner-recruit analysis below, the mortality caused by sea lions within each population on year $t$ (denoted $M_{t}$ ) is added into the recruits.

## Age Composition of Spawners

Age of spawning fish was determined through scale analysis. There were a total of 784 scales collected from 16 years. The composition of ages on a given year was applied to all populations. When age composition was missing for a given year, the average over all years with age data was used. The matrix of proportions of fish at age $=1,2,3, . .6$, on given years $(\mathrm{t})$ is denoted $A_{t, a}$ in the recruitment calculations below.

## Angling Mortality

There has not been a directed retention fishery on Willamette River winter steelhead since 1992. Following previous conservation planning efforts (ODFW 2008), harvest rates on winter steelhead in the Willamette River system up through 1992 were assumed to be $21 \%$, then decline to $5 \%$ to the present time for incidental mortality in fisheries targeting other stocks. A $2 \%$ incidental harvest rate is assumed in the Columbia River for all years. The vector of harvest rates ( 0.23 through 1993, 0.07 thereafter) it denoted $H R_{t}$ in the recruitment calculations below.

## Proportion of Hatchery-Origin Spawners

Hatchery winter steelhead have not be produced in the Willamette River since the late 1990s. The proportion of hatchery-origin fish spawning in the four focal populations in the 1980s and 1990s has been determined from scale analysis and used in previous conservation planning efforts (ODFW 2008, Appendix B). Specific values for each year and population can be found in the online supplement. Each population's vector of proportions of hatchery-origin spawners in year t is denoted $\mathrm{pHOS}_{t}$ in the recruitment calculations below. This is needed because hatchery-origin fish should not be counted as recruits of the naturally spawning population. The PVA simulates dynamics of naturally spawning fish only.

## Spawner-Recruit Analysis

The abundance of naturally produced ("wild") adult recruits associated with fish spawning on year $t$ is

$$
R_{S(t)}=\sum_{a=1}^{6} A_{t+a, a}\left(\frac{S_{t+a} *\left(1-p H O S_{t+a}\right)}{\left(1-H R_{t+a}\right)}+M_{t+a}\right)
$$

From here it is possible to fit nonlinear models of the relationship between recruits and spawners. Errors in such models are customarily lognormal, reflecting the multiplicative survival processes that gives rise to uncertainty in the number of recruits.

Bayesian methods were adopted for recruitment modeling for two related reasons. First, Bayesian analysis uniquely yields probabilistic interpretation of parameters. Second, the Markov chain Monte Carlo (MCMC) methods used to fit Bayesian models allow parameter uncertainty to be easily folded into a PVA simulations. JAGS software was used to run the MCMC. JAGS called from MATLAB using matjags.m.

Beverton-Holt models were fitted to these data, but the posterior distribution for the productivity parameters always exactly matched the noninformative priors. These data therefore do not contain sufficient information to reliably identify the Beverton-Holt productivity parameter. A Ricker models were used instead (Table 2). Data from all four populations were combined into a "single" recruitment model. Three such models were constructed that make different assumptions about the acrosspopulation independence of parameters (Table 2). Model 1 assumes all parameters, including error variance, are unique in each population. Models 2 and 3 assume that some parameters can be shared across populations. Model 2 assumes there is a single error variance shared by all four populations, but each population has a unique productivity ( $\alpha$ ) and rate of compensatory density dependence ( $\beta$ ). Model 3 assumes that productivity is identical across populations, while the magnitude of compensatory density dependence and error are unique to each population. In all three models, extremely diffuse (noninformative) uniform priors were used for $\alpha$ ( $\operatorname{Unif}(1,200)$ ), $\beta$ (Unif( $0,0.1$ )), and the standard deviation $\varepsilon(\operatorname{Unif}(0,4))$.

Table 2. Three Ricker recruitment models fitted to four populations of winter steelhead spawner-recruit data. The models make different assumptions about the number and structure of necessary parameters. WAIC measures relative out-of-sample predictive performance.

| ID | Model | \# Params | WAIC |
| :---: | :--- | :--- | :--- |
| 1 | $R_{t, p}=\alpha_{p} S_{t, p} e^{-\beta_{p} S_{t, p}} e^{\epsilon}, \epsilon \sim N\left(0, \sigma_{p}\right)$ | 12 | 224.8 |
| 2 | $R_{t, p}=\alpha_{p} S_{t, p} e^{-\beta_{p} S_{t, p}} e^{\epsilon}, \epsilon \sim N(0, \sigma)$ | 9 | 248.9 |
| 3 | $R_{t, p}=\alpha S_{t, p} e^{-\beta_{p} S_{t, p}} e^{\epsilon}, \epsilon \sim N\left(0, \sigma_{p}\right)$ | 9 | 217.6 |

Four MCMC chains per model were ran. The first 35,000 iterations were discarded as a "burn-in" period, and 10,000 samples per chain were retained after thinning 1:13 samples from the MCMC. Trace plots of the MCMC were visually inspected for signs of mixing and convergence. Extremely good estimates of the Gelman-Ruben diagnostic ( $\widehat{R}=1 \mp 0.0001$ ) were obtained.

Watanabe-Akaike Information Criterion (WAIC) can be used to assess the relative out-of-sample predictive performance of Bayesian models (Gelman, Whang, and Vehtari, 2013). Each iteration of the MCMC yields a draw from the multidimensional posterior distribution. This parameter vector can be used to compute the probability density of each datum in the data set. This produces I-by-S matrix of densities, where I is the number of data points (4 populations $X 32$ years $=128$ ), and $S$ is the arbitrary number of MCMC samples in the posterior. Armed with this matrix, the computed log pointwise predictive density is

$$
l p p d=\sum_{i=1}^{I} \log \left(\frac{1}{S} \sum_{S=1}^{S} p\left(y_{i} \mid \theta^{s}\right)\right)
$$

A correction for effective number of parameters to adjust for overfitting is obtained with

$$
\text { pwaic }=\sum_{i=1}^{I} V_{s=1}^{S}\left(\log p\left(y_{i} \mid \theta^{S}\right)\right),
$$

where V is the sample variance. Thus pwaic is just the posterior variance (across MCMC iterations) of the $\log$ predictive density for each data point, summed over all data points, and

$$
\text { WAIC }=-2^{*}(\text { lppd-pwaic }) .
$$

The units of WAIC can be interpreted like the more familiar AIC and DIC. Specifically, smaller values indicate better models. There are 31.4 units separating model Model 2 and Model 3, indicating that there is no empirical support whatsoever for Model 2 (Table 2). There are 7.3 units separating Model 1 and Model 3, indicating that Model 1 is considerably inferior to Model 3. Model 3 is therefore the only model used hereafter. Hilborn and Waters (1992, page 271-272) argued from first principles that productivities $(\alpha)$ should be similar within a species over much of its range. The model selection results presented here support Hilborn and Walters' (1992) assertion.

The fit of Ricker Model 3 to the spawner-recruit data is given in Figure 4. Uncertainty in Ricker parameters gives rise to multiple potential recruitment functions. Random draws from the MCMC output ensures that parameter values and parameter covariance are obtained in proportion to the associated posterior probability densities.


Figure 4. Spawner-recruit data and associated Ricker Model 3 fits. Thick green lines produced from the mean of the parameter posterior distribution. Thin grey lines produced from randomly chosen parameters in the posterior distribution. The blue diagonal line shows the 1:1 relationship between spawners and recruits.

The population viability analysis (PVA) model use here was also used in a previous assessment of coastal fall Chinook (ODFW 2011). The PVA is a computer model that uses information from the spawner-recruit analysis (see previous section) to project/simulate population abundances into the future. 100,000 repetitions of the 100-year simulation are conducted, and the fraction of these that result in an extinction event yields the probability of extinction. It is important to note that the word "extinction" refers to a population (i.e. "local extinction", or "extirpation"), not a species.

The PVA was ran under four different scenarios for each population. In the scenario called "No Sea Lions" (Table 1) it is assumed that there is no additional mortality beyond the incidental angling mortality during the adult life stage. This assumption holds for all 100 years in the simulation. The scenario called " 2015 Sea Lions" perpetuates the lowest mortality rate observed since 2014 for all 100 years of the PVA simulation. The scenario called "2017 Sea Lions" perpetuates the highest mortality rate observed since 2014 for all 100 years of the PVA simulation.

The Ricker recruitment function that is fitted to each population (Model 3) is the model of intergenerational population dynamics that is used within the PVA to simulate spawner abundances through time. However, in the spawner-recruit analysis, "recruits" are defined as pre-angling and presea lion adults. The very same inland mortality estimates that are used to estimate adult recruits from spawner abundances are also used by the PVA to convert adult recruits back into spawners. Indeed, the analytical steps used to estimate recruits for the spawner-recruit analysis are reversed inside the PVA. The PVA

1. takes a given spawner abundance on year $t$,
2. uses the recruitment function to compute adult recruits,
3. recruits are apportioned across years according to random permutations of the age composition data,
4. recruits are summed across ages within a year and then deflated by harvest rate sea lion mortality (if any).

A critically important aspect of all PVAs is the incorporation of stochasticty ("randomness"). Indeed, if stochasticity is neglected, then the steps outlined above would quickly result in static population and extinction risk would be zero. Stochasticity enters the PVA in several ways. First, the spawner-recruit data are ambiguous with respect to the parameters of the recruitment function (Figure 4). Thus, uncertainty in the estimates of recruitment parameters $\alpha$ and $\beta$ are simulated within the PVA by repeating simulations with 1000 different values of $\alpha$ and $\beta$. The 1000 different values of $\alpha$ and $\beta$ are selected in proportion to the probabilities of different values and their covariance. This is
accomplished by fitting the Ricker spawner-recruit model with MCMC methods in a Bayesian context. Samples of the MCMC are saved, and the PVA randomly selects parameter values out of this pool.

The spawner-recruit data are not fully explained by the Ricker recruitment function, even though parameter uncertainty is acknowledged. In Figure 4, this can be seen as the vertical distances between spawner-recruit "points" and the line(s) representing the recruitment function(s). These "residual" deviations must also be simulated in the PVA. These residuals are lognormally distributed (note that the errors, $\varepsilon$, are exponentiated in the recruitment functions described above) and contain temporal autocorrelation. After the PVA receives a set of values for $\alpha$ and $\beta$, the variance of the errors is computed as well as the lag-1 autocorrelation of the errors. A 100-year time series of residual errors is then simulated using:

$$
\varepsilon_{t}=\rho \varepsilon_{t-1}+\sqrt{\sigma^{2}} \sqrt{1-\rho^{2}} z_{t}
$$

where $\rho$ is the lag-1 autocorrelation of the errors, $\sigma^{2}$ is the variance of the errors, and $z_{t}$ is a standard normal random deviate (Morris and Doak 2002, p. 139). These simulations are repeated 100 times for each of the 1000 random parameter draws. There are therefore $100^{*} 1000=100,000$ repititions of a $100-$ year time series.

Extinction in the PVA model occurs when spawner abundance for four consecutive years falls below a "quasi-extinction threshold" (QET). A separate process called "reproductive failure threshold" (RFT) is used to zero-out recruitment at critically low spawner abundances. Both of these thresholds are implemented because processes like inbreeding depression, genetic drift, mate finding, and increased per-capita juvenile mortality will drive the population into extinction at critically low abundances. These negative density-dependent processes are very infrequently observed in nature, so they cannot be cannot be explicitly modeled. Collectively, both QET and RFT represent the boundary of an "extinction vortex" from which real populations are irrecoverable (Gilpin and Soulé1984, Courchamp et al. 2008, Jamieson and Allendorf 2012). The specific values used here are RFT=QET=100. The PVA counts the fraction of the 100,000 simulations where adult abundance falls below QET across 4 consecutive years.

The PVA model uses past abundances to infer extinction risk. Thus, the interpretation of the result is couched in the assumption that the conditions that were present when the data were collected will persist for 100 years. The model is not intended to capture effects of global warming, human population growth, or other anticipated future change. Of course, the future will not be like the past. Future food webs are uncertain, as is the adaptive potential of these fish. The purpose of the PVA is not to forecast the future; rather, the PVA is a comparison of two different sea lion scenarios while holding everything else constant across scenarios.

The PVA needs to replicate observed patterns of variation in spawner abundance. A crude but effective method to determine if the PVA adequately captures observed population dynamics is to simply plot a randomly selected 100 year time series of simulated abundances and then superimpose the empirically observed/reconstructed abundances (Figure 4). This visual test indicates that the PVA performs well. It simulates abundances that are greater and less than the empirical abundances, the volatility of these deviations seems to match the volatility of the empirical abundances, and the average simulated abundance approximates the average of the empirical abundances.


Figure 5. 100 year population simulation from the PVA (blue) with empirical spawner abundance (red). The PVA simulations of spawner abundances resembles the empirical time series.

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[^1]
[^0]:    * The 2017 sea lion predation estimate is a preliminary result.

[^1]:    http://www.dfw.state.or.us/fish/SeaLion/docs/Willamette Falls 2016 sea lion report.pdf

