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Title: Incorporating antenna detections into abundance estimates of fish

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Abstract:

Autonomous passive integrated transponder (PIT) tag antennas are commonly used to detect fish marked with PIT tags but cannot detect unmarked fish, creating challenges for abundance estimation. Here we describe an approach to estimate abundance from paired physical capture and antenna detection data in closed and open mark-recapture models. Additionally, for open models, we develop an approach that incorporates uncertainty in fish size, because fish size changes through time (as fish grow bigger) but is unknown if fish are not physically captured (e.g., only detected on antennas). Incorporation of size uncertainty allows for estimation of size-specific abundances and demonstrates a generally useful method for obtaining state-specific abundances estimates under state uncertainty. Simulation studies comparing models with and without antenna detections illustrate that the benefit of our approach increases as a larger proportion of the population is marked. When applied to two field data sets, our approach to incorporating antenna detections reduced uncertainty in abundance substantially. We conclude that PIT antennas hold great potential for improving abundance estimation, despite the challenges they present.

Keywords: abundance, antennas, capture-recapture, humpback chub, state uncertainty, fish

Introduction

Managers regularly require abundance estimates to assess population status and trends (Maxwell and Jennings 2005), inform management decisions (Walters 1986; Williams et al. 2002), trigger management actions (Bair et al. 2018; Donovan et al. 2019), and inform decisions to upgrade or downgrade the conservation status of taxa (Haines et al. 2013; Neel et al. 2012). When animals are rare or difficult to capture, abundance estimates can have poor precision and

be prone to bias. New technologies, such as camera traps or genetic mark-recapture techniques, can produce novel detection types that improve detection and abundance estimates yet differ from conventional detections (e.g., live captures, dead recoveries) and therefore require special considerations for mark-recapture modeling (Augustine et al. 2018; Macbeth et al. 2011). For fishes, autonomous passive integrated transponder (PIT) tag antennas have become a popular detection method, as these antennas are typically placed in aquatic environments to detect PIT tags of fish that swim by (Cooke et al. 2013; Zydlewski et al. 2006). Despite the potential for improved detection (Barbour et al. 2012), studies typically do not utilize antenna detections in abundance estimation because the characteristics of this detection type can make abundance estimation problematic. Here we describe some of the challenges and benefits of including PIT antenna detections in abundance estimation using mark-recapture modeling.

We start by highlighting two main challenges that arise from autonomous antennas. First, antennas produce an extreme form of capture heterogeneity where only fish with PIT tags can be detected. Thus, fish cannot be detected on antennas until after their first capture, when they are marked with a PIT tag. While it is relatively straight-forward to estimate abundance of the marked population (Fetherman et al. 2014; O'Donnell et al. 2010; Sloat et al. 2011), extending the abundance estimate to both marked and unmarked fish is more complicated. Second, antenna detections do not provide information about fish attributes commonly observed with physical capture, such as size, weight, disease status, or ripeness. Unknown size can be particularly problematic because size often substantially influences capture probabilities (Dauwalter and Fisher 2007; Hense et al. 2010; Korman et al. 2009; Millar et al. 2016) and antenna detection probabilities (O'Donnell et al. 2010; Saboret et al. 2021). Unaccounted for size effects on capture probabilities in mark-recapture models can be a source of individual

heterogeneity and produce negative bias in abundance estimates (Beamesderfer and Rieman 1988; Cubaynes et al. 2010; Otis et al. 1978). These challenges have hindered use of antenna data for abundance estimation (but see Dzul et al. 2017, Rudershausen et al. 2019, Conner et al. 2020 for exceptions), even though studies that use autonomous PIT antenna detections to estimate other parameters (namely survival and movement) have burgeoned (Hewitt et al. 2010; Horton et al. 2011; Rudershausen et al. 2014).

To estimate abundance, we develop and apply methods to combine antenna detections with physical captures. These two encounter types are complementary; physical captures sample both marked and unmarked fish (and thereby provide information about the proportion of fish that are marked), and antennas boost detection probabilities for previously marked fish. We hypothesize that adding antenna data to mark-recapture models will reduce uncertainty in estimated abundance based on two properties. First, adding antenna detections should reduce uncertainty in physical capture probability estimates, as antennas provide additional information about fish that were present in the study area but not physically captured (*i.e.*, fish that were just detected on antennas). Second, antennas can reduce uncertainty in abundance by increasing detection of marked individuals, since low detection probabilities inherently produce uncertainty (Dixon et al. 2005; MacKenzie et al. 2005), which can cause positive bias in estimated abundance.

Methods

In this study, we describe open and closed population models designed to estimate abundance from paired sampling that includes both antenna detections and physical captures. For the open model, we use a multistate model with state uncertainty where state refers to size category (*i.e.* size bin). We include code for simulations and applications as part of the

Supplementary Material 1. We use simulation to assess how adding antenna detections impacts abundance estimates under scenarios in which capture probability, antenna detection probability, survival probability, and proportion of previously marked fish are varied. We then apply models to capture-recapture data from field studies.

The assumptions of each of our approaches include: 1) all fish in the same state (i.e., size bin) in the sampling area have equal physical capture probabilities, 2) all marked fish in the same state in the sampling area have equal antenna detection probabilities, 3) antenna detections occur in discrete time, 4) only live fish are detected with antennas so that ghost tags are absent (Bond et al. 2019; Stout et al. 2020), and 5) antenna detections and physical captures are independent. These approaches are therefore designed for situations where antenna detections and physical captures occur within a short period of closure and where antennas are deployed throughout the study area to ensure all fish have equal detection probability. In practice, this modeling approach would be appropriate for studies where antenna detections most likely come from submersible antennas scattered throughout the sampling area and deployed for short periods (e.g., 1-10 days) or from mobile PIT antenna surveys where biologists actively move antennas through the aquatic habitat to detect PIT tags (O'Donnell et al. 2010; Sloat et al. 2011). These approaches are not developed for situations where antenna detections come from stationary antennas that are deployed continuously (e.g., antenna arrays that span the entire width of stream and detect fish moving between two rivers or sites), as often these data do not sample the entire study area, but rather only detect fish that move over the antennas. However, it is possible that under a set of circumstances, stationary antennas could be used with this method. Specifically, the following would have to be true: 1) all marked fish swim by the stationary antennas (and have a non-zero detection probability), 2) all fish (marked and unmarked) are exposed to physical sampling, and

3) there is population closure (i.e., no births, deaths, immigration, or emigration) between when fish moved over the stationary antennas and when fish were exposed to physical sampling. Most likely, this scenario would occur when estimating the population size of spawning fish. We apply our modeling approach to estimate abundance of bull trout (*Salvelinus confluentus*) in Hells Canyon, Snake River, from 2016-2018 (closed model) and humpback chub (*Gila cypha*) that spawn in the Little Colorado River (LCR; open model). Data generated during this study are available from the U.S. Geological Survey ScienceBase-Catalog (Dzul et al. 2021a).

Closed model simulation and modeling

Our simulated data for the closed model are based on a scenario where three days of sampling occurred. Some proportion of fish were marked with PIT tags before the start of the study. Each day, fish from a fixed population size (N) were exposed to capture by a physical gear type and antennas were deployed to detect marked fish. This leads to six passes for the simulated data set, with two passes - one corresponding to physical capture, the other corresponding to antenna detection - occurring each day. Fish that are marked prior to the study are detectable on antennas starting on day 1, but fish that are newly marked during the study cannot be detected on antennas until the day after marking. For example, consider the following capture history (00 10 01), where 1 and 0 denote detection and non-detection, respectively, and where paired numbers correspond to gear type (physical capture pass first, followed by pass of antenna detection) and spaces between pairs of numbers designate days. Thus, fish with the capture history 00 10 01 were physically captured on day 2 and detected on the antenna on day 3. The probability of this capture history depends on whether or not the fish was marked prior to day 1 of the study. If the fish had a previous mark, it has a nonzero antenna detection probability on all three days and thus the encounter history probability would be:

$$(1) \quad \frac{p_{cap}(1 - p_{cap})^2 \times p_{ant}(1 - p_{ant})^2}{p_{mark}^*}$$

$$(2) \quad p_{mark}^* = 1 - (1 - p_{cap})^3(1 - p_{ant})^3$$

where p_{cap} and p_{ant} represent the probability of capture and antenna detection (Table 1), respectively, and we assume that p_{cap} and p_{ant} are equal for all three days of sampling. Here p_{mark}^* is the trip encounter probability for marked fish, or probability that a marked fish was either detected on the antenna and(or) physically captured on at least one pass of the sampling occasion. Note that, by dividing the encounter probability by p_{mark}^* , the model conditions on fish that are encountered at least once so that abundance is a derived parameter (Huggins 1991). If the fish was not marked prior to the sampling occasion, it is first marked on day 2 and only detectable on antennas on day 3, thus the probability of its encounter history would be:

$$(3) \quad \frac{p_{cap}(1 - p_{cap})^2 \times p_{ant}}{p_{cap}^*}$$

$$(4) \quad p_{cap}^* = 1 - (1 - p_{cap})^3$$

Where p_{cap}^* is the trip encounter probability for unmarked fish, or the probability the fish was physically captured on at least one pass of the sampling occasion. Parameter estimates were obtained by maximizing the product of these encounter history probabilities across observed encounter histories. We fit models without antenna detections to help illustrate the (potential) benefit of antennas. Models were fit in R (R Core Development Team 2012) using maximum likelihood via the function ‘optim’ with Broyden-Fletcher-Goldfarb-Shanno method “BFGS”.

We calculated abundance ($\hat{N}$) and $SE(\hat{N})$ using two different methods, hereafter the single group and the separate group approaches. For the single group approach, no antenna detection data were used so $\hat{N} = \frac{c_{tot}}{p_{cap}^*}$ and $SE(\hat{N})$ was calculated using the Horvitz-Thompson

(HT) estimator in Equation 5 (this is a modified version of Equation 9.10 in McDonald et al. 2005), which requires the number of unique individuals encountered by physical capture (here referred to as c_{tot}), as well as estimates of the probability the fish was captured at least once during the sampling occasion (p_{cap}^*), and variance of p_{cap}^* (V) from the closed model:

$$(5) \quad SE(\hat{N}) = c_{tot} \left(\left(1 + \frac{3V}{p_{cap}^{*2}} + \frac{V^2}{p_{cap}^{*4}} \right) \frac{1 - p_{cap}^*}{p_{cap}^{*2}} + \frac{c_{tot}V}{p_{cap}^{*4}} \right)$$

For the separate group approach, abundance was calculated separately for previously marked and newly marked fish and then a multivariate version of the HT estimator was used to derive $\hat{N}$ and $SE(\hat{N})$. In the separate group method, catch and capture probabilities are calculated separately for previously marked and newly marked fish, and thus we replace scalars c_{tot} and p_{cap}^* above with vectors $\mathbf{c}$ and $\mathbf{p}^*$ and we replace V with the 2 x 2 variance-covariance matrix $\mathbf{\Omega}$ which represents the variances and covariances of $\mathbf{p}^*$. Here $\mathbf{c} = [c_{unmark}, c_{mark}]$, or the number of unique individuals that were captured as unmarked (c_{unmark}) and the number of unique individuals that were previously marked and either captured or detected on antennas (c_{mark}), and $\mathbf{p}^* = [p_{cap}^*, p_{mark}^*]$, or the encounter probabilities for unmarked and marked fish. Here $\hat{N} = \frac{c_{mark}}{p_{mark}^*} + \frac{c_{unmark}}{p_{cap}^*}$ and the multivariate HT estimator of $SE(\hat{N})$ is the summation of marked and unmarked groups ($J = 2$), and it accounts for covariance between p^* of marked and unmarked fish (McDonald et al. 2005).

$$(6) \quad SE(\hat{N}) = \sum_{j=1}^J c_j \left\{ \frac{(1 - p_j^*)}{p_j^{*2}} \left(1 + \frac{3\Omega_{jj}}{p_j^{*2}} + \frac{\Omega_{jj}^2}{p_j^{*4}} \right) + \sum_{k=1}^J \frac{c_k \Omega_{j,k}}{p_j^{*2} p_k^{*2}} \right\}$$

Simulation scenarios were similar to those used by Conner et al. (2020) and differed by the proportion of marked fish at the start of the study (10%, 20%, 30%, 40%, 50%), by daily capture probabilities ($p_{cap} = 10\%$ or 20%), and by daily antenna detection probabilities ($p_{ant} = 20\%$ or 60%). Results are based on 100 simulated datasets for each scenario. For each

197 simulated data set, we calculated three estimators of $(\hat{N})$ and $SE(\hat{N})$ and the precision of different
 198 estimators is presented using the relative standard error (RSE), here defined as $100 \times \hat{N}/SE(\hat{N})$.
 199 We also calculated relative bias, or $100 \times (\hat{N} - N)/N$, and coverage, or the percent of
 200 simulations where N was within the normal-based 95% CI of $\hat{N}$, for each estimator. The first
 201 estimator (E1) uses the single group approach and the model without antenna detections, the
 202 second estimator (E2) uses the single group approach and the model with antenna detections
 203 (i.e., the model is fit with antennas but N is estimated from physical captures only, so the
 204 estimator is $\hat{N} = \frac{c_{tot}}{p_{cap}^*}$), and the third estimator (E3) uses the separate group approach and models
 205 with antenna data. We hypothesize that, of the three estimators, E1 will have the worst
 206 precision because this model completely omits antenna detections. We further hypothesize that
 207 E3 will have the best precision because E3 has higher detection probability for marked fish
 208 compared to E2. We expect that the relative benefit of E3 over E2 will increase with higher
 209 proportions of marked fish.

210

211 Open model simulation and modeling

212 The open model used in our simulation is a conditional multistate population model
 213 (Arnason 1973; Schwarz et al. 1993) that includes three size states (small, midsize, and large) in
 214 form of size bins. The multistate model conditions on first capture, so that survival and capture
 215 probabilities are estimated from individuals marked with PIT tags (unmarked individuals are
 216 assumed to have survival and capture probabilities equal to those of marked fish). Unlike the
 217 closed model simulation, all fish in the open simulation are unmarked before the start of the first
 218 sampling occasion, so that both the capture probability and antenna detection probability cannot
 219 be estimated for the first sampling occasion. On the second occasion, capture and antenna

detection probabilities are obtained from information about fish marked during the first occasion, and on the third occasion these probabilities are estimated from fish marked during the first and second occasions, etc. This formulation is convenient for modeling antenna detections because fish must first be captured, given a PIT tag, and measured (so size is initially known) to enter the model so that there is no state (size) uncertainty for the first capture of each fish (i.e., no finite mixture parameter as in Pradel 2005) and fish in the model are detectable on antennas on all occasions following their first capture. Although unmarked individuals are not included in the model structure, the assumption that marked and unmarked fish have equal capture probabilities allows us to estimate abundance of unmarked individuals as a derived quantity.

The model exhibits a multistate structure that allows fish to transition among size states across sampling occasions. In our example with three size states, transitions between states are functions of apparent survival ($\phi_{i,t,s}$) and growth ($g_{i,t,s}$) probabilities for posterior draw i at time t and state s (note we include a dead state). We refer to the matrix elements in Equation 7 as $\psi_{i,t,s,v}$, which represent the transition probabilities between states s and v .

$$(7) \quad \begin{bmatrix} \phi_{i,t,1}(1 - g_{i,t,1}) & \phi_{i,t,1}g_{i,t,1} & 0 & (1 - \phi_{i,t,1}) \\ 0 & \phi_{i,t,2}(1 - g_{i,t,2}) & \phi_{i,t,2}g_{i,t,2} & (1 - \phi_{i,t,2}) \\ 0 & 0 & \phi_{i,t,3} & (1 - \phi_{i,t,3}) \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

The state transition matrix in Equation 7 is specific to our example where states correspond to size, but with modifications the multistate model structure can be used for modeling other states, such as breeding/nonbreeding, disease status, or age.

For the observation process, we use a multievent structure (Pradel 2005) where following initial capture, there are four possible types of detection for each size state on each sampling

occasion: captured only, captured and detected on antennas, only detected on antennas, or unobserved (i.e., not captured or detected on antennas). Note that there is state uncertainty for events where fish are only detected on antennas because size is unknown. For our simulation with three size states, there are eight possible events (here described by $Y_{j,t}$, which is the capture event observed for capture history j at time t). The detection probabilities for these eight events are listed in Table 2. We use a Bayesian approach where states are marginalized (Yackulic et al. 2020) and fit this model in Stan (Stan Development Team 2013).

Deriving abundance estimates from this model using the E3 approach is complicated because the size of many fish detected only on antenna is unknown and thus the number of fish detected in each size state is uncertain. Posterior samples of abundance, $N_{i,t,s}$, are derived for each posterior sample, i , time, t , and state, s , using the steps described below and analyzed across posterior samples to derive mean and standard error for $\hat{N}_{t,s}$ (Table 1). The first step in deriving abundance for a particular posterior draw, is to derive $\zeta_{i,j,t,s}$ which represents the likelihood that individuals with capture event $Y_{i,j}$ are in state s (out of Z possible states) at time t , conditional on the posterior draw i of relevant parameters (i.e., apparent survival, size transition, capture, and antenna probabilities). We estimate this likelihood using a forward conditional approach, which we briefly describe here (for a more detailed description and alternatives approaches see Yackulic et al. (2020)). During the interval when a fish is first captured and marked, the size class of a fish is known with certainty, so $\zeta_{i,j,t,s}$ is 1 for the observed size state and zero for all other size classes. So, for example, if a fish was first observed in the midsize state, the vector $\zeta_{i,j,t,1:Z}$ would equal $[0 \quad 1 \quad 0 \quad 0]$, where the terminal zero corresponds to the dead state. The likelihood values of being in state v for capture history j in subsequent time periods (i.e., $\zeta_{i,j,t+1,v}$) is calculated iteratively based on the vector of likelihoods in the previous time step ($\zeta_{i,j,t,1:Z}$), as

well as the array of state transition probabilities $\Psi_{i,t,s,v}$, and the conditional detection probability $p_{i,t+1,v,Y_{j,t+1}}$ which represents the probability of observed event $Y_{j,t+1}$ given state v :

$$(8) \quad \zeta_{i,j,t+1,v} = \left(\sum_{s=1}^Z \zeta_{i,j,t,s} \cdot \Psi_{i,t,s,v} \right) \cdot p_{i,t+1,v,Y_{j,t+1}}$$

Having derived all values of $\zeta_{i,j,t,s}$, the second step of this approach consists of estimating the probability, $\pi_{i,j,t,s}$, of being in state s , for capture history j , at time t , for posterior draw i via the following equation:

$$(9) \quad \pi_{i,j,t,s} = \frac{\zeta_{i,j,t,s}}{\sum_{k=1}^Z \zeta_{i,j,t,k}}$$

Note that whenever $Y_{j,t}$ corresponds to a physical capture, then $\pi_{i,j,t,s}$ will equal 1 for the element that corresponds to the observed size class and will equal 0 for all other elements. Thus, in practice, it is more efficient to import the physical capture data as a separate data matrix and only calculate $\pi_{i,j,t,s}$ when $Y_{j,t}$ corresponds to an antenna detection only (without physical capture). We refer to the subset of $Y_{j,t}$ that corresponds to antenna-only detections as A_t and then estimate, out of the number of fish with capture history j (f_j), how many were in each size state s at time t . Then we sum across all capture histories that were antenna-only detections at time t (i.e., $j \in A_t$) to obtain the expected number of antenna-only detections (c_{ant}) that were in size state s at time t for posterior draw i according to:

$$(10) \quad c_{ant,i,t,s} = \sum_{j \in A_t} f_j \pi_{i,j,t,s}$$

The last step requires generating random draws from a negative binomial distribution (King et al. 2016) and differs for the E1, E2, and E3 estimators. Parameters in the negative binomial were the number of successes (i.e., the number of unique individuals encountered) and the probability of success (i.e., capture probability and(or) detection probability). The random draws from the negative binomial distribution represented the expected number of failures (i.e.,

number of fish in each size state that were not captured), and this vector was added to the unique number that were captured and(or) detected on antennas to provide an estimate of $\hat{N}_{i,t,s}$.

The number of individuals encountered differed for E1, E2, and E3. Here, we partition the number of unique individuals that were physically captured ($c_{tot,t,s}$) into those that did not have a PIT tag before time t ($c_{unmark,i,t,s}$) and those that did ($c_{mark,i,t,s}$) (Fig 1). We also define the number of uncaptured fish for the total population ($u_{tot,i,t,s}$), the number of uncaptured, unmarked fish ($u_{unmark,i,t,s}$), and the number of uncaptured and undetected marked fish ($u_{mark,i,t,s}$). For E1 and E2 the single group approach was used, and thus only $c_{tot,t,s}$ and estimates of $p_{cap,i,t,s}^*$ were used to generate $u_{tot,i,t,s}$ using random draws from a negative binomial distribution::

$$(11) \quad u_{tot,i,t,s} \sim NB(c_{tot,t,s}, p_{cap,i,t,s}^*)$$

Estimates of unique unmarked, uncaptured fish ($u_{unmark,i,t,s}$) were also simulated from a negative binomial distribution with two parameters corresponding to the total number of successes ($c_{unmark,t,s}$) and the probability of success ($p_{cap,i,t,s}^*$). To get the number of unique, marked fish that were not encountered ($u_{mark,i,t,s}$), we summed the unique number of previously marked fish that were physically captured with the unique number of previously marked fish that were detected by antenna-only, and detection probability was the probability of being detected on antennas or physically captured:

$$(12) \quad u_{mark,i,t,s} \sim NB(c_{mark,t,s} + c_{ant,i,t,s}, p_{mark,i,t,s}^*)$$

Then, for E3, uncaptured fish (from both marked and unmarked groups) was added to catch from both groups to get $\hat{N}_{i,t,s}$:

308 (13) $\hat{N}_{i,t,s} = u_{unmark,i,t,s} + u_{mark,i,t,s} + c_{unmark,t,s} + c_{mark,t,s} + c_{ant,i,t,s}$

309 This entire process was repeated for each posterior draw to generate a distribution of abundance
 310 estimates. Then from this distribution, mean $\hat{N}_{t,s}$, RSE, relative bias, and coverage were
 311 calculated and summarized across 100 simulations.

312 We simulated capture histories for three different size states under two different
 313 scenarios: long-lived and short-lived. Simulated data included eight years of mark-recapture
 314 data with parameters (i.e., growth, survival, capture, and antenna detection probabilities) that
 315 were temporally constant but different among size states. Parameter values differed for long-
 316 lived and short-lived scenarios and specific values are listed in Table 3. Capture probabilities
 317 and antenna detection probabilities in the long-lived scenario were chosen to mimic patterns
 318 observed in humpback chub, where capture probabilities decrease but antenna detection
 319 probabilities increase as fish grow larger. The short-lived scenario is supposed to represent a
 320 salmonid population where the largest fish have both the highest capture and antenna detection
 321 probabilities and where survival is low and population turnover rates are relatively fast.

322 Starting population size was set to 2 000, 1 000, 2 000 for the three size states (long-lived
 323 scenario) or 5 000, 3 000, 750 (short-lived scenario). Each year, either 2 000 (long-lived
 324 scenario) or 10 000 (short-lived scenario) were recruited (or released) into the smallest size class
 325 of the population. These numbers caused a population trajectory that was more or less stationary
 326 (no large change in $N_{t,s}$ across years). All models were fit assuming growth and survival differed
 327 by size state but were constant across time, and that antenna detections and capture probabilities
 328 varied both by time (8 years, 7 intervals) and size state, thus resulting in a total of 47 parameters
 329 (2 growth probabilities, 3 survival probabilities, 21 capture probabilities, and 21 antenna
 330 detection probabilities).

331

332 Closed model – bull trout in Hells Canyon, Snake River

333 We estimated abundance of bull trout in a section of the Snake River, from the
334 confluence with the Salmon River to Hells Canyon, from 2016-2018. More detailed sampling
335 methods for this dataset can be found in the supplementary material of Conner et al. (2020). We
336 did not use PIT antenna detections from the Imnaha River reported by Conner et al. (2020)
337 because PIT antenna detections and physical captures did not occur sympatrically as required by
338 our method. Thus, we expect N estimates to be lower than estimates reported in Conner et al.
339 (2020). Briefly, bull trout were physically captured using angling from December to March in
340 2016-2018. During this same time, submersible antennas (Biomark, Inc., Boise, USA) were
341 distributed throughout the reach to detect bull trout marked with PIT tags. In each year, we
342 divide the sampling effort into four passes of angling and four passes of PIT antenna detections.
343 We then use E1, E2, and E3 to estimate abundance in 2016-2018 using closed models.

344

345 Open model – humpback chub that spawn in the Little Colorado River

346 This model only describes humpback chub that visit the LCR to spawn, and thus it is not
347 pertinent to humpback in western Grand Canyon, which are believed to spawn in the mainstem
348 (Van Haverbeke et al. 2018). Similar to the open model simulations, we include size states
349 (small subadult 100-149mm TL, large subadult 150-199mm TL, small adult 200-249mm TL, and
350 large adult >250mm TL) to account for variability in parameters relating to size. Unlike
351 simulations, we also include location states (LCR, observable CR, unobservable CR) to produce
352 twelve states that correspond to combinations of size and location. Fish sampling occurs in both
353 the observable Colorado River (in the Colorado River study site, located ~127-130 river

kilometers downstream of Glen Canyon Dam) and in the LCR. No sampling occurs in the unobservable CR (i.e., in the CR outside of the Colorado River study site), but fish from the unobservable CR may swim into the LCR and be captured.

This model includes mark-recapture data from sampling trips to the lower 13.56 km of the LCR (typically conducted in April, May, July, September, and October), as well as sampling trips to CR that are roughly timed to occur either in July, August, September, and October (2009-2011) or April/May, July, and September/October (2012-2020). Fish are captured using hoop nets (LCR, CR) or electrofishing (CR only), and all humpback chub >99mm TL are implanted with a PIT tag. Fish are only detectable on antennas following their first capture (i.e., after they receive a PIT tag).

This model is similar in structure to the model described in Yackulic et al. (2014) and we refer readers to this paper for more detailed methods and model description. This model differs from the model described in Yackulic et al. (2014) in the following ways: it 1) includes more years of data, 2) does not include fish with visual implant elastomer marks and omits the smallest size class (<100mm TL), 3) implements a Bayesian framework with temporal random effects on survival, movement, and growth parameters, 4) runs on a different time scale with three intervals per year (Apr- Jun, Jul – Sep, and Oct-Mar), 5) includes water temperature covariates for growth transition and capture probabilities in the Colorado River study site, and 6) incorporates antenna detections from eight submersible antennas in the fall of 2016 and spring, summer, and fall of 2018-2020. Antennas were suspended in the water column by tying antennas to an anchor on one end and a floating buoy on the other end. No antennas were deployed in 2017 due to complications with the antenna batteries. We use E1, E2, and E3 to estimate abundance from 2009-2020, but note that E2 and E3 are reduced to E1 from 2009-2015 and in 2017 because

antenna detection probabilities were fixed to zero in these years. Models were run for 3 chains (with 1 000 iterations each, with the first 500 discarded for burn-in) until convergence ($\hat{R} < 1.1$ for all parameters) in Stan from R using the package rstan (Stan Development Team 2013). We use E1, E2, and E3 to calculate abundance in fall for all adults (small and large adults) that spawn in the LCR.

Results

Simulation results

For simulations assessing the closed model, relative bias was low to negligible. When pass-specific physical capture probabilities were low (i.e., $p_{cap} = 10\%$), E1 had a +3 % relative bias across all values of proportions marked and antenna detection probabilities (note the proportion marked and antenna detection probabilities do not affect E1 because this estimator does not include antenna detections). Additionally, there was a +3% relative bias for E2 and E3 when $p_{cap} = 10\%$, the proportion marked was 10%, and $p_{ant} = 20\%$. However, once the proportion marked was >10% and(or) $p_{ant} = 60\%$, bias decreased to 0-1% for E2 and E3. When p_{cap} was higher (i.e., 20%), bias of all estimators was 0-1%. Coverage was $\geq 94\%$ for all estimators.

Comparison of precision illustrates that E3 consistently had the lowest RSE, followed by E2, then E1 (Fig 2). With both E2 and E3, RSE improved with higher proportions of marked fish. Also, as the proportion of marked fish increased, the RSE of E3 and E2 diverged, illustrating that E3 is particularly beneficial when a large proportion of fish are marked before the onset of the study. Increasing daily capture probability from 10% to 20% substantially

reduced RSE in all scenarios and led to a larger reduction in RSE compared to increasing daily antenna detection probability from 20% to 60%, a finding that was also observed by Conner et al. (2020).

For simulations assessing the open model, all three estimators displayed negligible bias in $\hat{N}$ for the long-lived scenario, where mean bias was between 0% and 2% and median bias was between -2% and 0% for all three size classes. For the short-lived scenario, bias was low with mean bias between 0% and 2% and median bias between -1% and 1% for the midsize and large size classes, but there was moderate negative bias in abundances of the smallest size class and this bias was consistent across all three estimation methods. Specifically, mean bias was between -8% and -7% and median bias was between -8 and -10 %. Coverage was >95% for all estimators and scenarios. Similar to closed model simulations, comparison of RSE estimates shows that often E3 had the lowest RSE, followed by E2, and then E1. However, the relative benefit of each estimator depended on size state, year, and scenario. For the long-lived scenario, differences in RSEs from the three estimators were negligible for small fish and more pronounced for midsize and large fish (Fig 3). Also, with midsize and large fish, the benefit of E2 and E3 tended to increase as more years of data were accumulated (hereafter the 'year effect') so that RSE decreased gradually from year 2 to year 7. The proportion of large fish that were marked increased from 11% (year 2) to 55% (year 7). For large fish under the long-lived scenario, in year 7 simulations showed a 51% reduction in RSE for E3 compared to E1 (i.e., RSEs for E1 and E3 were 13.6% and 6.7%, respectively). The short-lived scenario differed from the long-lived scenario in that the RSE of E1 was lower for all size states, the benefits of the E2 and E3 were more apparent, and the year effect was shorter-lived (i.e., RSE decreased from years 2-4 but did not decrease much after year 4; Fig 4). The proportion marked for large fish in the

short-lived scenario started at 34% (year 2), grew quickly to 65% (year 4), then grew gradually to 77% (year 7). Large fish under the short-lived scenario saw a 38% reduction in RSE in year 7 for E3 compared to E1 (i.e., RSEs for E1 and E3 were 9.4% and 5.8%, respectively).

Closed model – bull trout in the Snake River

Abundance estimates were relatively similar across years. All three estimators produced similar $\hat{N}$ in 2016 (367-386), whereas estimators from models with antenna data (i.e., E2 and E3) produced nominally lower $\hat{N}$ in 2017 and 2018 compared to the E1 estimator from the model without antenna detections. Specifically, in 2017 $\hat{N}$ was 294 (E1), 242 (E2), and 237 (E3), and in 2018 $\hat{N}$ was 388 (E1), 291 (E2), and 280 (E3). Importantly, however, 95% CIs did overlap substantially for all estimators. Furthermore, E2 and E3 both produced more precise $\hat{N}$ in all years compared to E1, and E3 was slightly more precise than E2 (Fig 5). Specifically, compared to E1, use of E2 for $\hat{N}$ reduced the width of the 95% CI by 37-50% and use of E3 reduced the width by 44-57% depending on the year. The model estimates that the proportion of bull trout marked before the start of the study was 19%, 14%, and 23% in 2016-2018, respectively.

Open model – Humpback chub that spawn in the Little Colorado River

General trends for all three estimators are similar over the 2009-2020 period (Fig 6). Abundance estimates were similar across all three estimators prior to 2016, as antennas were not implemented in the sampling design until 2016. We therefore focus on differences between estimators observed in 2016- 2020, after antennas were deployed as an additional gear type. Generally, there was little difference among mean abundance estimates across methods. Notably, there were differences in the precision of E3 compared to E1 and E2 in 2016, 2018, 2019, and 2020 – the four years antennas were deployed. In these years, $\hat{N}$ from E3 had much

better precision compared to E1 and E2 and displayed a 32-48% reduction in the width of the 95% CI compared to E1 and a 32-44% reduction compared to E2. During the fall sampling trips where antennas were deployed, capture probabilities ranged between 2-5% (small adults) and 1-3% (large adults) and antenna detection probabilities were 9-24% (small) or 19-53% (large). The model estimates that approximately 31-55% of small adults and 56-77% of large adults were marked from 2016-2020, suggesting that a high proportion of individuals are marked.

Discussion

Results from closed and open simulations illustrate how including PIT antenna detections in abundance estimation can be advantageous for precision if a substantial proportion of the population is marked. If only a small proportion (e.g., <10%) of fish are marked however, PIT antennas will have little influence on precision of $\hat{N}$ regardless of whether or not PIT antenna detection probabilities are high. The proportion of marked fish is influenced by p_{cap} , because fish must be first physically captured to receive a mark, the exception being stocked fish that are released with marks. Accordingly, improving physical capture probabilities will always benefit estimation of N , but antennas can still improve precision in $\hat{N}$ under some circumstances.

For open model simulations, we divided results into three different outcome categories, the best-case, mid-case, and worst-case outcomes, which described the benefit of using PIT antenna detections for N estimation. The best-case outcome pertained to large fish in the long-lived scenario. The best-case outcome arises from the relatively high physical capture probabilities for small and midsize fish, and this leads to a high proportion of marked fish in the large size state. Additionally, large fish exhibit high survival, low physical capture probability, and high antenna detection probability. Large fish from the short-lived scenario represent the mid-case outcome. Fish in the mid-case outcome had relatively high capture probabilities

compared to fish in the best-case outcomes and thus better RSE without antennas (E1) so that the room for improvement was narrower for E2 and E3. Small fish in the long-lived and short-lived scenarios represent worst-case outcomes where the benefit of antenna detection was negligible. For this group, the benefit of antennas was low due to the low proportion of marked fish (~10%). Importantly, small fish in the short-lived scenario were problematic as bias was more substantial compared to other groups (-8% relative bias in mean $\hat{N}$). This bias was relatively consistent across E1, E2, and E3 and likely due to small sample sizes (i.e., low numbers of recaptures for fish in the smallest size class), which in turn was likely the result of low survival, high growth, and low capture probabilities for this size class.

Similar to our simulations, both applied examples illustrated that incorporation of antenna detections into mark-recapture models improved the precision of abundance estimates so that E2 and(or) E3 had higher precision compared to E1. In the bull trout example, the proportion of marked individuals was relatively low (14-23%), and there was little difference in the benefit of E2 versus E3. Incorporation of antennas reduced uncertainty in $\hat{N}$ by improving precision on $\hat{p}_{cap}(2016, 2017, 2018)$ and also producing higher values of $\hat{p}_{cap}(2017, 2018)$. In contrast, the benefit of E3 over E2 and E1 was clear in the example of humpback chub that spawn in the LCR, likely because a larger proportion of fish were marked (31-71%). This applied example is similar to the best-case simulation scenario in that adult humpback chub tended to have low capture probabilities and high antenna detection probabilities.

While the above-described method improved estimation of N , we stress that the independence of PIT antenna detections and physical capture probabilities are necessary for these approaches and achieving this independence must be addressed at the design stage of a study. For instance, minimizing dependence of antennas and other gear types can be achieved by

moving submersible antennas frequently so that all fish within the sampling area have equal antenna detection probabilities. In addition, fish captured in hoop nets or trammel nets that are set overnight may have a much lower probability of having an antenna detection because once captured these fish cannot swim freely and encounter antennas. Accordingly, using these gear types in conjunction with antenna detections may be problematic, particularly for closed models. For open models, passive gears, such as hoop nets or trammel nets, could be permissible with certain caveats. In our humpback chub examples, physical capture data and antenna detections were pooled across passes (i.e., across days) within the same sampling occasion so that for each sampling occasion there was one pass of antennas and one pass of physical capture. For these examples, the main consideration is that the probability of being captured at least once by the physical gear type is independent from the probability of being detected at least once by the autonomous antennas. Accordingly, if physical capture probabilities are generally low and the sampling design includes multiple passes, the bias induced by dependence of sampling gears may be negligible. Another limitation of this method is that it does not address the problem of ghost tags (i.e., tags of dead fish), and further modifications may be necessary to help with this issue.

PIT tags are commonly used to mark fish because they are small in size, provide a unique identifier for each individual tag, and are relatively inexpensive (Cooke et al. 2013). Consequently, millions of PIT tags have been implanted in fish in watersheds in the Pacific Northwest (primarily salmonids) and in the Colorado River Basin (Conner et al. 2020). In these systems, antennas are increasingly being used to monitor fish movement and survival (Cathcart et al. 2018; Pennock et al. 2018; Sloat et al. 2011). While it is apparent that managers and

biologists are embracing the use of autonomous antennas to detect fish, incorporating antenna detections into long-term monitoring efforts is still relatively uncommon.

Extending the benefit of increased detection (from antennas) could improve statistical power of monitoring designs and better enable biologists to detect increasing or decreasing population trends (Peterman 1990; Taylor and Gerrodette 1993; Wagner et al. 2013). Power analysis could be used to evaluate the statistical power of competing sampling designs (e.g., Carlson and Schmiegelow 2002; Dzul et al. 2013) to determine whether or not antennas are beneficial. Specifically, rough estimates of physical capture probabilities, antenna detection probabilities, and the proportions of fish that are marked can be incorporated into simulations to estimate statistical power and assess sampling tradeoffs. In cases where the proportion of marked fish is high, it may make sense to allocate more effort towards deploying antennas in lieu of additional days/nights fishing with the same gear types.

Other studies have used antenna detections to fit spatial mark-recapture models and assess environmental effects on movement (Raabe et al. 2013), to assess movement patterns on multiple spatial scales (Kanno et al. 2020), and to separate permanent emigration from survival (Horton et al. 2011). Importantly, there are numerous mark-recapture applications where antenna detections may be useful, though much of the statistical groundwork for model development in these areas remains unexplored. Specifically, antennas can act as a supplemental gear type that can be used to assess individual heterogeneity in capture probabilities, evaluate potential for trap-happy or trap-shy behaviors (Bunch and Stewart 2020), or inform availability (Dzul et al. 2021b). We hope future studies will leverage the potential for antennas to act as a supplemental source of detections to help learn more about fish life history and inform management decisions.

540

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553 Data availability: Data for both humpback chub applications will be made publicly available as
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Closed model

<i>Par.</i>	<i>Estimator</i>	<i>Description</i>
p_{cap}	E1,E2,E3	Pass-specific capture probability
p_{ant}	E2,E3	Pass-specific antenna detection probability
c_{tot}	E1,E2	Catch - or total number of unique individuals that were physically captured
p_{cap}^*	E1,E2,E3	Trip capture probability (only includes probability of being captured)
V	E1,E2	Variance of p_{cap}^*
p_{mark}^*	E3	Trip capture probability for marked fish (includes probability of being captured and(or) detected on antennas)
c_{mark}	E3	Number of unique previously marked fish that were captured and(or) detected on antennas
c_{unmark}	E3	Number of unique unmarked fish that were captured
$\mathbf{c}$	E3	Vector (c_{unmark} and c_{mark})
$\mathbf{p}^*$	E3	Vector (p_{cap}^* and p_{mark}^*)
$\mathbf{\Omega}$	E3	Variance-covariance matrix for $\mathbf{p}^*$
N	E1,E2,E3	Total abundance

Open model

<i>Par.</i>	<i>Estimator</i>	<i>Description</i>
i	-	Subscript indicating posterior draw
t	-	Subscript indicating sampling occasion or interval
s	-	Subscript indicating size state at time t
v	-	Subscript indicating size state at time $t+1$

j	-	Subscript indicating row of capture history matrix
ϕ	E3	3-d array of apparent survival probabilities for each posterior draw, time, size state
g	E3	3-d array of growth transition probabilities for each posterior draw, time, size state
Y	E3	Capture history matrix
ξ	E3	4-d array of likelihoods for each posterior draw, unique row of Y , time, size state
Ψ	E3	4-d array describing the state transition matrix for each posterior draw and time
π	E3	4-d array of rescaled likelihoods (ξ) or state probability vector for antenna-only detections
A	E3	Ragged 2-d array of indices describing which rows of Y are antenna-only detections at each time
f	E3	Vector of frequencies that correspond to the number of individuals observed with particular capture history
c_{ant}	E3	3-d array of 'catch' for antenna-only detections for each posterior draw, time, and size state
c_{unmark}	E3	2-d array of physical catch of unmarked fish for each size state and time
c_{mark}	E3	2-d array of physical catch of previously marked fish for each size state and time
c_{tot}	E1,E2	2-d array of the total number of unique individuals that were physically captured for each size state and time
u_{unmark}	E3	3-d array of the number of unmarked, uncaptured fish for each posterior draw, time, and size state
u_{mark}	E3	3-d array of the number of marked, uncaptured and undetected fish for each posterior draw, time, and size state
u_{tot}	E1,E2	3-d array of the number of uncaptured fish for each posterior draw, time, and size state
p_{cap}^*	E1,E2,E3	3-d array of physical capture probability for each posterior draw, size state, and time
p_{mark}^*	E3	3-d array of encounter probability (includes physical capture and antenna detection probabilities) for marked fish for each posterior draw, time, and size state
N	E1,E2,E3	3-d array describing total abundance for each posterior draw, time, and size state

Table 1. Description of model parameters for closed and open models that include antenna detection and physical capture data. Parameters (Par.) could be used in abundance estimation for estimators E1 (no antenna model), E2 (model fit with antennas but abundance estimated from physical captures only), and E3 (model fit with antennas and abundance estimated from physical captures and antenna detections).

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<i>Event number</i>	<i>Size</i>	<i>Captured?</i>	<i>Detected on antennas?</i>	<i>Probability</i>
1	small	Y	N	$p_{cap,1} (1-p_{ant,1})$
2	small	Y	Y	$p_{cap,1} p_{ant,1}$
7	small	N	Y	$(1-p_{cap,1}) p_{ant,1}$
8	small	N	N	$(1-p_{cap,1}) (1-p_{ant,1})$
3	midsize	Y	N	$p_{cap,2} (1-p_{ant,2})$
4	midsize	Y	Y	$p_{cap,2} p_{ant,2}$
7	midsize	N	Y	$(1-p_{cap,2}) p_{ant,2}$
8	midsize	N	N	$(1-p_{cap,2}) (1-p_{ant,2})$
5	large	Y	N	$p_{cap,3} (1-p_{ant,3})$
6	large	Y	Y	$p_{cap,3} p_{ant,3}$
7	large	N	Y	$(1-p_{cap,3}) p_{ant,3}$
8	large	N	N	$(1-p_{cap,3}) (1-p_{ant,3})$

Table 2. Probabilities of events for three different size classes in simulations. Events are determined by whether or not a fish was captured and detected on antennas (Y= yes, N = no), as well as the size bin of the fish if the fish was captured. Capture probabilities (p_{cap}) and antenna detection probabilities (p_{ant}) are indexed by subscripts referring to the size state : 1 (small), 2 (midsize), and 3 (large).

<i>Parameter</i>	<i>Size state</i>	<i>Long-lived</i>	<i>Short-lived</i>
Growth	S to M	50%	70%
Growth	M to L	20%	30%
Survival	S	60%	30%
Survival	M	80%	40%
Survival	L	90%	50%
p_{cap}	S	30%	25%
p_{cap}	M	20%	25%
p_{cap}	L	10%	40%
p_{ant}	S	30%	30%
p_{ant}	M	40%	40%
p_{ant}	L	50%	50%

Table3. Parameter values used in simulations of a multi-state model with antenna detections. Parameters were temporally constant but varied by size state (S = small, M = medium, L = large). Parameters for detection probability include p_{cap} – or the probability of physical capture, and p_{ant} - the probability of an antenna detection.

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Figure 1. Conceptual diagram that describes how to calculate the number of unique individuals in each size class for capture history j [1 1 7 4 8 5 7] that was observed with frequency f_j , where 1 = captured as small fish and not detected on antennas, 2 = captured as small fish and detected on antennas, 3 = captured as midsize fish and not detected on antennas, 4 = captured as midsize fish and detected on antennas, 5 = captured as large fish and not detected on antennas, 6 = captured as large fish and detected on antennas, 7 = only detected on antennas (size unknown), and 8 = not captured and not detected on antennas. The probabilities fish transition between states are a function of apparent survival (ϕ) and growth (g) probabilities. For each sampling occasion (t), illustrations depict whether or not the fish was detected on antennas, whether or not the fish was captured (and at what size), and whether this observation would be included in number of unique individuals that were physically captured but unmarked at capture (c_{unmark}), the number that were physically captured and previously marked (c_{mark}), or the number that were only detected on antennas (c_{ant}). Here, numeric subscripts refer to posterior draw i , then time (second index), then state (third index). Note that, for antenna-only detection at $t = 3$, size is unknown and thus c_{ant} must include the probability (π) capture history j is in states 1 and 2, but for the antenna-only detection at $t = 7$ the fish is known to be large based on previous captures.

Figure 2. Comparison of the relative standard error (RSE) for different abundance estimation methods. Estimates of RSE depend on the proportion of fish that are marked with PIT tags (x-axis), as well as the pass-specific probability of physical capture (p_{cap}) and pass-specific antenna detection probability (p_{ant}). Results are based on 1000 simulations from models with three passes of antenna detections and three passes of physical capture. Abundance estimation methods include the E1 (no antennas), E2 (antennas used in model fitting but not in abundance calculation), E3 (antennas used in both model fitting and abundance calculation), and the RSE

from a method described by Conner et al. (2020) who use PIT antenna detections to calculate abundance. Similar to the current method, Conner et al. (2020) give marked and unmarked fish different encounter probabilities but unlike the current method, Conner et al. (2020) do not separate physical capture and antenna detection probabilities.

Figure 3. Relative standard error (RSE) for abundance estimates from the long-lived scenario for three different size classes (small, midsize, and large) by year. Abundance was estimated using three different estimators: E1 (no antennas), E2 (antennas in model but not abundance calculation), and E3 (antennas in model and abundance calculation).

Figure 4. Relative standard error (RSE) for abundance estimates from the short-lived scenario for three different size classes (small, midsize, and large) by year. Abundance was estimated using three different estimators: E1 (no antennas), E2 (antennas in model but not abundance calculation), and E3 (antennas in model and abundance calculation).

Figure 5. Population size estimates and 95% credible intervals of bull trout in Hells Canyon (Snake River) in the winter of 2016, 2017, and 2018. Abundance estimates come from three different estimators: E1 (no antennas), E2 (antennas used in model but not abundance estimation), and E3 (antennas used in both models and abundance estimation).

Figure 6. Mean abundance estimates and 95% credible intervals from three different methods for adult humpback chub that spawn in the Little Colorado River. Three different estimators were used to estimate abundance: E1 (no antennas), E2 (antennas used in model fitting but not abundance estimation), and E3 (antennas used in both model fitting and abundance estimation).

Figure 1. Conceptual diagram that describes how to calculate the number of unique individuals in each size class for capture history j [1 1 7 4 8 5 7] that was observed with frequency f_j , where 1 = captured as small fish and not detected on antennas, 2 = captured as small fish and detected on antennas, 3 = captured as midsize fish and not detected on antennas, 4 = captured as midsize fish and detected on antennas, 5 = captured as large fish and not detected on antennas, 6 = captured as large fish and detected on antennas, 7 = only detected on antennas (size unknown), and 8 = not captured and not detected on antennas. The probabilities fish transition between states are a function of apparent survival (ϕ) and growth (g) probabilities. For each sampling occasion (t), illustrations depict whether or not the fish was detected on antennas, whether or not the fish was captured (and at what size), and whether this observation would be included in number of unique individuals that were physically captured but unmarked at capture (c_{unmark}), the number that were physically captured and previously marked (c_{mark}), or the number that were only detected on antennas (c_{ant}). Here, numeric subscripts refer to posterior draw i , then time (second index), then state (third index). Note that, for antenna-only detection at $t = 3$, size is unknown and thus c_{ant} must include the probability (π) capture history j is in states 1 and 2, but for the antenna-only detection at $t = 7$ the fish is known to be large based on previous captures.

338x190mm (96 x 96 DPI)

Figure 2. Comparison of the relative standard error (RSE) for different abundance estimation methods. Estimates of RSE depend on the proportion of fish that are marked with PIT tags (x-axis), as well as the pass-specific probability of physical capture (p_{cap}) and pass-specific antenna detection probability (p_{ant}). Results are based on 1000 simulations from models with three passes of antenna detections and three passes of physical capture. Abundance estimation methods include the E1 (no antennas), E2 (antennas used in model fitting but not in abundance calculation), E3 (antennas used in both model fitting and abundance calculation), and the RSE from a method described by Conner et al. (2020) who use PIT antenna detections to calculate abundance. Similar to the current method, Conner et al. (2020) give marked and unmarked fish different encounter probabilities but unlike the current method, Conner et al. (2020) do not separate physical capture and antenna detection probabilities.

219x146mm (300 x 300 DPI)

Figure 3. Relative standard error (RSE) for abundance estimates from the long-lived scenario for three different size classes (small, midsize, and large) by year. Abundance was estimated using three different estimators: E1 (no antennas), E2 (antennas in model but not abundance calculation), and E3 (antennas in model and abundance calculation).

181x154mm (300 x 300 DPI)

Figure 4. Relative standard error (RSE) for abundance estimates from the short-lived scenario for three different size classes (small, midsize, and large) by year. Abundance was estimated using three different estimators: E1 (no antennas), E2 (antennas in model but not abundance calculation), and E3 (antennas in model and abundance calculation).

181x154mm (300 x 300 DPI)

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146x146mm (300 x 300 DPI)

Figure 6. Mean abundance estimates and 95% credible intervals from three different methods for adult humpback chub that spawn in the Little Colorado River. Three different estimators were used to estimate abundance: E1 (no antennas), E2 (antennas used in model fitting but not abundance estimation), and E3 (antennas used in both model fitting and abundance estimation).

212x134mm (300 x 300 DPI)