Leveraging Angler Effort to Inform Fisheries Management: Using Harvest and Harvest Rate to Estimate Abundance of White Sturgeon

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Abstract

Traditional methods for estimating abundance of fish populations are not feasible in some systems due to complex population structure and constraints on sampling effort. Lincoln's estimator provides a technique that uses harvest and harvest rate to estimate abundance. Using angler catch data allows assumptions of the estimator to be addressed without relying on methods that could be prohibitively field-intensive or costly. Historic estimates of White Sturgeon *Acipenser transmontanus* abundance in the Sacramento-San Joaquin River basin have been obtained using mark-recapture methods. However, White Sturgeon population characteristics often cause violations of model assumptions, such as population closure and independent capture probabilities. We developed a version of Lincoln's estimator using a joint likelihood, estimated abundance of White Sturgeon in the Sacramento-San Joaquin River basin in 2015 using this method and empirical data, and assessed accuracy and precision of estimates in a simulation study. Estimating abundance using harvest and harvest rate, as represented by our model framework, has the potential to be precise and accurate. The joint likelihood-based approach fitted using Bayesian methods is advantageous because all sources of variation are included in a single model. Precision of abundance estimates was low when the model was applied to White Sturgeon in the Sacramento-San Joaquin River basin and to similar conditions in a simulated dataset. Using simulation, precision and accuracy increased with increases in the number of high-reward and standard tags released, tag reporting rate, tag retention rate, and harvest rate. Results demonstrate potential sources of error when using this approach and suggest that increasing the number of tagged fish and tag reporting rate are potential actions to improve precision and accuracy of abundance estimates of the model.

Keywords Lincoln's estimator, White Sturgeon, fish abundance, harvest, Sacramento-San Joaquin River

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Introduction

Monitoring the status and trends in fish abundance is a primary component of fisheries management. Monitoring allows scientists to evaluate the effects of management actions and measure progress relative to objectives (Radomski and Goeman 1996; Pope et al. 2010). Fish abundance can be estimated both indirectly and directly through relative indices or absolute measures. Relative abundance is often assessed using catch per unit effort (CPUE; Pope et a. 2010). Catch per unit effort assumes that the number of fish captured is proportional to sampling effort and that capture probability is constant (Hilborn and Walters 1992). However, varying gear selectivity, saturation, and variation in environmental conditions can result in biased estimates because of unequal capture probabilities (Hangsleben et al. 2013; Korman et al. 2017; Stewart et al. 2017). Estimates are also sensitive to sampling design and the need for standardization often limits comparisons over a long period (Maunder and Punt 2004).

Considering the drawbacks of relative indices, several advantages of estimating absolute abundance are apparent. First, absolute abundance estimates often do not assume that capture probability is constant, thus producing more reliable trends in abundance. In addition, absolute abundance can be used as a reference point for population models, which are especially important for species at risk (Naujokaitis-Lewis et al. 2009). Management goals often target absolute abundance, such as escapement goals for Pacific salmon *Oncorhynchus* spp. populations in the Pacific Northwest (Wright 1981). Absolute abundance can be estimated with techniques such as depletion, census methods, or capture-recapture (Ricker 1975; Holmes et al. 2006; Clabough et al. 2012; Stewart et al. 2019). The effectiveness of depletion methods depends on the size of the system, fish species, and other stream characteristics (Peterson et al. 2011; van Poorten et al. 2017; Stewart et al. 2019). Census methods are often limited to systems with infrastructure to enumerate fish passage and are also subject to bias and incomplete counts (Putt et al. 2021). Traditional capture-recapture methods rely on a thorough understanding of population structure and movement dynamics (Seber 1982). Addressing critical assumptions, such as population closure and independent capture probabilities, can result in field-intensive and costly sampling designs (Gwinn et al. 2011). Managers aim to maximize accuracy and precision of abundance estimates while minimizing cost; thus, the method used to evaluate abundance may depend on many factors (e.g., population traits, data availability, agency resources).

Mark-recapture methods remain among the most fundamental techniques in fisheries management to estimate abundance and other population parameters. The Lincoln-Petersen model represents the foundation of most mark-recapture methods where a sample of n_1 fish is caught, marked, and released (Lincoln 1930; Pollock 1990). Later a second sample (n_2) of fish is captured, of which m have been marked, and absolute abundance ($\widehat{N}$) is estimated as $\widehat{N} = \frac{n_1 n_2}{m}$. The Lincoln-Petersen estimator relies on the assumptions that (*i*) the population is closed, (*ii*) all the individuals are equally likely to be captured in each sample, and (*iii*) marks are not lost. Numerous other mark-recapture models, of varying complexity, have been developed which can be used to account for assumption violations (Jolly 1965; Seber 1965; Otis et al. 1978; Pollock et al. 1990; Pine et al. 2003). However, cost and effort can be major limitations of implementing appropriate mark-recapture methods for large, complex systems and when capture probabilities are low.

Estimating abundance using the total number of fish harvested and harvest rate can be a potential alternative to mark-recapture methods that rely on effort by investigators. This method was first introduced by Lincoln (1930) and was used to estimate Mallard *Anas platyrhynchos* abundance. The estimator, in its simplest form, is analogous to the Lincoln-Petersen estimator

$$\widehat{N} = \frac{n_1 n_2}{m} \text{ or } \widehat{N} = \frac{bH}{r},$$

where b is the number of newly tagged individuals, H is the total number of individuals harvested, and r is the number of tags that are retrieved and reported by anglers. As with the Lincoln-Petersen estimator, Lincoln's estimator has several critical assumptions; however, random sampling, population closure, and complete harvest and tag reporting (i.e., all harvested fish as well as captured tags are reported) are the most important (Alisauskas et al. 2009). Of course, in the context of Lincoln's estimator, fishing mortality is explicitly accounted for since harvest and harvest rate are essential to estimating abundance. Tag-return models have been further developed, but primarily estimate mortality using data supplied by members of the general public involved in the exploitation process (Brownie et al. 1993; Liljestrand et al. 2019). One of the advantages of tag-return models is that the sample of recovered fish is drawn from a large geographic area which may encompass the entire range of the population (Pollock et al. 1990). Thus, if effort from anglers is well-distributed spatially and temporally within large, complex systems, assumptions of population closure and independent capture probabilities may not be an issue. Further, when capture probability using a fishery-independent mark-recapture study is low, the number of recaptured tags may be higher using Lincoln's estimator if angler effort and tag reporting rates are sufficiently high. The estimation of angler reporting rate of tags using reward-tag programs have also been widely researched (Pollock et al. 2001) and estimation of tag loss can be easily incorporated using double-tagging studies (Seber 1982; Fabrizio et al. 1999; Livings et al. 2007). When the total number of fish harvested is known, advances in modeling of the tag-return process can be incorporated within Lincoln's estimator to estimate abundance from harvest and harvest rate (Dux et al. 2019; Hansen et al. 2019).

This paper presents a case study of population estimation for White Sturgeon *Acipenser transmontanus* in the Sacramento-San Joaquin (SSJ) River basin by adapting the approach originally used by Lincoln (1930). White Sturgeon in the SSJ have a complex life history and population structure (Schreier et al. 2013; Klimley et al. 2015). Generally, adults move into the lower Sacramento and San Joaquin rivers from November–January and migrate upriver to spawn from February–May (Jackson et al. 2016; Miller et al. 2020). White Sturgeon leave the lower Sacramento River and enter the delta shortly after spawning, but some adults remain in the San Joaquin River during the summer. White Sturgeon are found in San Francisco Bay throughout their entire lifespan with limited movement into the Pacific Ocean (Welch et al. 2006). Recruitment of early life stages is often highly variable, which can lead to a complex age structure and variable population growth (Gingras et al. 2013; Hatten et al. 2018). White Sturgeon also exhibit periodic spawning and females are thought to spawn every 2–10 years (Semakula and Larkin 1968; Chapman et al. 1996). Spawning periodicity introduces challenges for mark-recapture studies as there may be unequal capture probabilities between individuals that migrate to spawn and those that do not (Haxton and Friday 2019). Moreover, very few White Sturgeon in the SSJ have been recaptured during the fishery-independent mark-recapture program, with less than two recaptures during each annual sampling period in recent years (DuBois et al. 2011).

Absolute abundance estimates are needed for White Sturgeon in the SSJ to track progress toward management goals, as directed by the Central Valley Project Improvement Act (CVPIA; U.S. Fish and Wildlife Service 1995). Absolute abundance estimates can also be used in population models to evaluate effects of variable exploitation and recruitment on White Sturgeon population growth and status (e.g., Blackburn et al. 2019; Ulaski et al. 2022). Historically, the

California Department of Fish and Wildlife (CDFW) has attempted to monitor White Sturgeon abundance through multiple-census and Petersen mark-recapture methods (DuBois et al. 2011). Fishery-independent, closed population mark-recapture models have been used for other anadromous White Sturgeon populations in the unimpounded portion of the Columbia River and Fraser River (Devore et al. 1995; Nelson et al. 2013). Mark-recapture programs appear to provide reasonable estimates of abundance for White Sturgeon in the Columbia and Fraser rivers because these systems are (*i*) less complex and (*ii*) many more White Sturgeon are tagged and recaptured throughout their distribution. However, due to prohibitive costs, the amount and distribution of sampling effort is limited for White Sturgeon in the SSJ, making the assumptions of population closure and the problem of insufficient recaptures difficult to overcome.

Estimating abundance of White Sturgeon in the SSJ using harvest and harvest rate may have several advantages. First, the estimator capitalizes on data already being collected to evaluate fishery dynamics (Blackburn et al. 2019). California Department of Fish and Wildlife estimates harvest rate using a high-reward tag-return program and White Sturgeon harvest is monitored through the sale and submission of Sturgeon Report Cards (DuBois and Gingras 2011). Second, tag-returns from anglers have been higher than recaptures of tags by agency mark-recapture surveys. Finally, the wide distribution of angler harvest throughout the year and across the population's range can help meet assumptions of population closure and independent capture probabilities. The purpose of this paper was to (1) develop a model to estimate abundance based on Lincoln's estimator and modern tag-return models using a joint likelihood to incorporate all variances in a single model, (2) use the model to estimate abundance of White Sturgeon in the Sacramento-San Joaquin, and (3) evaluate the effect of the biological and observation process on the accuracy and precision (i.e., bias and variance) of the model.

Methods

White Sturgeon in the Sacramento-San Joaquin River basin

We estimated the abundance of harvestable White Sturgeon (102–152 cm fork length), harvest, harvest rate, and tag reporting rate in the SSJ in 2015 using tag-return and harvest reporting data collected by CDFW. White Sturgeon sampling occurred previously by CDFW and in Suisun and San Pablo bays during August–October (Figure 1). During sampling, White Sturgeon measuring 84–204 cm fork length that bore no prior tags had a Carlin disc-dangler reward tag inserted through the musculature proximal to the dorsal fin. Each tag was labeled with a monetary value of US$50, $100, or $150 and a return address. We used tag-return data of fish that were tagged from August–October 2015 that were available for harvest from August 2015–July 2016. We informed estimates of the average reporting rate for each reward tag (i.e., $50 or $100) and harvest rate from fish tagged in 2015 that were harvested and reported from August 2015–July 2016. We assumed a 100% return rate for high-reward tags, which has been shown to illicit a near-100% reporting rate (i.e., $150; Nichols et al. 1991; Meyer et al. 2012; Blackburn et al. 2019). We excluded reports of tagged fish that were caught and released by anglers because fish were not harvested. Mandatory harvest reporting was implemented by CDFW in 2007 using report cards where anglers are required to submit by January 31 of the following year (DuBois et al. 2013). Most fish are harvested by anglers from November–April and approximately one in four fish of harvestable size are released. The proportion of fish that are released is fairly consistent throughout the season. Tag returns occurred from August 2015–July 2016, but the sale and submission of report cards are reported by calendar year. Therefore, we included the White

Sturgeon report cards purchased from January 2015–July 2016 and the number of White Sturgeon harvested from August 2015–July 2016 (*Supplemental Material*, Table S1 & Table S2).

Estimating abundance using harvest and harvest rate

Lincoln's estimator of abundance is simply the ratio of harvest, C, and harvest rate, $\hat{\mu}$ (Lincoln 1930):

$$\widehat{N}_t = \frac{C}{\hat{\mu}}, \tag{1}$$

where $\widehat{N}_t$ is the population size at time of tagging. Harvest rate can be expressed in terms of instantaneous fishing (F) and natural (M) mortality; therefore, Lincoln's estimator can be rearranged to form Baranov's catch equation (Baranov 1918) as:

$$C = \frac{F}{F+M}\left(1 - e^{-(F+M)l}\right)N_t\,, \tag{2}$$

where l is the proportion of the year when the study occurs. Natural mortality was assumed to be zero since the natural mortality of adult White Sturgeon is very low (i.e., 0.05; Blackburn et al. 2019). However, including M within the model allows the inclusion of non-zero estimates.

High-reward tagging programs can be used to estimate fishing mortality rates and reporting rate of standard tags (Pollock et al. 2001; Meyer and Schill 2014). The tag-return process can also be expressed in terms of F and M such that the probability of a tagged fish being harvested and reported ($\hat{p}_i$) is:

$$\hat{p}_i = \frac{F}{F+M}\left(1 - e^{-(F+M)l}\right)\hat{\lambda}_i\hat{\gamma}, \tag{3}$$

where λ_i is the probability a tagged and harvested fish is reported with reward-level i, and γ is the probability a tagged fish retains an individual tag. Assuming a 100% return rate of high-reward tags (i.e., $\lambda_q = 1.0$), the reporting rate of standard tags can be estimated as:

$$\hat{\lambda}_i = \frac{R_i g_q}{R_q g_i}, \tag{4}$$

where R_i and R_q denote the number of tags with reward-level i and high-reward tags harvested and reported, and g_i and g_q indicate the number of fish tagged and released with reward-level i and high-reward tags (Pollock et al. 2001). Failure to account for loss of tags may lead to biased estimates of fishing mortality and population size (Wetherall 1982). Tag-retention probability (γ) can be estimated by releasing a group of double-tagged fish (Wetherall 1982) or can be informed by previous studies.

If harvest has a Poisson distribution and R_i is binomially distributed, the final model can be written as:

$$N_{t+l} = N_t \times e^{-(F+M)l} \tag{6}$$

$$C \sim Poisson\left(\frac{F}{F+M}\left(1 - e^{-(F+M)l}\right)N_t\right) \tag{7}$$

$$for\ i = 0, 1 \ldots q$$

$$R_i \sim Binomial\left(g_i, \frac{F}{F+M}\left(1 - e^{-(F+M)l}\right)\lambda_i \gamma\right) \tag{8}$$

where N_{t+l} is the population size at the end of the study period (l) and λ_i is equal to 1 for high-reward (q) tags or

$$\lambda_i = \begin{cases} \lambda_i, & if\ i \neq q, \\ 1, & if\ i = q \end{cases}.$$

The White Sturgeon recreational fishery in the SSJ occurs year-round; therefore, we set l equal to one. If we assume that mean harvest per angler of anglers who did and did not submit harvest report cards are equal, we can incorporate incomplete harvest reporting in the model as

$$a_r \sim Binomial(a_p, \delta) \tag{9}$$

$$C_{obs} \sim Binomial(C, \delta), \quad (10)$$

where a_p is the number report cards purchased by anglers from January 2015–July 2016, a_r is the number of those report cards that were returned by anglers, δ is the probability that a report card is returned, and C_{obs} is reported harvest from August 2015–July 2016. Therefore, the model estimates several parameters including C, F, N_t, λ, γ, and δ using the datasets R, g, C_{obs}, a_r, and a_p. Assuming independence of individual observations and independent retention, harvesting, and reporting probabilities, the likelihood $[L(R, g, C_{obs}, a_r, a_p | C, F, N_t, \lambda, \gamma, \delta)]$ of the model is the product of the likelihoods for individual datasets (Edward 1992).

We used Bayesian inference to approximate solutions and fit all models using the program JAGS (Plummer 2003) interfaced with the software program R (R Core Team 2018; see *Supplemental Material*, Text S1). A prior continuous uniform distribution was used including $U(0{,}1000000)$ for N_t and $U(0{,}5)$ for F and a prior beta distribution of $Beta(1{,}1)$ was used for λ_i and δ. The estimate of γ relied on a prior distribution of $Beta(10{,}1.111)$ with a mean of 0.90 (Rien et al. 1994). The inferences reported are based on 100,000 simulated samples from each of three independent chains after 50,000 burn-in samples. We assessed model convergence using the ratio of the estimated pooled posterior variance and within-sequence variation, where a ratio of less than 1.05 supported model convergence (Brooks and Gelman 1998).

Simulations

We assessed the accuracy and precision of estimated abundance using the model by conducting a simulation study. Harvest and tag returns were simulated over one year for a population of size N_t = 100,000, which was approximate to the posterior mean when the model was applied to empirical data. The purpose of the simulation was to assess the effects of variables in the data-generating model on accuracy and precision of abundance estimates by incrementally changing each variable while all other variables were held constant (Table 1). We analyzed the effect of harvest rate, reporting probability, number of standard and reward tags, tag retention, and natural mortality and we limited variables to values reported in the literature. The number of reward tags and standard tags were assessed at a range of reasonable values (i.e., g_0 = 50–500, and g_q = 50–500). The variables not being assessed were held constant to closely resemble the White Sturgeon empirical model. For example, we held harvest rate and reporting probability of standard tags constant at the approximate mean posterior distributions of estimated parameters when the model was applied to empirical data (i.e., μ = 0.10, λ_1 = 0.45). Similarly, the number of standard and reward tags released were set to reflect the number of tags released in the White Sturgeon empirical model (i.e., g_0 = 100, and g_q = 50). Natural mortality was held constant at zero because the natural mortality of adult White Sturgeon is very low (Blackburn et al. 2019) and tag retention was set at 0.90 (Rien et al. 1994).

We simulated harvest as a Poisson random variable as in Eq. 7, where instantaneous fishing mortality (F) is equal to $-\ln(1-\mu)$. The return of standard (R_0) and high-reward (R_q) tags was simulated as two binomial random variables as in Eq. 8. We did not incorporate nonresponse of harvest reporting in simulations, thus the likelihood $[L(C,R,g|F,N_t,\lambda,\gamma)]$ of the model estimating abundance from the data-generating model differs slightly than the model applied to empirical data. Simulations were repeated for 1,000 iterations. Simulations were excluded if less than one reward and one standard tag were returned, which typically comprised <1% of iterations. Finally, we estimated bias for each iteration, i, as $\widehat{N}_{t_i}-N_t$ and precision as the root mean squared error (RMSE):

$$RMSE = \sqrt{\sum_{i=1}^{r} \frac{(\widehat{N}_{t_i} - N_t)^2}{r}}\,. \tag{11}$$

Results

White Sturgeon abundance in the SSJ

Of 92,204 anglers that purchased White Sturgeon harvest report cards for January 2015–July 2016, approximately 30% of anglers reported their catch (n = 28,373 anglers) accounting for 2,115 White Sturgeon harvested. White Sturgeon harvest was reported throughout most of the year from the Sacramento-San Joaquin River basin to San Francisco Bay (Figure 1), with most fish harvested during November–April (Figure 2). Mean harvest per angler of the response stratum was 0.07 fish/angler (SD = 0.31 fish/angler). Total harvest (e.g., both reported and non-reported harvest) during the study period was estimated by the model as 6,875 fish (95% CI = 6,628–7,130 fish). Approximately 50 tags were released at each reward level and few tags were returned (i.e., R_1 = 1, R_2 = 2, R_3 = 4; Table 2). The model estimated reporting probability of $50 tags as 0.43 (95% CI = 0.06–0.94) and the reporting probability of $100 tags as 0.59 (95% CI = 0.14–0.98). Instantaneous fishing mortality was estimated as 0.09 (95% CI = 0.04–0.19), thus the annual harvest rate was also 0.09 (95% CI = 0.04–0.17). The model estimated abundance of harvestable adult White Sturgeon (102–152 cm fork length) in the SSJ as 95,889 fish (95% CI = 39,133–188,812).

Simulations

Precision and accuracy of the model's estimate of abundance from the simulated data varied widely depending on the levels of variables (i.e., harvest rate, annual natural mortality, number of reward tags, number of standard tags, tag reporting rate, and tag retention rate) simulated in the exercise (Figure 3). Mean absolute bias varied from approximately 640–79,000 fish across all levels of variables and RMSE varied from approximately 15,000–120,000. Precision and accuracy of abundance estimates were relatively low when variables were similar to levels estimated for White Sturgeon in the SSJ in 2015 (i.e., bias = 35,000; RMSE = 71,000). However, mean bias and RMSE decreased non-linearly with increases in harvest rate, number of reward tags, number of standard tags, tag reporting rate, and tag retention rate. For example, bias decreased by 77% and RMSE decreased by 68% when the number of fish released with a reward tag increased from 50 to 250 tags. Natural mortality had a relatively small effect on precision and accuracy, though RMSE increased slightly when fish were removed from the population.

Discussion

Estimating abundance using harvest and harvest rate (Lincoln 1930), as represented by our model framework, has the potential to be precise and accurate. Precision of abundance estimates was low when the model was applied to White Sturgeon in the SSJ and to similar conditions in a simulated dataset. Very few tags were returned by anglers during the tag-return program for White Sturgeon in the SSJ and harvest rate was low, resulting in imprecise abundance estimates as predicted by the simulation study. Further, results of the simulation study indicate the abundance estimate for White Sturgeon in the SSJ is likely biased high. Although, precision and accuracy increased in the simulation study with increases in the number of high-reward and standard tags released, tag reporting rate, tag retention rate, and harvest rate. Similar effects have been found in studies estimating exploitation and tag reporting rate. Therefore, increasing the number of tagged fish and improving tag reporting rate are actions that can be used to improve precision and accuracy of abundance estimates. For example, simulations of a Red Snapper *Lutjanus purpureus* fishery revealed that uncertainty and bias in exploitation estimates improved as true exploitation rates increased and with the number of high-reward tags (Sackett and Catalano 2017). Similarly, uncertainty of tag reporting rates was high when a low number of high-reward tags were returned by Idaho anglers (Meyer et al. 2012). Finally, the joint likelihood-based approach fitted using Bayesian methods is advantageous because all sources of variance were included in a single model, thereby providing a robust estimate of uncertainty. Thus, results of our study demonstrate potential sources of error when using this approach.

Obtaining a robust estimate of abundance for White Sturgeon in the SSJ is notoriously difficult and provides a fitting example for how Lincoln's estimator can be applied. Historically, White Sturgeon abundance was estimated by CDFW using a mark-recapture program and Lincoln-Petersen estimator (Kohlhorst 1980; Schaffter and Kohlhorst 1999). However, the assumptions of the mark-recapture design, such as population closure, were likely not met (DuBois et al. 2011). For instance, White Sturgeon are sampled every year with trammel nets in August–October in Suisun and San Pablo bays. As a result, recaptures of tagged fish are limited to a small portion of the distribution of White Sturgeon and there is a high probability of losses due to movement outside of the study area (Miller et al. 2020). In contrast, contemporary abundance estimates by CDFW were estimated as the ratio of reported harvest and estimated harvest rate (Dubois and Gingras 2011). We expanded their method to reduce potential bias of abundance estimates by accounting for tag loss and nonreporting of tags and harvest. In addition, we propagated the uncertainty of all parameters to the credible interval of the abundance estimate, providing a more robust estimate of uncertainty.

Several components of estimating White Sturgeon abundance using angler tag-returns and harvest data appear advantageous over the Lincoln-Petersen estimator supported by fishery-independent surveys. First, in the last decade very few White Sturgeon have been recaptured during surveys (DuBois et al. 2011). For example, during the White Sturgeon surveys from August–October 2015, only two White Sturgeon were recaptured from an ongoing mark-recapture study that began in the 1970s. In comparison, seven tags were returned by anglers during the tag-return program from August 2015–July 2016. Second, sampling of White Sturgeon during mark-recapture surveys are limited to San Pablo and Suisun bays during a brief time each fall, presumably due to constraints on time and resources. Given White Sturgeon migrate upriver to spawn the assumptions of the Lincoln-Petersen estimator are likely violated. In comparison, angler effort occurs throughout most of the year and throughout the distribution of White Sturgeon in the SSJ as reflected by the distribution of angler harvest (Figures 1 and 2). Third, though estimates of White Sturgeon abundance were imprecise, increasing the number of reward tags and improving tag reporting rate could increase precision of estimates and would likely be more cost-effective than dramatically increasing the amount of survey effort required to support a more sophisticated mark-recapture design. Specifically, the simulation study indicates that increasing the number of high-reward and standard tags to approximately 200 tags each could greatly increase precision of estimated abundance.

Despite advantages of the estimator, several assumptions should be carefully considered. Random sampling, independent capture probabilities, population closure (with the exception of fishing mortality), and 100% reporting of harvest and tags are the most important assumptions of Lincoln's estimator (Alisauskas et al. 2009). We did not explicitly test whether or not assumptions were met for our model but have relied on information about the movement and distribution of White Sturgeon and anglers to support the rationale behind these assumptions. First, we assumed that tagged White Sturgeon represented a random sample of harvestable White Sturgeon and the probability of harvesting a tagged and untagged fish was approximately the same. If capture probabilities during the tagging and recapture processes are not independent, estimates of exploitation can be biased (Ricker 1975). For example, if tagged fish are more likely to avoid subsequent capture by anglers then exploitation would be underestimated. However, by tagging a random sample of the population, the probability of violating assumptions of independent capture probabilities is reduced. The majority of White Sturgeon aggregate in San Francisco, Suisun, and San Pablo bays during the fall before mature adults migrate up the Sacramento River and San-Joaquin rivers to spawn from winter to spring (Jackson et al. 2016; Miller et al. 2020). Therefore, when sampling occurs from August to October in Suisun Bay it is likely that a random sample of adult White Sturgeon are tagged with reward tags. However, a more representative sample could be obtained by increasing effort to tag fish across a wider area including San Pablo Bay, San Francisco Bay, and the lower Sacramento. Another component of tag-return studies that can introduce unequal capture probabilities is tagging mortality. Although the effect of tagging on survival of White Sturgeon is negligible (Rien et al. 1994; Robichaud et al. 2006) and was not included in our model, tagging mortality for other species should be evaluated and included in estimates of harvest rate if necessary (Miranda et al. 2002).

Second, we assumed that natural mortality or losses to movement outside the harvest area was zero, which may be an appropriate assumption if instantaneous natural mortality is very low or the study occurs over a short period (Alisauskas et al. 2014). If this assumption is violated, natural mortality could be estimated with an alternative method such as an integrated tagging and catch-at-age analysis (Maunder 2001). Alternatively, natural mortality can be estimated using a proxy from von Bertalanffy growth parameters (e.g., Hoenig 1983; Jensen 1996; Hewitt and Hoenig 2005). Natural mortality for White Sturgeon is very low (i.e., 0.05; Blackburn et al. 2019), thus simulation results more appropriately indicate losses to movements outside of the harvest area. For White Sturgeon in the Sacramento-San Joaquin River basin, there are a few cases in which individuals could become unavailable for recapture. For instance, rare cases of White Sturgeon making extensive migrations have been documented (Welch et al. 2006). However, studies have shown the majority of White Sturgeon stay within their natal rivers and estuaries (Miller 1972; Kohlhorst et al. 1991; Veinott et al. 1999). In addition, a few areas are closed to fishing both seasonally and year-round including an upper portion (~100 mi) of the Sacramento which is closed year-round (Figure 1). But reproductive adults represent a small fraction of the population that migrate to spawn each year and do not represent permanent emigration since sturgeon return rapidly after spawning (Schaffter et al. 1997). Therefore, the probability of losses to movement are low, especially since the fishery is open year-round and anglers harvest White Sturgeon across their distribution. Regardless, the effect of natural mortality or losses to movement on accuracy and precision of abundance estimates was minimal (Figure 3). For example, when annual natural mortality increased from 0.00 to 0.50, RMSE only increased by ~6%. Bias did not increase substantially because estimates of both catch and exploitation decrease proportionally with increasing natural mortality, assuming mortality is equal between tagged and untagged individuals (Cooch et al. 2021).

Third, we assumed that high-reward tags illicit a near 100% reporting rate. Lincoln's estimator relies on complete tag reporting, so robust estimates of tag reporting rates are important. High-reward tagging studies provide a useful method to estimate standard tag reporting rates (Pollock et al. 2001; Meyer et al. 2012). Accurate estimates of tag reporting rates assume 100% reporting of tagged fish with a high reward. For example, if high-reward tags have a reporting rate of 0.60, the percent error in estimated reporting rate is over 40% and results in a downward bias of harvest rate (Sackett and Catalano 2017). Thus, high-reward tags must have a value sufficient to illicit a near 100% reporting rate. Evidence suggests that a high-reward of approximately US$150 should be sufficient to acquire a near 100% reporting rate (Nichols et al. 1991; Meyer et al. 2012). However, the value of high-reward tags could be increased to evaluate whether $150 is a large enough reward to illicit a near 100% reporting rate and should be re-evaluated to adjust for inflation (Pollock et al. 2001).

The abundance of harvestable White Sturgeon in the SSJ (102–152 cm fork length) was estimated with the model, though 95% credibility intervals were large. The main source of uncertainty in the abundance estimate originates from the low number of tags returned by July 2016 from harvested fish that were tagged in August–October 2015. Seven tags were reported with only four high-reward tags reported, which resulted in very imprecise estimates of reporting probabilities (e.g., 95% CI = 0.06–0.94). As the number of high-reward tags returned decreases, uncertainty in tag reporting increases (Pollock et al. 2001). For example, if five high-reward tags were returned instead of four, the estimate of abundance would decrease by 15% (i.e., 85,000 fish). Further, the simulation study demonstrated that abundance estimates are likely biased high when harvest rate is low and few reward tags are released. Ultimately, if few reward tags are reported, the probability that abundance of White Sturgeon is overestimated increases. A robust estimate of abundance for White Sturgeon in the SSJ requires an increase of the number of tags released and strategies to increase reporting rate of tags (DuBois and Gingras 2011). A second source of uncertainty is the rate of tag loss which has been estimated previously at approximately 0.90 (Rien et al. 1994). However, if a portion of White Sturgeon were double tagged, tag loss could be directly estimated by the model which can both reduce uncertainty and slightly increase overall tag returns. A third source of uncertainty is the low proportion of harvest report cards returned by anglers. We could not address bias in harvest reporting which may be a source of error for harvest estimates, especially when harvest reporting is low (e.g., 30%). Successful anglers may be more likely to submit harvest report cards, resulting in an overestimation of harvest and abundance (Carline 1972; Alisauskas et al. 2014). In addition, the number of permits sold was used as an estimate of the number of anglers, but many who purchase permits may not fish and may be less likely to return report cards. Negative or positive incentives could be effective in increasing harvest reporting rate such as suspending anglers who do not return cards from the fishery for a period of time (Kilpatrick et al. 2005; Johnston et al. 2007). Regardless, harvest reporting biases can be quantified and incorporated in the analysis framework (Pollock et al. 1994). For example, surveys can be used to estimate angler participation and reporting biases.

We provide an alternative method to estimate abundance using harvest and harvest rate that has the potential to be precise and accurate, and the technique provides a robust estimate of uncertainty. We emphasize that the abundance estimate for White Sturgeon in the SSJ that we presented here is highly uncertain, and may be biased high as demonstrated by the simulation study. However, a more precise and accurate estimate could be obtained with relatively straightforward, simple improvements to the tag-return and harvest reporting programs. Precision of abundance estimates may also be higher in populations that support a higher harvest rate. A number of population characteristics can result in traditional mark-recapture methods (e.g., robust mark-recapture) being prohibitively field-intensive and costly (Gwinn et al. 2011). For populations with complex movements (e.g., salmonid populations with resident, fluvial, and adfluvial life-history types) or low capture probabilities, effort and coverage of the resampling period can be expanded with minimal increase in cost and effort by fisheries scientists. Assumptions of population closure and independent capture probabilities can be more easily addressed with Lincoln's estimator by distributing tagging efforts proportional to the population in space and time (Ricker 1975). Finally, for many exploited fish populations, monitoring harvest and harvest rate are already central to managing the fishery. Therefore, an enormous benefit of using this method is that it can be easily implemented within existing management infrastructures.

Supplemental Material

Text S1 Model estimating White Sturgeon *Acipenser transmontanus* abundance in the Sacramento-San Joaquin River basin in 2015 using the program JAGS, interfaced with the software program R.

Available: https://doi.org/10.3996/JFWM-22-057.S1 (26 KB PDF)

Table S1 Reported White Sturgeon *Acipenser transmontanus* harvested per angler (harvest_per_angler) from the Sacramento-San Joaquin River basin and San Francisco Bay-Delta area, California, from August 2015–July 2016.

Available: https://doi.org/10.3996/JFWM-22-057.S2 (222 KB XLSX)

Table S2 The number of anglers in California who purchased (A) and reported (R) White Sturgeon *Acipenser transmontanus* report cards from January 2015–July 2016 and the response rate of reported harvest (response_rate).

Available: https://doi.org/10.3996/JFWM-22-057.S3 (1 KB PDF)

Reference S1. U.S. Fish and Wildlife Service. 1995. Working paper on restoration needs: habitat restoration actions to double natural production of anadromous fish in the Central Valley of California, Volume 3. U.S. Fish and Wildlife Service, Stockton, CA.

Available: https://doi.org/10.3996/JFWM-22-057.S4 (17.350 MB PDF)

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Tables

Table 1. Summary of each variable incrementally changed in data-generating model for White Sturgeon *Acipenser transmontanus* abundance estimates. The table includes what value the variable was held at for other simulations, the range of the variable simulated, and the increments at which it was simulated. References that are NA indicate variables that were set to reasonable levels (https://frasersturgeon.com/wp-content/uploads/2019/01/Direct_delayed_mortality_of_WS_in_three_gear_types_LFR.pdf [Accessed August 2023]).

Variable	Constant	Range	Increment	References
Harvest rate	0.10	0.05–0.65	0.05	Miranda et al. 2002; Slipke et al. 2003; Schill et al. 2007; Sullivan and Vining 2011; Meyer and Schill 2014; Kerns et al. 2015; Bisping and Thompson 2017; Lewandoski et al. 2017; Sackett et al. 2018; Briggs et al. 2020
Natural mortality	0.00	0.00–0.50	0.05	Isermann et al. 2005; Lewandoski et al. 2017; Thorley and Andrusak 2017
Number of reward tags	50	50–500	50	NA
Number of standard tags	100	50–500	100	NA
Tag reporting rate	0.45	0.15–0.95	0.10	Denson et al. 2002; Miranda et al. 2002; Henry et al. 2005; Isermann et al. 2005; Meyer and Schill 2014; Quinn and Andrews 2016; Lewandoski et al. 2017
Tag retention rate	0.9	0.70–1.00	0.05	Miranda et al. 2002; Slipke et al. 2003; Henry et al. 2005; Sullivan and Vining 2011; Henderson and Fabrizio 2014; Meyer and Schill 2014; Kerns et al. 2015; Lewandoski et al. 2017; Thorley and Andrusak 2017; Sackett et al. 2018

Table 2. Summary of tagged fish released and reported, and the reporting probability of varying reward values (US$) for White Sturgeon *Acipenser transmontanus* in San Pablo and Suisun bays, California, in 2015. Numbers in parentheses are 95% credibility intervals of reporting probabilities.

Reward value (US$)	Tagged	Reported	Reporting probability
50	52	1	0.43 (0.08, 0.90)
100	47	2	0.59 (0.19, 0.95)
150	50	4	1.00

Figure Captions

Figure 1. Map of the Sacramento and San Joaquin rivers as they enter the San Francisco Bay–Delta Estuary, California. The number of White Sturgeon *Acipenser transmontanus* harvested and reported by anglers from August 2015–July 2016 are illustrated by color for each harvest region and regions with no reported harvest are shown in grey. Areas closed to White Sturgeon fishing seasonally are depicted with white stripes and areas closed year-round are shown with red and white stripes.

Figure 2. The number of White Sturgeon *Acipenser transmontanus* harvested and reported by anglers (light grey) and the number of harvestable White Sturgeon sampled by the California Department of Fish & Game in the Sacramento-San Joaquin River basin during August 2015–July 2016 (dark grey).

Figure 3. The mean bias and root mean squared error (RMSE) of estimated fish abundance using harvest and harvest rate (i.e., Lincoln's estimator) compared to a data-generating model at varying levels of natural mortality, harvest rate, number of standard tags, number of reward tags, tag reporting rate, and tag retention rate (r = 1,000). The data-generating model simulated data similar to empirical data collected for White Sturgeon *Acipenser transmontanus* in the Sacramento-San Joaquin River basin from August 2015–July 2016. Each variable was changed incrementally while all others were held constant (constant values depicted by vertical, dashed lines) and the ranges of variables were limited to values reported in the literature. Boxes in the left column represent the 1st and 3rd quartiles of bias of estimated abundance and the red line is at zero bias. Points in the right column denote RMSE of abundance estimates and grey bars indicate the number of iterations that returned a sufficient number of tags to calculate bias and RMSE. Lines were fit using locally estimated scatterplot smoothing.

Figures

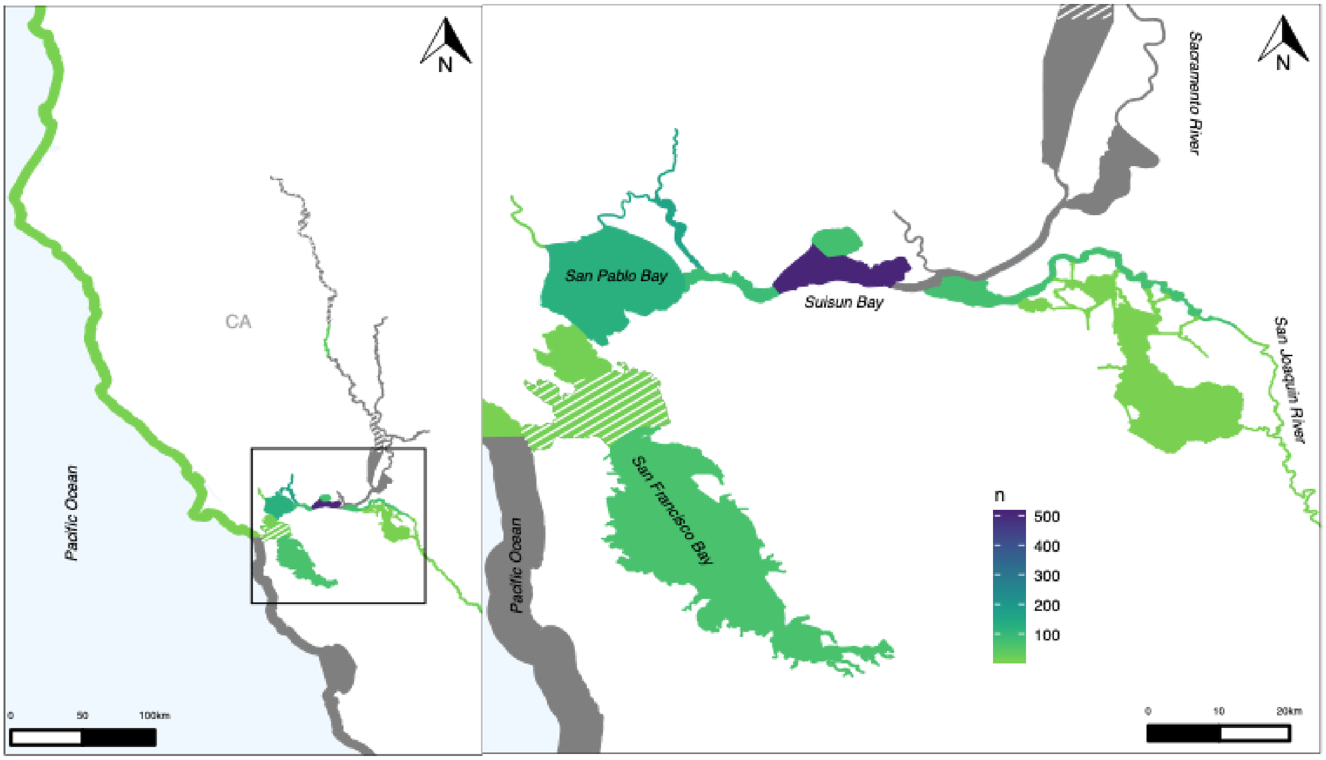

Figure 1

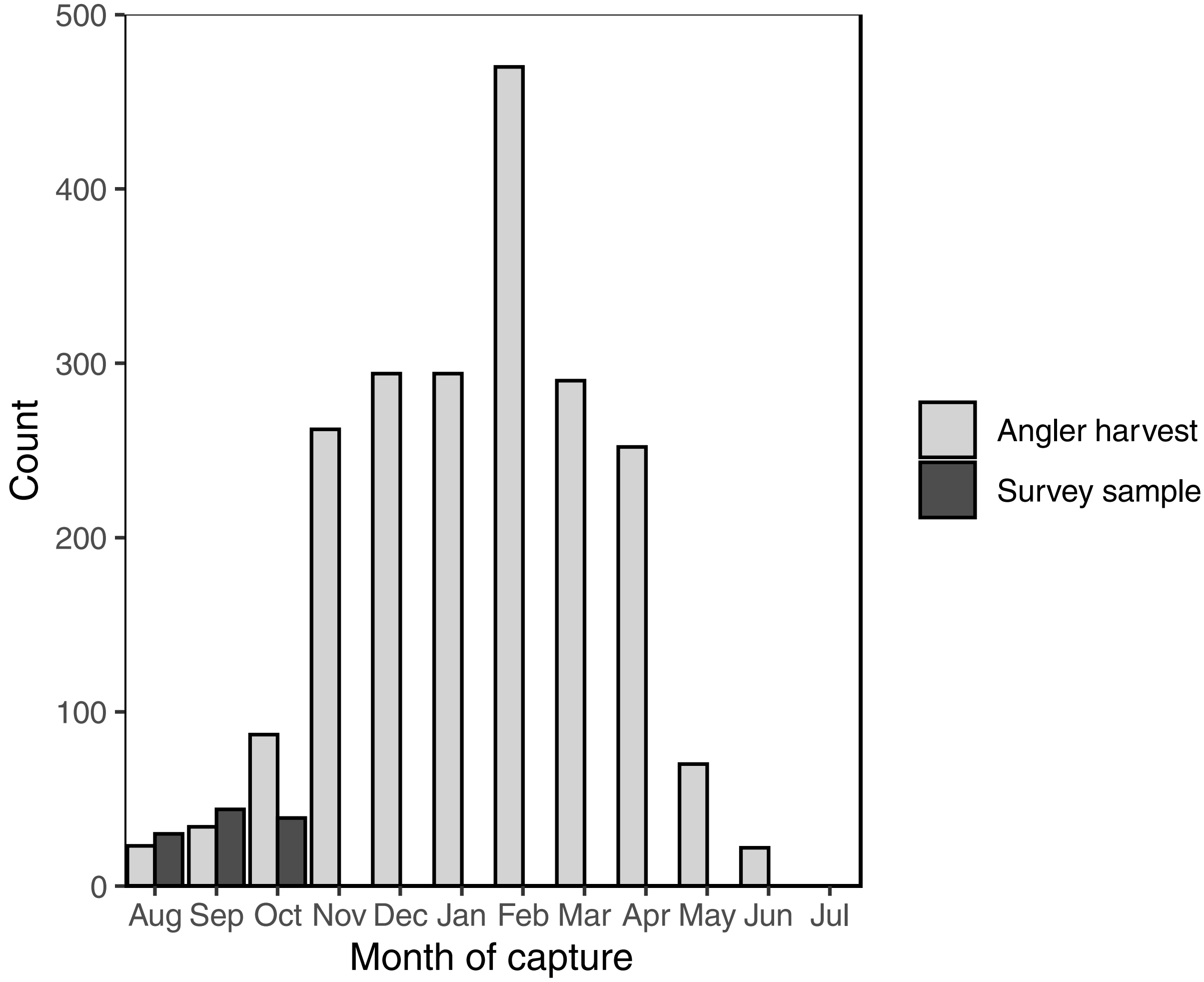
500
400
300
200
100
0
Count
Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul
Month of capture
Angler harvest
Survey sample

Figure 2

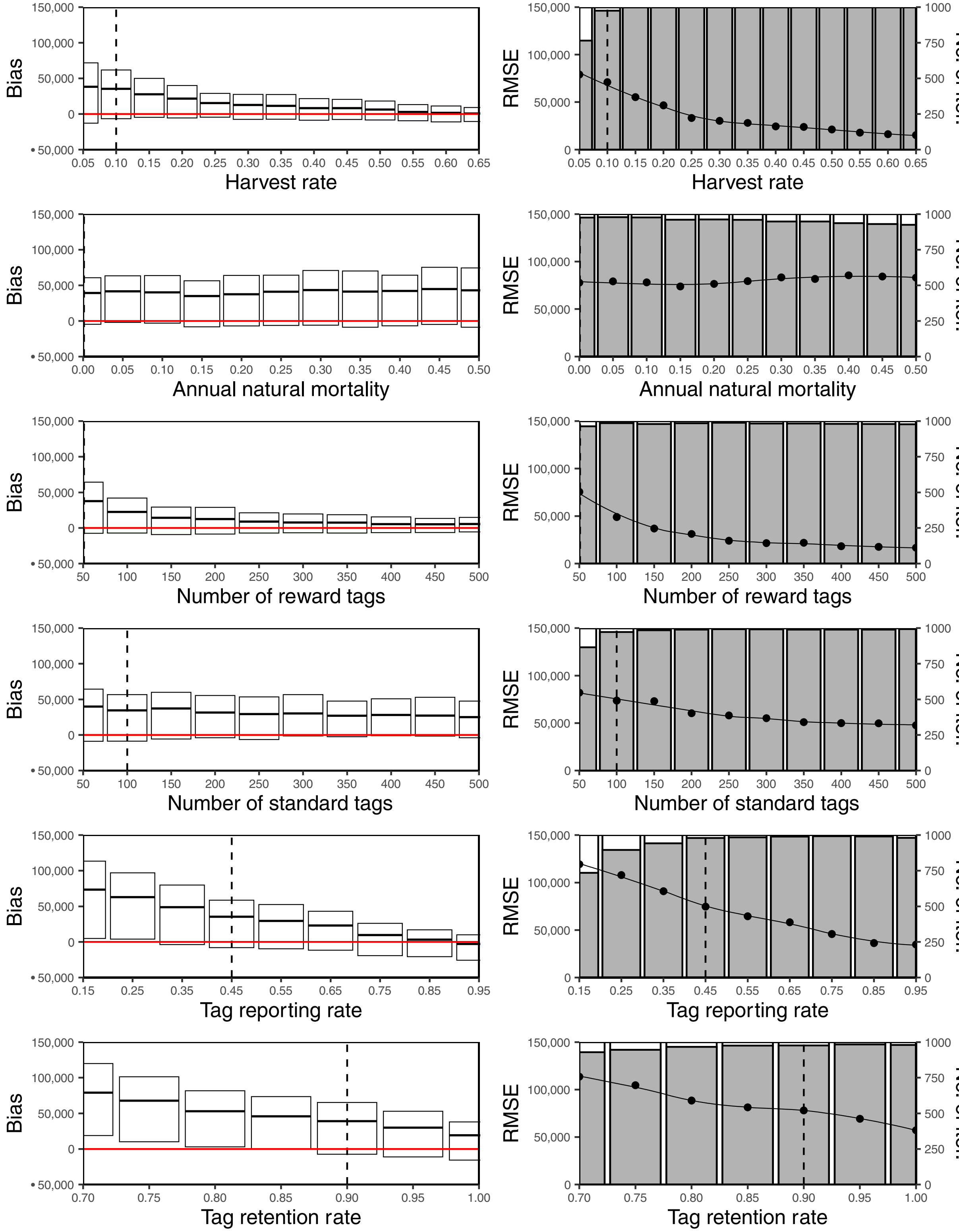
Bias
RMSE
No. of iter.
Harvest rate
Annual natural mortality
Number of reward tags
Number of standard tags
Tag reporting rate
Tag retention rate

Figure 3