

1 **Quantifying uncertainty when extrapolating the relationship between snorkel**
2 **counts and mark-recapture estimates of juvenile salmonids**

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20 **Abstract**

21 Snorkel surveys are frequently used to monitor stream-dwelling fish. Inferring local abundance from
22 snorkel surveys is complicated by two primary factors: variable fish detection probabilities and the
23 relative abundance of fish in habitat types below the recommended minimum depth for snorkeling. We

24 examine these factors across three salmonid species (*Oncorhynchus* spp.), 4 years, and 113 location-
25 years in Oregon coastal streams. We calibrate snorkel counts to mark-recapture estimates and develop
26 mathematically explicit expressions that convert a new snorkel count into a probability density of
27 abundance for streams containing mixed habitat types that were and were not snorkeled. Snorkelers
28 detected 63%, 47%, and 39% of juvenile coho salmon (*O. kitsutch*), steelhead trout (*O. mykiss*), and
29 cutthroat trout (*O. clarkii clarkia*) estimated by mark-recapture, respectively, but uncertainty within and
30 among sampling units was high. Further, analytics developed here can be used to infer abundance and
31 uncertainty for habitat types that were not snorkeled. Our quantification of uncertainty arising from
32 using snorkel counts as a proxy for abundance will help managers balance biological risks with available
33 resources.

34 **Keywords**

35 Salmonid monitoring, snorkel surveys, Bayesian mark-recapture, density-dependent habitat selection

36 Introduction

37 Snorkel surveys are widely used to monitor juvenile salmonid abundance (Crawford 2011,
38 Jonasson et al. 2016, Poole et al. 2019). The purpose of snorkel surveys ranges from the
39 evaluation of recovery efforts (e.g., McElhany et al. 2000; Flitcroft et al. 2012, 2014, O'Neal et
40 al. 2016) to examination of ecological relationships (Hicks and Hall 2003, May and Lee 2004).
41 Snorkel surveys are often performed because they cost less than electrofishing or mark-
42 recapture and thus may be conducted with greater replication in time and/or space (Schill and
43 Griffith 1984, Hankin and Reeves 1988, Dolloff et al. 1993). Furthermore, snorkeling can be
44 conducted in habitats that are too deep or complex to effectively sample with techniques that
45 require fish to be captured (Gardiner 1984, Hicks and Watson 1985). Snorkeling also poses less
46 risk of mortality than methods that require capture, making it well suited for monitoring
47 species listed under the Endangered Species Act (ESA; O'Neal 2007).

48
49 Inference from snorkel counts is confounded by two primary factors. First, the detection
50 probability of snorkeling is often unknown (e.g., Hankin and Reeves 1988, Walters et al. 1999),
51 or can vary with differing survey types and species (Staton et al. 2022), environmental
52 conditions (Hayes and Baird 1994, Mullner et al. 1998), and fish densities (Hillman et al. 1992,
53 Roni and Fayram 2000). Second, a depth of at least 20cm is recommended for snorkeling
54 (O'Neal 2007). The proportion of fish distributed into habitats below this recommended depth
55 is often unknown and can exhibit inter-annual variation, complicating an attempt to infer local
56 abundance within a reach using detection-adjusted snorkel counts (Constable and Suring 2023).

57 Previous attempts to quantify variation in abundance between sample units that can and
58 cannot be snorkeled are rare.

59
60 The need to address these factors was motivated by management concerns in Western Oregon,
61 where coho salmon (*Oncorhynchus kisutch*) are listed under the ESA and co-occur with
62 steelhead (anadromous *O. mykiss*) and cutthroat trout (*O. clarkii clarkii*). In response to the ESA
63 listing, a large-scale monitoring effort was initiated in 1998 under the Oregon Plan for Salmon
64 and Watersheds (OPSW) that yields snorkel counts of all three species (State of Oregon 1997).
65 The OPSW monitoring area includes 16,700 km of streams in three coho salmon Evolutionarily
66 Significant Units (ESUs) and four steelhead Distinct Population Segments (DPSs; Figure S6).
67 Snorkeling was used to monitor this area because of its increased spatial coverage relative to
68 other methods. Snorkeling was also favorable because coho salmon prefer pools (Nickelson et
69 al. 1992, Bisson et al. 1997), which typically provide adequate depths for snorkeling but can be
70 too deep or complex to efficiently sample for methods that require fish capture (Mullner et al.
71 1998, Satterthwaite 2002). Further, stream visibility and temperatures in this area were
72 conducive to snorkeling (Hillman et al. 1992, Mullner et al. 1998, Roni and Fayram 2000). Under
73 the OPSW protocols, snorkeling is only conducted in pools that are ≥ 20 cm deep. Other
74 protocols similarly sample only in pools (e.g., Flitcoft et al. 2014, Tualatin River Watershed
75 Council 2015) or pools and glides (e.g., Ebersole et al. 2009).

76

77 The OPSW monitoring data are used to assess trends in the distribution and abundance of
78 salmonids (Constable and Suring 2022) and inform the status of coho salmon (Wainwright et al.
79 2008, Stout et al. 2012). For trend monitoring, a method should be sufficiently precise and have
80 consistent bias (Temple and Pearsons 2007). Counts from snorkel surveys have demonstrated
81 repeatability (Thurow 1994). Resurveys of OPSW snorkel sites have indicated that snorkel
82 counts are precise (Constable and Suring 2022) but less was known about snorkel survey bias.
83 The magnitude of snorkeler detection probability was previously thought to change according
84 to visibility conditions (Rodgers et al. 1992), species, life stage, and number of fish (Hillman et
85 al. 1992). Several studies have compared snorkel counts to electrofishing removal estimates
86 (e.g. Roni and Fayram 2000. Ebersole et al. 2009). However, electrofishing estimates also have
87 variable biases related to both fish and stream attributes (Peterson et al. 2004, Rosenberger
88 and Dunham 2005). Until now, little has been done to compare the accuracy snorkel counts of
89 coho salmon with known numbers of fish or methods with less bias, such as mark-recapture,
90 since the assessments of Rodgers et al. (1992) and Hillman et al. (1992). The accuracy of OPSW
91 steelhead and cutthroat counts is unknown, and we are unaware of any attempt to infer
92 uncertainties in abundance in fast-water habitats (e.g., riffles and rapids) for these three
93 species given snorkel counts in pools for any protocol.

94
95 Here, we address the two factors that confound inference from snorkel counts by developing
96 techniques to convert a new snorkel count into a probability distribution of abundance in
97 stream reaches containing a mix of habitats that were and were not snorkeled. From 2016 –
98 2019 we sampled 18 stream reaches (Supplement 1). In 66 pools, both snorkel and mark-

99 recapture estimates were conducted. Mark-recapture estimates were conducted in an
100 additional 47 fast-water units. We develop novel analytics to quantify uncertainty of fish
101 abundance in pool habitats that were snorkeled and in fast-water units where snorkeling was
102 not conducted.

103

104 **Materials and methods**

105 *Ongoing OPSW Monitoring*

106 The OPSW monitoring protocol employs a generalized random tessellation stratified design to
107 select random, spatially balanced sites that are representative of the sampling frame (Stevens
108 and Olsen 2004). The OPSW sampling frame includes all 1st-3rd order streams within coho
109 salmon and steelhead rearing distributions. Selected sites were surveyed using a snorkeling
110 protocol developed by Rodgers (2000) and a stream habitat survey protocol developed by
111 Moore et al. (1997). Surveying took place during daylight hours of the summer base flow period
112 (mid-July to early October). Snorkelers began at the downstream end of the site and proceeded
113 upstream (Thurow 1994). The type of each habitat unit was determined following Moore et al.
114 (1997). Fast-water units had slopes >0, turbulent surface water, and were more uniform in
115 channel bed form, relative to pools. Pools had a slope of 0, still surface water, and contained a
116 well-defined scour within the channel bed form or an impounding feature, such as a beaver
117 dam or log jam. The length, width, and depth of each fast-water unit (e.g. riffles, rapids,
118 cascades) and pool was measured. Fast-water units were not snorkeled under OPSW protocols
119 because the majority (78%, Constable, ODFW, unpublished data) of these habitats in the

120 program's sampling frame did not meet the recommended 20 cm minimum depth criteria. Only
121 pools that were ≥ 20 cm in maximum depth and ≥ 6 m² in surface area were snorkeled. Pools
122 meeting these criteria were surveyed in a single snorkeling pass, during which snorkelers made
123 separate counts of cutthroat trout and juvenile steelhead ≥ 90 mm fork length (FL), and juvenile
124 coho salmon regardless of length. Juvenile steelhead and cutthroat trout < 90 mm FL were not
125 counted because they cannot be reliably distinguished by snorkelers in this size range (Hawkins
126 1997, Roni and Fayram 2000). Steelhead adults were rarely observed during snorkel surveys
127 because spawning run timing does not coincide with the survey period (reviewed by Busby et
128 al. 1996). Resident *O. mykiss* (rainbow trout) are also rare in OPSW project area, occurring
129 mainly in habitats that are upstream of barriers to anadromy (Busby et al. 1996), which are
130 outside of the sampling frame. In most years, 10-15% of surveyed sites were resurveyed to
131 determine adherence to survey protocols and the count precision.

132

133 *Data Collection*

134 In our study, streams containing juvenile coho salmon, juvenile steelhead, and cutthroat trout
135 from past OPSW surveys were chosen to conduct concurrent snorkel counts and mark-
136 recapture estimates. Within chosen streams, a reach was identified that contained four pool
137 habitat sampling units (hereafter "pool") with fast-water units between each pool. Thus, four
138 pools and three fast-water units could be surveyed in sequence. Pools were required meet the
139 OPSW depth and surface area criteria for snorkeling. Once this reach was located, block nets
140 were placed to establish closed populations (Peterson et al. 2005). Block nets were placed at

141 the top and bottom of the reach and at the transition between each pool and fast-water unit to
142 prevent fish from moving between sampling units. The integrity of each block net was
143 examined by a snorkeler. This configuration allowed for a snorkel count in each pool and a
144 mark-recapture data collection in each pool and in each fast-water unit. Though block nets are
145 not typically present during snorkeling, we assumed their presence would not significantly bias
146 snorkel counts. This assumption was based on OPSW field observations and the work of
147 Korman et al. (2010), who observed steelhead remaining stationary for visual observations.
148 Additionally, mark-resight studies with observations find few fish from the focal reach in
149 adjacent reaches the day after marking (Tim Copeland, Idaho Fish and Game, personal
150 communication).

151
152 Snorkel counts preceded mark-recapture estimates. Snorkel counts were made following
153 OPSW protocols described above (Rodgers 2000). Visibility and hiding cover were rated on an
154 ordinal scale by the snorkeler, considering water clarity and any other factors that could
155 impede the ability to observe fish (Rodgers 2000; Crawford 2011). After snorkeling was
156 completed, the reach was allowed to recover 2 – 2.5 hours before the first phase of mark-
157 recapture began. Fish were captured by electrofishing with 1-3 Smith Root, Inc. model 12-B
158 backpack electrofishers. Mode switches were set at G-5 (40Hz at a 25% duty cycle) and voltage
159 settings ranged from 100 to 300V; depending on stream depth, temperature, conductivity, and
160 fish response. Each pool and fast-water was electrofished until the entire area of the pool was
161 covered. Fish were identified to species, counted, and marked for recapture. Fish captured in
162 pool units were marked differently than fish captured in fast-water units. When captured fish

163 had recovered and when electrofishing and marking was completed in the subsequent
164 upstream habitat unit, fish were released back into the unit where they were captured. Fish
165 recaptured from outside the unit in which they were marked were not included in mark-
166 recapture estimates. Mortalities recorded in the marking phase were not available for
167 recapture and were not included in mark-recapture estimates. Mortalities recorded in the
168 recapture phase were included in mark-recapture estimates.

169
170 When the marking phase was complete, the reach was allowed to recover ~24 hours before
171 the recapture phase began (Temple and Pearsons 2007). The duration of this recovery period
172 should satisfy our subsequent mark-recapture modeling assumption that capture efficiency was
173 similar between passes (Peterson et al. 2004, Rosenberger and Dunham 2005) and similar
174 among marked and unmarked individuals. Block nets remained in place during this time and
175 were inspected periodically and cleaned of debris. Each pool and fast-water unit was
176 electrofished using similar effort as the first phase, covering all areas of the habitat unit with a
177 goal of recovering approximately 50% or more of the marked fish (Rodgers et al. 1992).
178 Numbers of marked and unmarked fish were recorded for each species and mark location was
179 recorded to determine if fish had migrated past block nets (violating mark-recapture
180 assumptions). As with the marking phase, fish were held in buckets within the unit where they
181 were captured and released when they had recovered and when electrofishing was completed
182 in the subsequent upstream unit.

183

184 *Mark-recapture Analysis*

185 There are four possible capture histories for an individual sampled on two occasions: {1,1},
 186 {1,0}, {0,1} and {0,0}, where 1 indicates that the individual is observed, 0 indicates that it was
 187 unobserved, and commas within a capture history {} separate first and second sampling
 188 occasions. A simple model for these data assumes that capture probability, p , is a constant for
 189 all individuals within a sampling unit, and constant across sampling occasions (but not
 190 necessarily constant across sampling units). Thus, under the constant p assumption, the four
 191 possible capture histories listed above should occur with frequency p^2 , $p(1-p)$, $(1-p)p$, and $(1-p)^2$,
 192 respectively. The foregoing can be further simplified into just three kinds of observations. An
 193 individual can be observed on both occasions, $x=2$, with probability p^2 ; observed once, $x=1$, with
 194 probability $2p(1-p)$; or never observed, $x=0$, with probability $(1-p)^2$. These arithmetic facts are
 195 also given by the binomial distribution

$$196 \quad f(x;2,p) = \binom{2}{x} p^x (1-p)^{2-x}, \quad (1)$$

197 where x is 0, 1, or 2, indicating the number of times an individual was observed. The number 2
 198 in Equation 1 indicates two sampling occasions in which individuals are available for
 199 observation. Finding the value of p that maximizes the likelihood of data x is problematic
 200 because the number of individuals with capture history {0,0} is axiomatically unknown and so
 201 the number of instances in which $x=0$ is thus unavailable. Huggins (1991) addressed this issue
 202 for maximum likelihood analyses by developing a likelihood that conditions estimation of p only
 203 on observable capture histories.

204

205 Data augmentation with Bayesian techniques also provides a work-around to the problem of
 206 unknown number of individuals with the {0,0} capture history. With data augmentation (Royle
 207 et al. 2007), we add an arbitrary number of “synthetic” individuals with capture history {0,0} to
 208 the observed data set. The analytical task becomes estimating the proportion of real animals in
 209 the augmented data set. To do this, we introduce a parameter, ψ , for the inclusion probability
 210 that a given individual in the augmented data set is a real individual. For all individuals i in the
 211 augmented data set we have

$$212 \quad z_i \sim \text{Bernoulli}(\psi) \quad (2)$$

$$213 \quad x_i \sim \text{binomial}(p \cdot z_i, \text{trials}=2) \quad (3)$$

214 and the sum over z is the estimate of abundance (Kéry and Schaub 2012). We augmented all
 215 species-and-unit data sets with 100 synthetic individuals.

216

217 Here, we extend the data augmentation technique to accommodate our multiple sampling
 218 units (j), each having unique covariates and observed snorkel counts. The inclusion probability
 219 of synthetic individuals was assumed to vary across units, and flat prior distribution was used:
 220 $\psi_j \sim \text{Beta}(1,1)$. We checked that posteriors of ψ were not truncated at 1 to verify that data were
 221 sufficiently augmented. Three alternative models are

$$222 \quad \text{Model 1: } p_j \sim \text{beta}(1,1) \quad (4)$$

$$223 \quad \text{Model 2: } p_{fast} \sim \text{beta}(1,1) ; p_{pool} \sim \text{beta}(1,1) \quad (5)$$

$$224 \quad \text{Model 3: } \text{logit}(p_j) = b_0 + b_1 * \text{Clarity} + b_2 * \text{Cover}; b_i \sim \text{Normal}(\mu=0, \sigma=32), \quad (6)$$

225

226 where the distributions stated within each model are Bayesian prior distributions. The large
227 standard deviation ($\sigma=32$) is equivalent to a vague precision of 0.001. Note that Model 1
228 estimates p uniquely for each of the j sites; Model 2 estimates p twice for sites dichotomously
229 classified as either “fast” or “pool”; Model 3 derives p for each of the j units using a logit-linear
230 model with the covariates *clarity* and *cover*. Thus, in Model 3, the value of p at unit j depends
231 on the across-unit relationship between p and covariates *clarity* and *cover*.

232

233 A posterior distribution for the proportion of the local abundance at a site that is observed by
234 a snorkeler is obtained simply by defining the quantity

$$235 \quad p_{snorkel,j} = \frac{Observed_{snorkel,j}}{\hat{N}_j}, \quad (7)$$

236 and then including this node in the Markov chain Monte Carlo (MCMC) algorithm. The other
237 derived quantities, mean abundances across sites on different years, mean abundances across
238 years in different habitat types (pool vs. fast) and mean ratios of abundance in fast vs pool
239 sampling units for different years can be similarly estimated with uncertainty inside the MCMC
240 algorithm without needing to specify additional priors.

241

242

243

244 If the snorkel count is informative of abundance, then the snorkel count data can be
 245 integrated directly into the abundance estimate. Rather than estimating abundance across sites
 246 *and then* quantifying the relationship with the associated snorkel counts, as in Equation 7, it is
 247 also possible to *leverage* a potential relationship when estimating abundance at each site.
 248 Specifically, we can replace Equation 7 with

$$249 \quad \text{Observed}_{snorkel,j} \sim \text{Binomial}(p_{snorkel,j}, \hat{N}_j) . \quad (8)$$

250 In this case, we estimate abundance \hat{N}_j jointly in Equation 9 and over the sum of z in the data
 251 augmentation. This joint estimation of abundance from two different data sources is known as
 252 an integrated model (Schaub and Abadi 2011). In Table 1 and throughout, Models 1, 2, and 3
 253 that are fitted using Equation 9 instead of Equation 7 (those that integrate the snorkel counts)
 254 are denoted with the letter “b”.

255
 256 In Model 3, we ask whether mark-recapture capture probability is related to the stream
 257 habitat covariates *clarity* and *cover*. We may also ask whether these covariates affect snorkel
 258 detection probability. This is done with:

$$259 \quad \text{Logit}(p_{snorkel,j}) = \gamma_0 + \gamma_1 * \text{Clarity} + \gamma_2 * \text{Cover}; \gamma \sim \text{Normal}(\mu=0, \sigma=32). \quad (9)$$

260 For simplicity, using stream covariates on snorkel detection probability was implemented only
 261 when the mark-recapture capture probability was treated as a unique random variable in each
 262 mark-recapture study (Model 1 above). We call this Model 4b below.

263

264 Model comparisons were made with two different information-theoretic metrics. The
 265 deviance information criterion (DIC; Spiegelhalter et al. 2002) computed with package R2jags
 266 (Su and Yajima 2021) uses half the variance of the deviance as an approximation for the
 267 effective number of parameters. We also calculated Watanabe-Akaike information criterion
 268 (WAIC). This was done by recording the point-wise predictive density of each datum x_i in a
 269 species-specific data set of size N ,

$$270 \quad D_i = \text{binomial}(x_i, p \cdot z_i, \text{trials}=2) \quad (10)$$

271 across all iterations, s , of the MCMC, yielding $D_{i,s}$. Following Gelman et al. (2014), we computed
 272 WAIC from the posterior samples after completing the MCMC:

$$273 \quad WAIC = -2 \sum_{i=1}^N \log \left(\frac{1}{S} \sum_{s=1}^S D_{i,s} \right) - \sum_{i=1}^N \frac{1}{S-1} \sum_{s=1}^S \left(\log(D_{i,s}) - \overline{\log(D_i)} \right)^2 \quad (11)$$

274 The “b” versions of the models contain two densities.

275

276 Model goodness of fit (GoF) was assessed with a posterior predictive check (Bayesian p-
 277 value, Gelman et al. 1996). For all real and augmentation individuals, i , we recorded Freeman-
 278 Tukey (FT) statistics

$$279 \quad FT.obs_i = \left(\sqrt{x_i} - \sqrt{E(x_i)} \right)^2 \quad (12)$$

$$280 \quad FT.sim_i = \left(\sqrt{x.sim_i} - \sqrt{E(x_i)} \right)^2 \quad (13)$$

281 at each iteration of the MCMC, where $E(x_i) = p_i * z_i * 2$ and $x.sim_i \sim \text{Binomial}(p_i * z_i, \text{size}=2)$. We
 282 summed $FT.obs$ and $FT.sim$ over individuals and checked for the proportion of MCMC
 283 iterations where $FT.sim > FT.obs$.

284
 285 Models were implemented with R Statistical Software (V4.2.3; R Core Team 2023) and JAGS
 286 (V4.3.0; Plummer 2003). For each model formulation-by-species cross ($7*3=21$ models), we ran
 287 50,000 iterations of three MCMC simulations with a 15,000 iteration burn-in period. Chains
 288 were thinned to 1:5, resulting in 21,000 posterior samples per parameter per model per
 289 species. A high-performance computer server at the University of Idaho was needed to prevent
 290 memory overload and had an additional benefit of running all 63 MCMC chains simultaneously.

291

292 *Inferring abundance in pool sample units*

293 We desire a probability density function for the abundance of fish in a pool given a new
 294 snorkel count in a pool. This is possible using our empirical estimates of the proportion seen by
 295 snorkelers. Denoting a new snorkel count as SC and the now estimated proportion seen by
 296 snorkelers as PS , our estimator of abundance in the pool is

$$297 \quad \widehat{N}_{pool} = \frac{SC}{PS}. \quad (14)$$

298 We assume the new snorkel count comes from a pool unit drawn randomly from the collection
 299 of pools sampled for this study. We now develop a probability density function for \widehat{N}_{pool} that
 300 includes uncertainty arising from random sampling of pool unit as well as uncertainty in the

301 proportion of fish seen by snorkelers. Uncertainty in the proportion of fish seen by snorkelers
 302 across all units is given in the right-hand column of Figures 1-3. We note right skew in these
 303 posterior distributions arising from a few sites where snorkelers observed a relatively high
 304 proportion of available fish. We therefore selected a gamma distribution to generalize the
 305 empirical posterior distribution of the among-sites proportion of fish seen by snorkelers. Given
 306 that we have a gamma distribution in the denominator of Equation 14, it is not trivial to find the
 307 density function for abundance in the pool given some new snorkel count. The change-of-
 308 variables technique provides the solution. Let $w()$ denote the inverse function, and $w'()$ be the
 309 derivative of the inverse function. The change-of-variables technique stipulates that

$$310 \quad g(\widehat{N}_{pool}) = f(w(\widehat{N}_{pool})) * |w'(\widehat{N}_{pool})|. \quad (15)$$

311 Noting that the inverse function of Equation 14 is

$$312 \quad w(\widehat{N}_{pool}) = PS = \frac{SC}{\widehat{N}_{pool}}, \quad (16)$$

313 and $f()$ is the gamma function parameterized with shape α and rate β , we obtain

$$314 \quad g(\widehat{N}_{pool}; SC, \alpha, \beta) = \frac{\frac{sc}{\widehat{N}_{pool}}^{\alpha-1} e^{-\beta \frac{sc}{\widehat{N}_{pool}}} \beta^\alpha}{(\alpha-1)!} * \left| -\frac{SC}{\widehat{N}_{pool}^2} \right|. \quad (17)$$

315 To implement, we find values for α and β that maximize the likelihood of our MCMC posterior
 316 samples for the species of interest. These values are inserted into Equation 16. We may also
 317 insert any value for new snorkel count SC and obtain

$$318 \quad \int_0^\infty \frac{\frac{sc}{\widehat{N}_{pool}}^{\alpha-1} e^{-\beta \frac{sc}{\widehat{N}_{pool}}} \beta^\alpha}{(\alpha-1)!} * \left| -\frac{SC}{\widehat{N}_{pool}^2} \right| d\widehat{N}_{pool} = 1, \quad (18)$$

319 indicating that we have a proper posterior probability. From here, we can use numerical
 320 procedures to find the 95% highest probability density interval (HPDI) for \widehat{N}_{pool} . This is done by
 321 numerically integrating Equation 18 across variable ranges of the x-axis (\widehat{N}_{pool}) and retaining the
 322 range integrating to 0.95 that is higher on the y-axis (probability density) than all other
 323 0.95 integral values.

324

325 *Inferring abundance in fast sample units*

326 We desire a probability density function for the abundance of fish in a fast unit given a new
 327 snorkel count in a pool unit. This is possible using our empirical estimates of the proportion
 328 seen by snorkelers (PS) and the empirical estimates of the ratio of abundance in fast and pool
 329 units ($RatioFP$) which was calculated as a derived parameter in the MCMC procedure.

330

331 We begin by noting that

$$332 \quad \widehat{N}_{fast} = \frac{SC}{PS} * RatioFP, \quad (19)$$

333 where the first term on the right-hand side is the pool abundance (Equation 14). We pool
 334 MCMC samples of $RatioFP$ across all years and then once again fit a gamma distribution using
 335 maximum likelihood. This yields a closed-form parametric model for the second term on the
 336 right-hand side of Equation 19. Since we already have a closed-form solution for the first term
 337 on the right side of Equation 19 (viz. Equation 17), we could proceed with known methods for
 338 calculating a product distribution. However, a more straightforward approach follows from

339 noting that the distribution of the quotient of two gamma-distributed random variables is beta-
 340 prime distributed

$$341 \quad \frac{RatioFP}{PS} \sim \frac{(x/\sigma)^{\alpha-1}(1+x/\sigma)^{-\alpha-\beta}}{B(\alpha,\beta)}, \quad (20)$$

342 where B is the Beta function, α and β are the shape and rate parameters, respectively, of
 343 $RatioFP$, and σ is the rate parameter of PS divided by the rate parameter of $RatioFP$.

344
 345 The parametric form in Equation 20 is multiplied by a constant (SC) to obtain a posterior for
 346 \widehat{N}_{fast} . We employ the change-of-variables technique again to obtain

$$347 \quad h(\widehat{N}_{fast}; SC, \alpha, \beta, \sigma) = \frac{\left(\frac{\widehat{N}_{fast}}{SC+\sigma}\right)^{\alpha-1} \left(1 + \frac{\widehat{N}_{fast}}{SC+\sigma}\right)^{-\alpha-\beta}}{B(\alpha,\beta)} * \left|\frac{1}{SC}\right|. \quad (21)$$

348 This solution for the posterior distribution of \widehat{N}_{fast} can be confirmed with Monte Carlo
 349 techniques (Appendix A). With this closed-form posterior for \widehat{N}_{fast} we can compute 95% HPDI
 350 for any given snorkel count in pool sample units.

352 *Density-dependent snorkel detection*

353 Our mark-recapture models make no assumption about the relationship between pool
 354 sampling unit abundance and snorkel detection probability. To determine whether snorkel
 355 detection varies with abundance, we regress year-by-pool point estimates of the proportion
 356 seen by snorkelers, $p_{snorkel}$, against the associated point estimate of abundance for that pool
 357 and year. This is repeated for each species' Model 1, 1b, 2, 2b,3, and 3b.

358

359 *Density-dependent habitat selection*

360 Density-dependent habitat selection could cause the relative abundance of fish in fast and
 361 pool sampling units to change as site-level abundance changes across space or time. Such a
 362 response would add complexity when using snorkel counts (collected in pools) to infer
 363 abundance in fast sampling units or even site-level abundance. Simply plotting the abundance
 364 ratio (Fast:Pool) over site abundance is confounded by different sites having different numbers
 365 of sampling units in fast and pool sampling units. To remove the effect of different proportion
 366 of fast-water versus pool units within a reach, we calculate the mean abundance ratio of
 367 Fast:Pool for a given site and year (y-axis) as

$$368 \frac{\frac{1}{F} \sum_{f=1}^F N_f}{\frac{1}{P} \sum_{p=1}^P N_p},$$

369 where N is all posterior samples of abundance in fast (f) and pool (p) sampling unit. Aggregating
 370 the posterior samples across sampling units enables calculation of a 95% HPDI. We plot this
 371 over the mean unit abundance per site,

$$372 \frac{1}{F+P} \sum_i^{F+P} N_i,$$

373 where N_i are posterior samples of abundance across all units i within the given site and year,
 374 regardless of the number of units within that site and year that are fast (F) and pool (P). We
 375 report the standard error of the point estimates of abundance among all units (fast and pool)
 376 within the site. We used Type I and Type II regression to test for an effect of mean unit
 377 abundance per site on the Fast:Pool ratio to determine if site-level abundance affects the

378 distribution of fish between pool and fast-water units. We also explored using the inverse of
379 the range of the 95% envelope of the Fast:Pool ratio in a weighted regression.

380

381 **Results**

382 Pool and fast-water unit specific fin clips indicated 0.2% of coho salmon, 0% of steelhead, and
383 1.8% of cutthroat trout were recaptured outside of the unit in which they were marked,
384 suggesting block nets contained fish within their original sampling unit. Of all fish handled for
385 mark-recapture, 0.7% of coho salmon, 0.8% of steelhead, and 0.3% of cutthroat trout were
386 electrofishing related mortalities. These data indicated closed population assumptions for
387 mark-recapture were met. Snorkelers did not observe fish crowding at block nets, suggesting
388 that fish did not attempt to escape pools during snorkeling.

389

390 Model convergence was verified by visually inspecting trace plots. The maximum Gelman-
391 Rubin (1992) convergence diagnostic R_{hat} across all 6384 monitored parameters was less than
392 1.05. The 10th, 50th, and 90th percentiles of the effective number of samples per parameter
393 were 820, 11,000, and 21,000, respectively. No mark recapture model formulation consistently
394 outperformed others when looking across species and information theoretic criteria (Table 1).
395 However, there were generally small differences in parameter estimates across mark recapture
396 models for coho (Figure 1) as well as steelhead (Figure S1) and cutthroat trout (Figure S2). All
397 models had satisfactory goodness of fit (Table 1). For simplicity, we hereafter highlight Model
398 3b because it had good information theoretic and goodness of fit metrics. Supplement 1

399 contains percentiles of posteriors for all parameters, as well as the associated Rhat and
400 effective MCMC sample sizes for all models and species.

401

402 Integrating the snorkel count into the estimate of abundance did not systematically affect the
403 abundance estimate (Figure 1, S3, and S4). However, as noted above, units with sparse mark-
404 recapture data had poor goodness of fit unless the snorkel count was integrated into the
405 abundance estimate. Generalizing the proportion of fish seen by snorkelers across sample
406 units is given in the right-hand columns of Figures 1, S3, and S4. Using Model 3b, the mean of
407 these distributions for coho, steelhead, and cutthroat trout are 63%, 47%, and 39%,
408 respectively. However, uncertainty within and across sample units was high.

409

410 The mean unit abundance varied considerably across years for coho, with higher abundances
411 on odd years (Figure 2). In contrast, steelhead and cutthroat trout displayed more consistent
412 mean unit abundances across the four years of study (Figure 2). On average, pool sample units
413 contained 3.3 times more coho than fast-water units (Figure 3). Steelhead had equitable
414 abundances in pool and fast-water units, but uncertainty in all estimates was high (Figure 3).
415 Cutthroat trout had slightly higher abundances in pools than fast-water units, and there was
416 more variation in abundance across pool units than fast-water units (Figure 3). The proportion
417 of coho residing in pools was greater than that of steelhead and cutthroat trout (Figure 4). All
418 three species exhibited some interannual differences in the fast:pool abundance ratio, but the
419 magnitude of annual differences was less than the differences among species (Figure 4).

420

421 The mean unit abundance at a site consisting of multiple sample units did not predict the ratio
422 of abundances among pool and fast-water units (Figure 5). Type I and Type II linear regressions
423 fit to these points were not significant at $\alpha = 0.05$. Using the inverse of the range of the 95%
424 HPDI as weights in a linear regression similarly yielded insignificant effects of site abundance on
425 the ratio of abundances among the site's pool and fast-water units. We thus did not find a
426 significant signal of density-dependent habitat selection for all three species but note that
427 slopes were negative for all three species.

428

429 We used the analytical framework developed above to infer abundance in fast-water units.
430 Using equation 16, we generated a posterior distribution of the abundance of fish in a pool
431 given a snorkel count of 10 fish (Figure 6). Application of Equation 20 to a future coho snorkel
432 count in a pool yields abundance in a fast-water unit (Figure 7). This extrapolation includes
433 uncertainty in proportion seen by snorkelers and hence the associated pool abundance. It also
434 includes uncertainty in the ratio of abundances between pool and fast-water units (3.3x, Figure
435 3). Due to extreme uncertainty inferring cutthroat and steelhead abundance in pools, we make
436 no attempt to apply Equation 20 and extrapolate abundance to fast-water units for these
437 species.

438

439 The proportion of fish seen by snorkelers generally declined with increasing abundance in the
440 pool for coho (Figure S3) and cutthroat (Figure S4), but not necessarily steelhead (Figure S5).

441 We once again note small differences between the alternative mark-recapture model
442 formulations (rows of Figures S3-S5), and whether or not snorkel counts are integrated into the
443 abundance estimate or not (columns of Figures S3-S5). The effect of cover and clarity on
444 snorkel detection were not statistically significant for any of the three species, but posteriors
445 for both covariates were negative for all three species (Supplement 4).

446

447 **Discussion**

448 Our analysis of multiple mark-recapture and snorkel counts shares some features of a novel
449 analysis first developed by Staton et al. (2022). Both analyses use Bayesian techniques to
450 integrate uncertainty in mark-recapture estimates into the snorkel detection probability. We
451 further develop estimators for uncertainty in abundance in fast-water units, which may not be
452 snorkeled under all protocols. By quantifying the relative abundance of fish in pool and fast-
453 water units with a fuller accounting of uncertainty, we facilitate estimation across stream unit
454 types and enable the calibration of snorkel counts to population estimates when there is a
455 management need, e.g., management of steelhead fisheries on Southwest Oregon rivers
456 (Oregon Department of Fish and Wildlife 2021). In pools, snorkelers observed, on average, 63%
457 of the mark-recapture estimate for coho salmon. This result is very similar to a previous result
458 indicating that snorkelers observed 64% of the mark-recapture estimate (Rodgers et al. 1992),
459 suggesting that snorkeler detection probability has remained consistent over time for OPSW
460 monitoring.

461

462 We found a negative effect of abundance on the proportion of juvenile coho and cutthroat
463 seen by snorkelers across all models. Some of the variance in snorkel detection probability can
464 thus be attributed to variance in abundance. However, knowledge of the relationship between
465 abundance and snorkel detection probability has little practical utility because local abundance
466 will generally not be known when a snorkel count is made. In future scenarios when only a
467 snorkel count exists, inference about abundance in the pool should proceed via Eqs. 14 and 17
468 without further attempt to “account” for effects of abundance on the snorkel detection
469 probability. Since cover or clarity had insignificant effects on snorkeler detection probability for
470 all three species, these measures may provide only weak improvement in estimates of
471 abundance derived from snorkel counts.

472
473 Density-dependent habitat selection can influence population regulation (Pulliam and
474 Danielson 1991, McPeck et al. 2001), species interactions (Danielson 1992), evolutionary
475 processes (Holt 1987), and the resulting eco-evolutionary dynamics (Morris 2011). Our study
476 was able to detect whether the relative abundance in pools and fast-water units within a site
477 changed with overall abundance in the site. We found no such evidence of density-dependent
478 habitat selection within the range of naturally changing abundances that occurred during our
479 study. However, we note that coho exhibit a strong positive relationship between abundance
480 ratio of units (fast:pool) and the mean unit abundance across years. We do not consider this
481 evidence of density-dependent habitat selection because pooling data across units obscures the
482 spatial scale over which habitat selection occurs (i.e. a site composed of multiple pool and fast-
483 water units). Density-dependent habitat selection of spawning Chinook salmon (*O.*

484 *tshawytscha*) has been documented in our study region (Falcy 2015), but remains poorly
485 understood for juvenile coho, steelhead, and cutthroat trout.

486

487 We focus herein on estimating uncertainty profiles for abundance at the scale of pools and
488 fast-water units, given a pool snorkel count. Managers may desire information at larger spatial
489 scales. For example, a stream reach comprised several pool and fast-water units. The
490 abundance at the scale of the entire stream reach is the sum of abundances in all the pool units
491 (presumably snorkeled) plus the sum of all the abundances in all the fast-water units. The
492 average of the pool snorkel counts could be used in Equation 20 to generate an abundance
493 profile for each fast-water unit in the reach. Let the median of the resulting distribution be the
494 point estimate. If there are four fast-water units, then the point estimate for abundance in all
495 the fast-water units within a stream is simply the point estimate multiplied by 4. Treating each
496 fast-water unit as an independent random variable, we can easily leverage the fact that
497 variances are additive. That is, the variance of the sum of multiple random variables is equal to
498 the sum of the individual variances. Estimating the variance of the sum of several correlated
499 random variables is also highly tractable: simply add the variances and twice all the pairwise
500 covariances (see Bienaymé's identity). Generating a probability density function for the sum of
501 multiple correlated random variables is less tractable and may require the application of
502 moment generating functions. Regardless, the analytics developed here at the scale of habitat
503 units can be rolled up into an estimate with uncertainty at the scale of an entire stream reach.
504 Estimates at the reach scale can then be used to estimate abundance at larger scales, such as

505 stratum, by extrapolating to the extent of species distribution within the monitored area
506 (Stevens and Olsen 2004).

507
508 Monitoring decisions are ideally motivated by a desire to reduce uncertainty around
509 management actions (Nichols and Williams 2006) while also optimizing costs (Falcu 2018).
510 Additional work on the efficiency of snorkel surveys could entail simulating management
511 decision-making with uncertainty about biological trends. Our analysis provides the estimation
512 uncertainty that could be used in such a management strategy evaluation (Punt et al. 2016) of
513 an ESA listed species.

514

515 **Acknowledgements**

516 We thank Jeff Rodgers for initiating our snorkel survey program. We also thank Scott Kirby and
517 Alex Neerman who were instrumental in the field work over the course of our study. Tim
518 Copeland and three anonymous journal reviewers provided useful feedback on an earlier
519 version of this manuscript.

520

521 **Author statements**

522 The use of trade, firm, or product names is for descriptive purposes only and does not imply
523 endorsement by the U.S. Government. Fish sampling in this study was done in an ethical
524 manner and in accordance with Oregon Administrative Rule 635-011-0066 and within the

525 confines of ODFW's permitted fisheries research programs (National Marine Fisheries Service
526 permit numbers 19958, 20822, 21768, and 22446).

527

528 Competing interests: The authors declare there are no competing interests.

529

530 Author contributions: MF developed and implemented the analytical methods and lead the
531 writing. RC developed field methods, supervised data collection, and contributed to the writing.

532

533 Funding: This research was supported by the Oregon Department of Fish and Wildlife and the
534 Oregon Plan for Salmon and Watersheds. MF developed analytical methods while employed by
535 the US Geological Survey.

536

537 Data availability: Additional figures are given in Supplement 1. Raw data are given in
538 Supplement 2. R and JAGS code for all species and models are in Supplement 3. Raw model
539 outputs are given in Supplement 4. Code for generating all figures is given in Supplement 5.

540

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776

777 **Appendix A**778 Using the R programming language, define shape and rate parameters for *RatioFP* and *PS*:779 `shape1<-14.00224 #(shape on RatioFP; numerator)`780 `shape2<-12.0917 #(shape on PS; denominator)`781 `rate1<-47.79727 #(rate on RatioFP; numerator)`782 `rate2<-19.13105 #(rate on PS; denominator)`

783

784 Simulate observations

785 `RatioFP<-rgamma(100000,shape1,rate1)`786 `PS<-rgamma(100000,shape2,rate2)`787 `SC<-20`788 `Obs.sim<-(SC/PS)*RatioFP`

789

790 Calculate the probability density

791 `fast<-seq(1,30,by=0.001)`792 `Obs.calc<-dbetapr(fast/20,shape1,shape2,scale=rate2/rate1)*abs(1/20)`

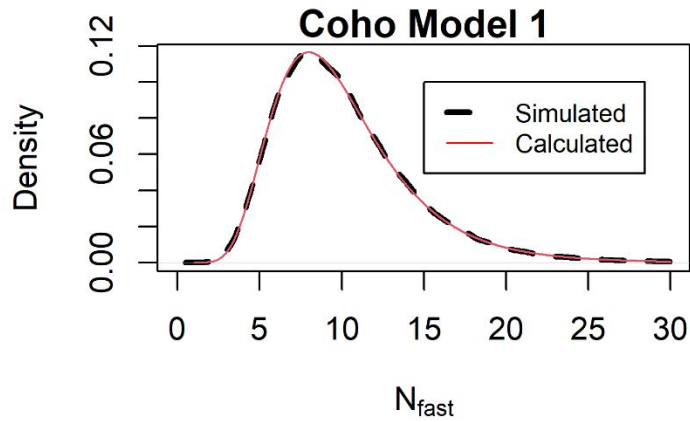
793

794 Compare Obs.sim and Obs.calc in Fig. A1 for a demonstration of concordance between the

795 derived mathematical function and the simulation.

796

797



798

799 **Figure A1.** Concordance between simulated and calculated functions for the abundance of fish
 800 in a pool unit.

801

802 We further note that our closed-form posterior numerically integrates to 1 with absolute error

803 $< 1.4E-06$

```
804 f<-function(x){dbetapr(x/20,shape1,shape2,scale=rate2/rate1)*abs(1/20)}
```

```
805 integrate(f,0, Inf)
```

806

807

808

809 **Tables**

810 Table 1. Two information-theoretic criteria (DIC and WAIC) were calculated separately for each
 811 species and model type (1-3 vs. 1b-4b). GoF is goodness of fit as described in equations 12 and
 812 13 of main text. The R code for generating these metrics is given in Supplement 6.

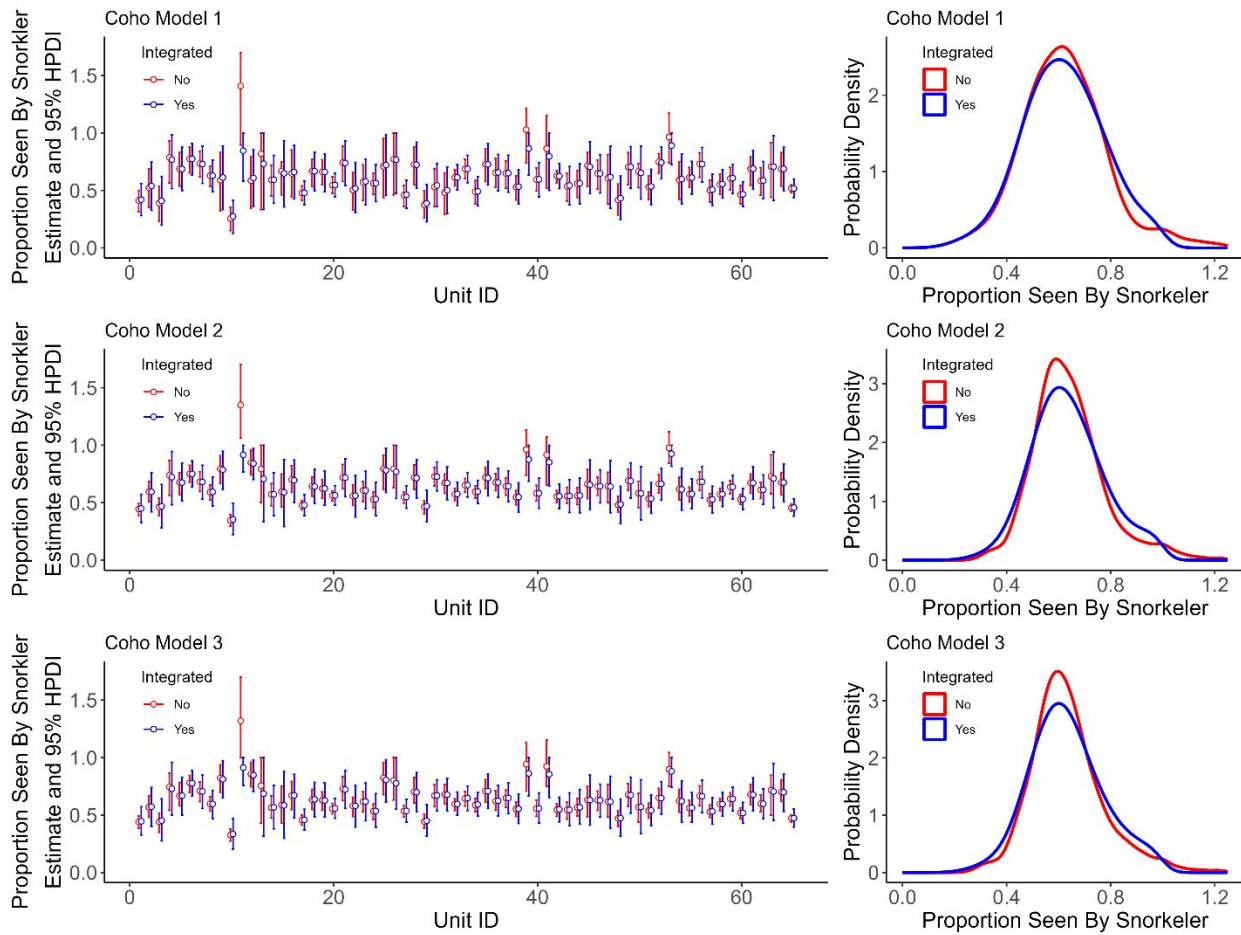
	Coho			Steelhead			Cutthroat		
	Δ DIC	Δ WAIC	GoF	Δ DIC	Δ WAIC	GoF	Δ DIC	Δ WAIC	GOF
1	1458	423	0.23	0	403	0.27	0	380	0.27
2	49	23	0.36	1990	18	0.37	894	0	0.39
3	0	0	0.36	1220	0	0.39	1100	15	0.37
1b	1547	392	0.31	158	319	0.52	0	274	0.50
2b	0	44	0.42	1659	66	0.62	627	26	0.60
3b	184	0	0.45	0	0	0.70	201	0	0.63
4b	782	492	0.25	315	340	0.37	337	305	0.37

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814

815 **Figures**

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818 Figure 1. Point estimates and 95% highest probability density intervals (HPDI) for the proportion

819 of juvenile coho seen by snorkelers at each pool unit where mark-recapture and snorkel counts

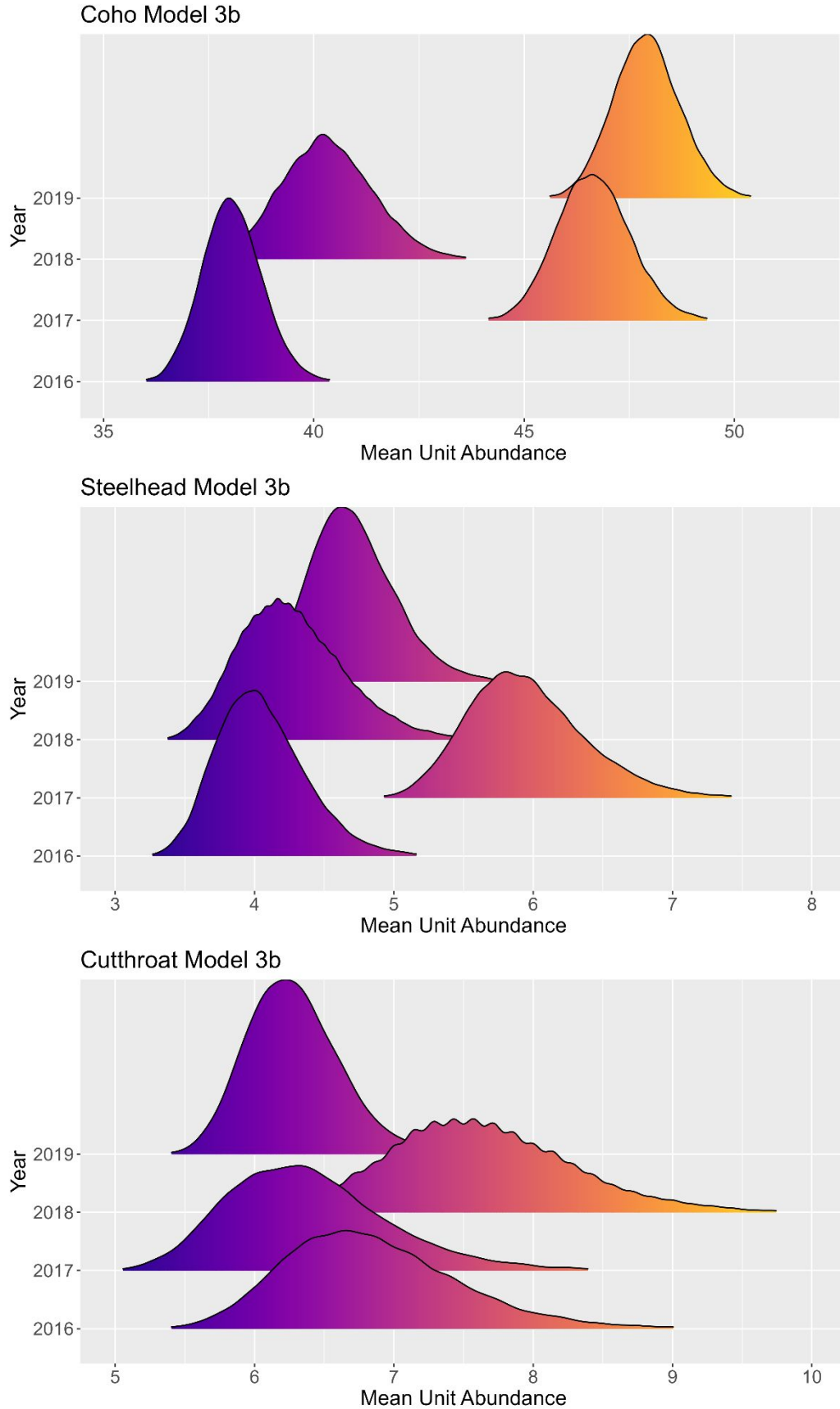
820 were conducted concurrently (left column). The integrated models in blue include the snorkel

821 count in the estimation of local abundance (denoted “b” in the main text). Alternative model

822 formulations (rows) produce similar results. Aggregating uncertainty within and across sampling

823 unit results in the probability density distributions for the proportion of fish seen by snorkelers
824 given in the right-hand column.
825

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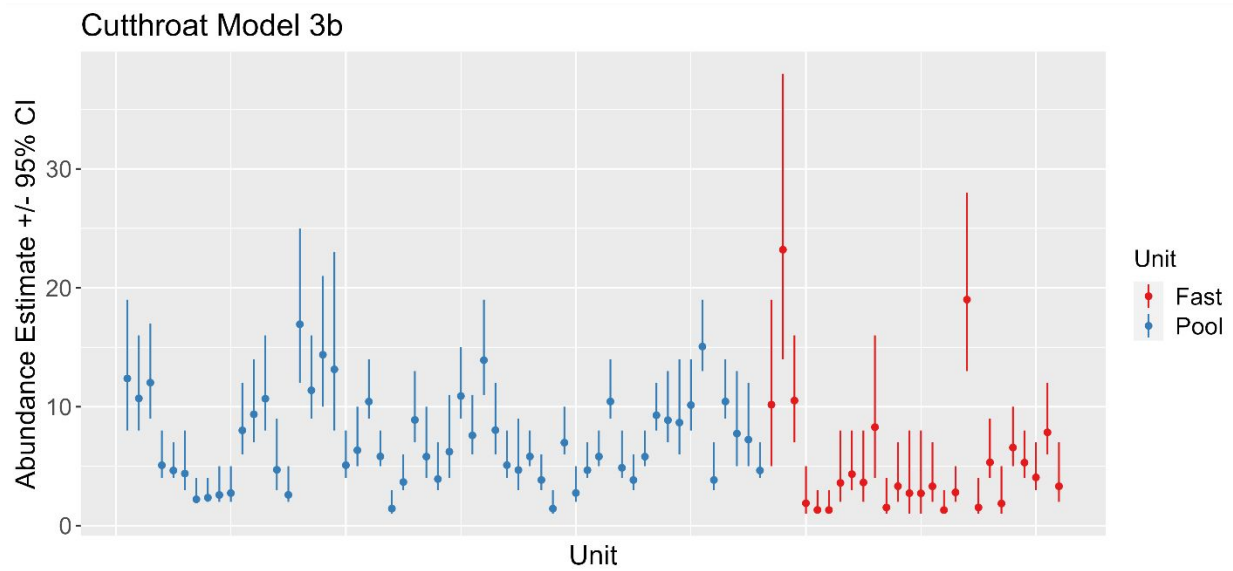
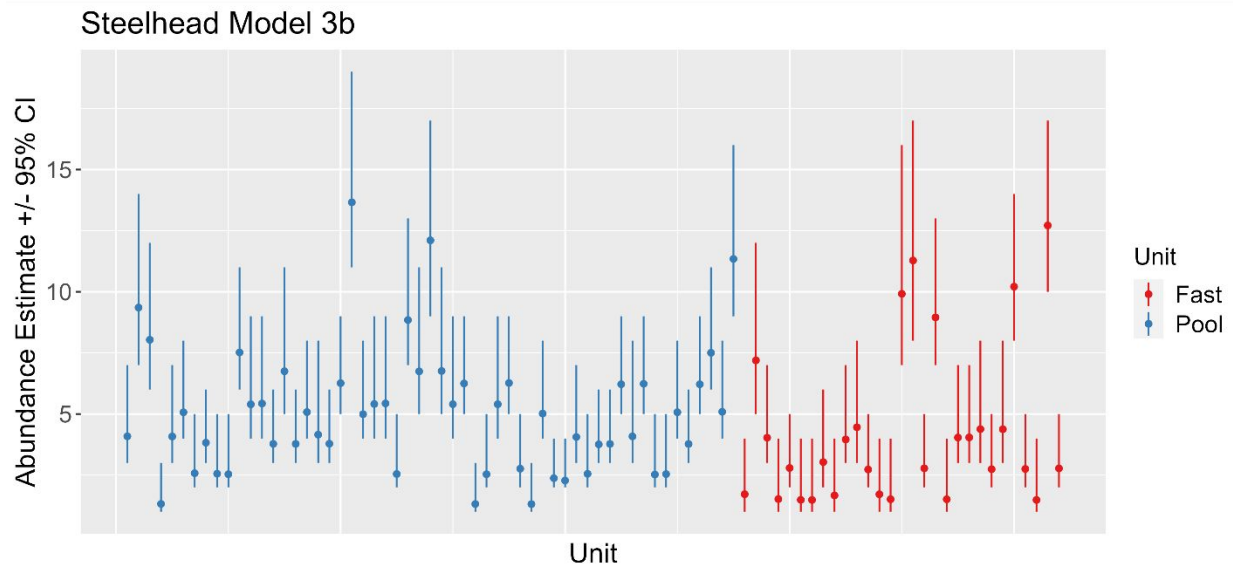
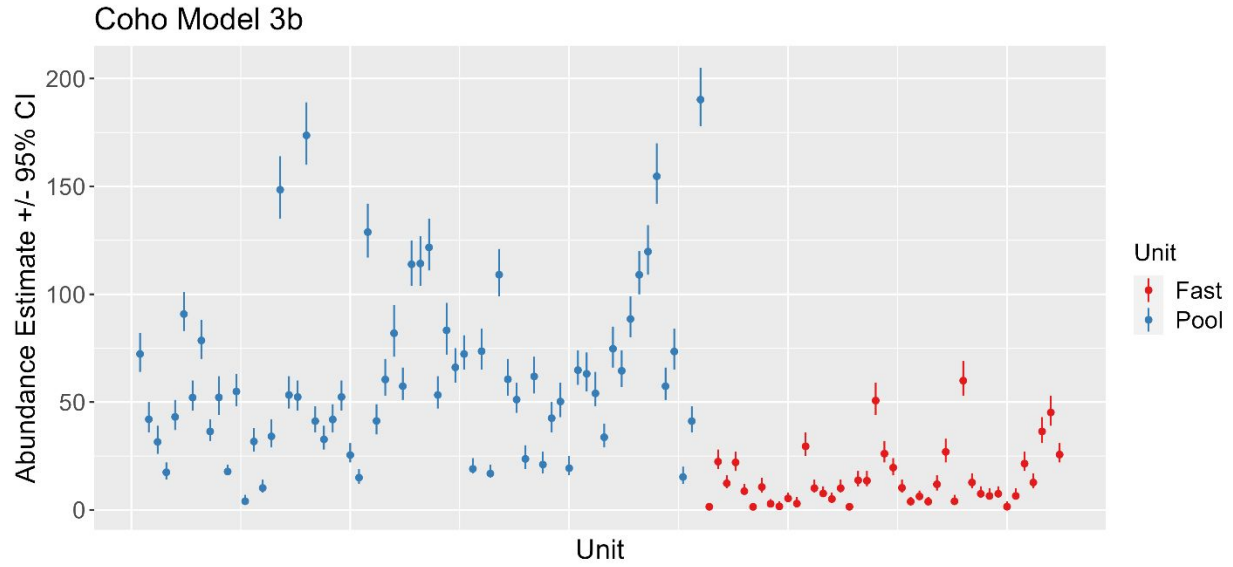


827 Figure 2. Mean unit abundance (x-axis) for each of three species (panels) and four years (y-axis).

828 All estimates were generated with Model 3b.

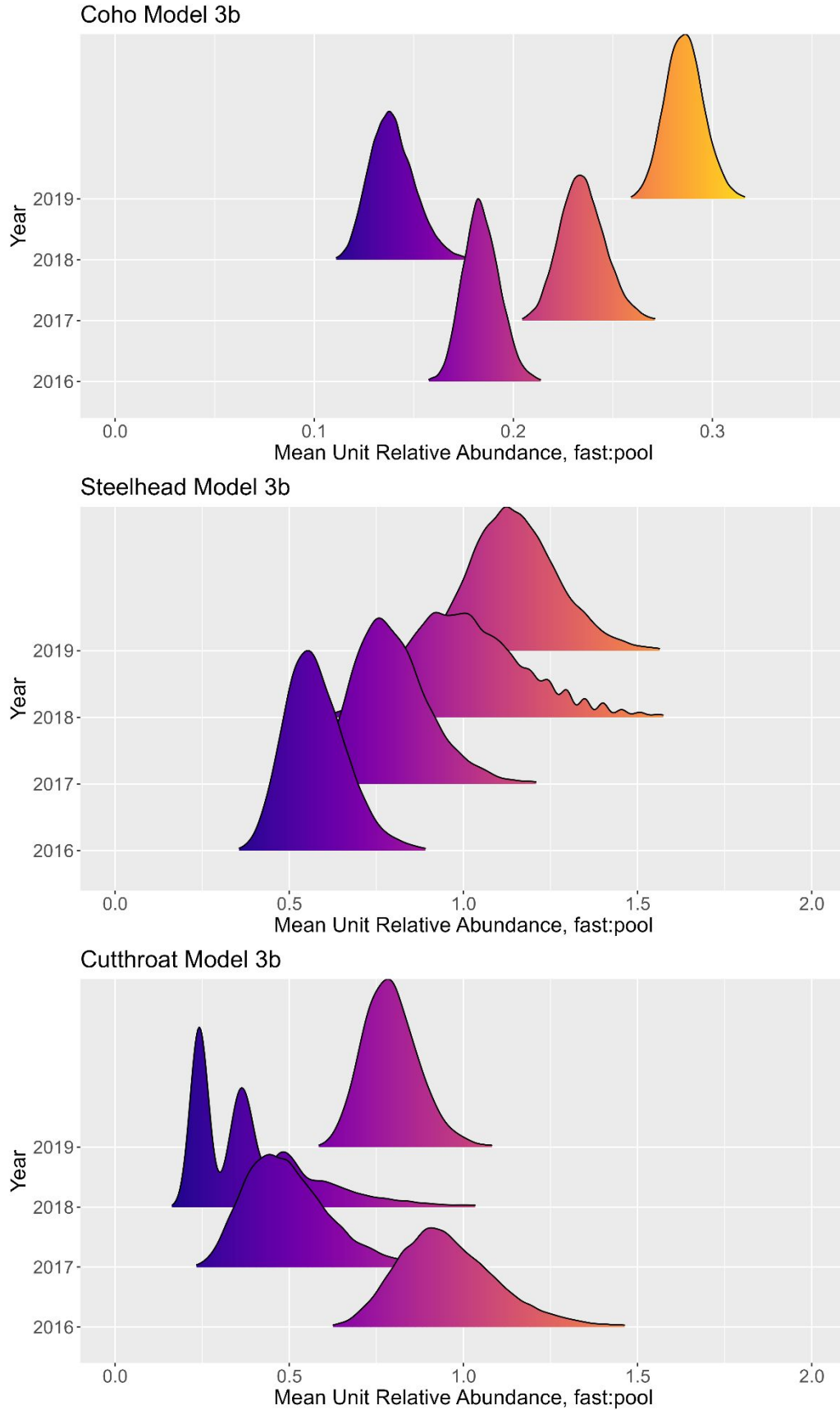
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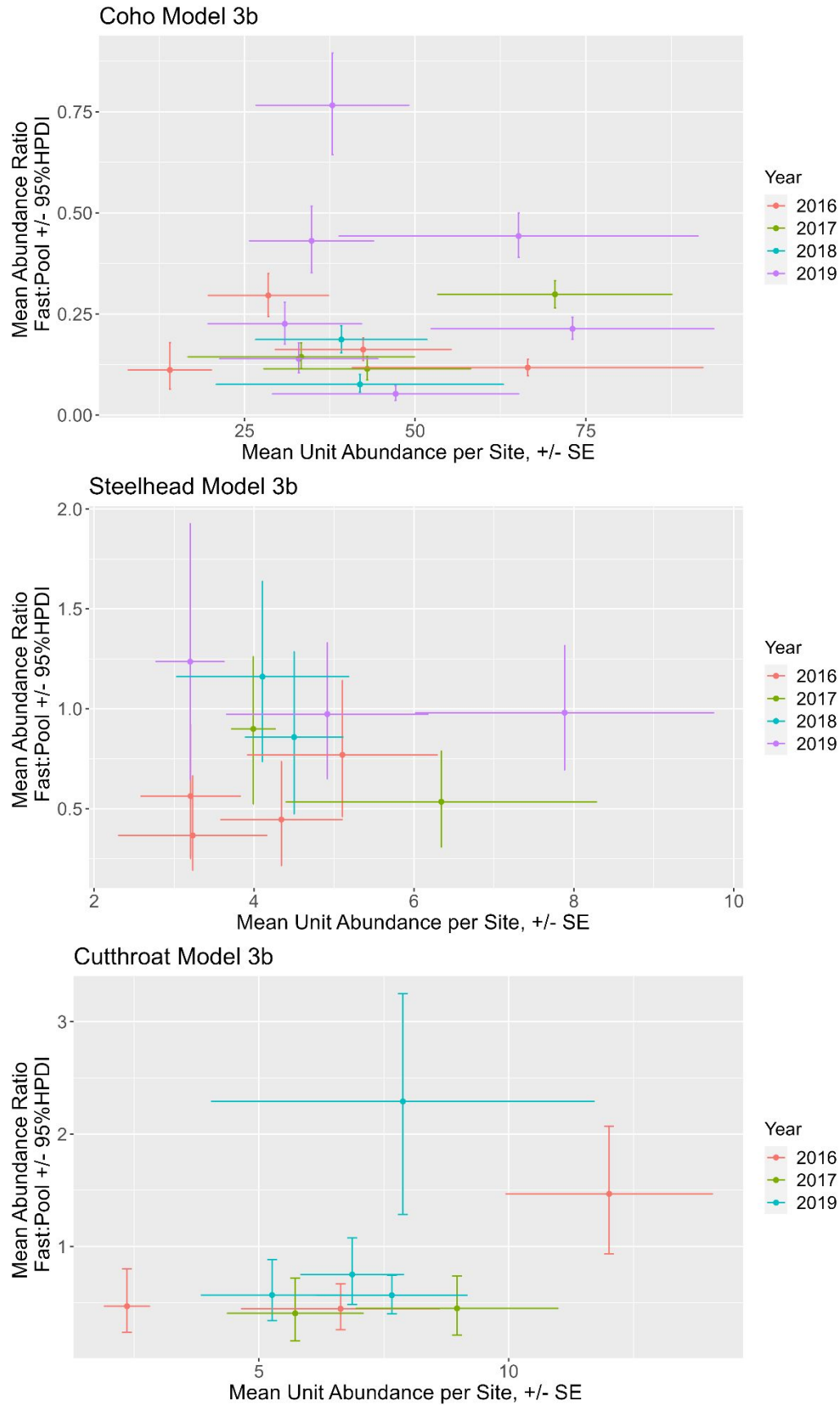


831 Figure 3. Point estimates and 95% highest probability density intervals (HPDI) for three species
832 (rows) in pool (blue) and fast-water (red) units. All estimates were generated with Model 3b.
833

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835 Figure 4. The ratio of abundances in fast-water units relative to pool units for three species
836 (panels) and four years (y-axis). Note difference in scale on the x-axis. Values less than 1
837 indicate greater abundance in pool units. These distributions include uncertainty within and
838 among sampling units. All estimates were generated with Model 3b.
839

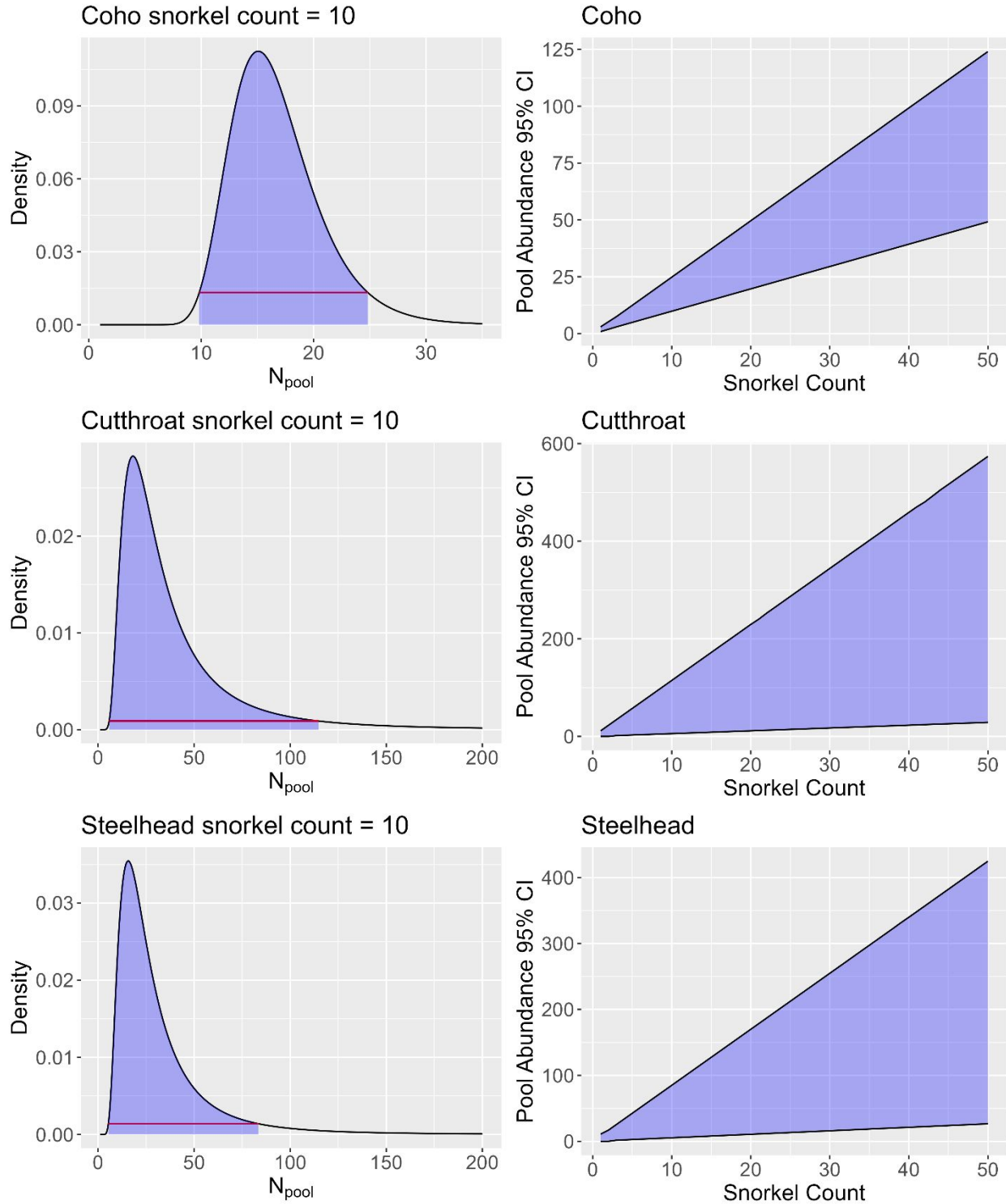


841 Figure 5. Search for density-dependent habitat selection. The average unit abundance at a site
842 does not significantly predict the ratio of abundances between pool and fast units within that
843 site. All estimates were generated with model 3b.

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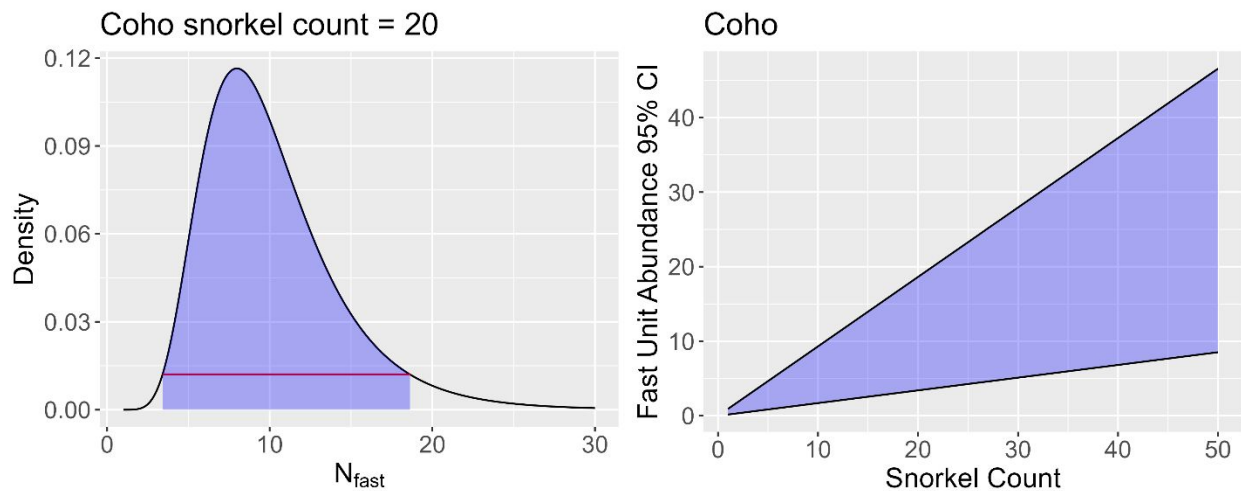
848 Figure 6. Probability density for the estimate of the number of juvenile fish of each three

849 species (rows) in a pool given a snorkel count of 10 (left column). The 95% highest probability

850 density interval (HPDI) is given by the red horizontal line and blue shading. The 95% HPDI

- 851 envelope for pool abundance is given for snorkel counts ranging from 1 to 50 (right column). All
852 estimates generated with Model 3b.

853



854

855 Figure 7. Abundance in a fast-water unit is derived from a snorkel count in a pool by accounting
 856 for the snorkeler detection probability within and among pool units, and the ratio of
 857 abundances between pools and fast-water across all years. The left-hand column illustrates a
 858 pool snorkel count of 20 coho. The red horizontal bar and the blue shading give the 95% highest
 859 probability density interval (HPDI). The 95% HPDI envelope for fast-water abundance is given
 860 for snorkel counts ranging from 1 to 50 (right column). All estimates were generated with
 861 Model 3b.

862