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1 Integrating underwater video into traditional fisheries indices using a hierarchical

- 2 formulation of a state-space model
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- 4 Daniel C. Gwinn^{a,b*}, Nathan M. Bacheler^c and Kyle Shertzer^c
- 5

^a Biometric Research, 3 Hulbert Street, South Fremantle 6162, Western Australia, Australia.

^b The University of Western Australia, School of Biological Sciences, Perth, Western

8 Australia, Australia.

9 ^c National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, North

- 10 Carolina, United States of America.
- 11

^{*}Corresponding author: Daniel C. Gwinn, dgwinnbr@gmail.com

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14 Abstract

Indices of abundance are commonly used in fisheries stock assessment models to 15 represent trends in population size over time; however, an index can misrepresent such trends 16 17 when catchability varies, sampling gears change or spatial sampling frames shift. Here we develop a state-space model in a Bayesian framework that combines both chevron trap 18 19 catches and video counts into a single integrated index. The modeling approach accounts for 20 variation in sampling efficiency (catchability) of both sampling gears and adjusts for aspects of changes in the spatial sampling frame (sampling intensity and spatial coverage) through 21 time due to monitoring program development. We validate the model using a simulation 22 23 study and then demonstrate its utility using data on vermilion snapper *Rhomboplites* aurorubens from the period 1990-2016. The index suggests high variation in the abundance 24 of vermilion snapper, particularly for years previous to 2000 and a systematic decline in 25

26	abundance between the early 1990s and 2016. This pattern culminates (2016) with vermilion
27	snapper at about 16% of their average early 1990s abundance which is a stronger decline than
28	is indicated by the current index used for stock assessment of the species.
29	
30	Keywords: Vermilion snapper, abundance index, Bayesian model, catchability
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33 1. Introduction

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Fisheries harvest policies are typically based on the results of fitting population 35 dynamics models with a variety of data types (Hilborn and Walters, 1992; Walters and 36 Martell, 2004). One essential piece of information used in many fisheries stock assessments 37 is a metric that indexes changes in total stock size through time (Maunder and Punt, 2004). 38 39 These indices are typically derived from some form of fishery-dependent or -independent catch or count per-unit-effort data and are assumed to change in proportion to abundance, and 40 41 thus reflect a scaled version of the total stock size. The resultant indices are used to "tune" stock assessment models, affecting estimates of population dynamics quantities and 42 management reference points, such as harvest targets. Due to their importance for effective 43 44 fisheries management, much attention has been paid to fisheries index development (e.g. 45 Maunder and Starr, 2003; Maunder and Punt, 2004; Maunder et al., 2006); however, obtaining efficacious indices reflecting true changes in total stock size can be quite difficult 46 47 (Kimura and Somerton, 2006). Analysts face many challenges when developing abundance indices for stock 48 assessments, particularly regarding the assumption of proportionality. One of the simplest 49

50 representations of an abundance index is $I_t = N_t q$, where the index I_t is the product of the

51 true abundance N_t and the catchability q (i.e. the proportion of N_t sampled). As long as

52 catchability is constant through time, the assumption of proportionality is met and the index

53 will have the desirable property of reflecting true proportional changes in abundance.

54 However, when catchability varies, changes in q (or q_t) are confounded with changes in N_t ,

such that I_t may not adequately represent true abundance trends. Complicating this matter is

that q (almost) always varies when sampling fish for a variety of reasons (Monk, 2013;

57 Gwinn et al., 2016). For example, the influence of vessel effects on catchability and fishery-

58	dependent indices is well known with variation in q related to variables such as vessel size,
59	crew size, GPS technology, power of motor, and specific gear characteristics (Maunder,
60	2001; Maunder and Punt, 2004; Thorson and Ward, 2014). Fisheries-independent data for use
61	in developing abundance indices are generally recognized as superior to fishery-dependent
62	data (e.g. Dennis et al., 2015), however, these data are similarly vulnerable to variable q . For
63	example, the catchability of reef fish with common baited traps can be strongly related to
64	environmental variables such as temperature, depth, soak time, and substrate characteristics
65	(Coggins et al., 2014; Bacheler et al., 2014; Shertzer et al., 2016). At best, these influences on
66	catchability add noise into catch data but can also result in spurious patterns in I_t that do not
67	reflect N_t when influential variables change systematically across space and time (e.g.
68	Walters and Maguire, 1996; Ward, 2008; Langseth et al., 2016).
69	Shifts in sampling design elements such as the spatial frame of sampling and
70	sampling methods commonly occur in long-term monitoring programs. Typically intended to
71	improve sampling, these idiosyncrasies can also create challenges when developing fisheries
72	indices (Conn et al., 2017). Similar to changes in catchability, changes in the spatial sampling
73	frame and associated environmental characteristics can influence the component of the stock
74	targeted by sampling (e.g. Walters and Maguire, 1996; Langseth et al., 2016). This is also
75	true for changes in sampling gears and is the reason why there is a continuous development
76	of methods to create spatially-explicit indices (e.g. Walters, 2003; Cao et al., 2017;
77	Ducharme-Barth et al., 2018) and indices that integrate multiple sampling methods (e.g.
78	Conn, 2010; Gibson-Reinemer et al., 2017; Kotwicki et al., 2018; Ono et al., 2018). Thus,
79	methods that are robust to variation in catchability due to environmental variables, as well as
80	shifts in sampling frame and sampling methods, are important tools for stock assessment
81	scientists (Maunder and Piner, 2015).

82 The management of many economically important reef fisheries along the southeast 83 U.S. Atlantic coast rely on indices derived from surveys using fishery-independent chevron traps. These traps have been used in this region since 1990 but were fitted with video cameras 84 85 beginning in 2011 to further understand the quality of chevron trap catch data for indexing reef fish abundance, including species that do not enter traps (Bacheler et al., 2013a; Shertzer 86 et al., 2016). The use of underwater video to assess the properties of various sampling gears 87 88 is becoming increasingly common in the literature (e.g. Ward, 2008; Parker et al., 2016; Streich et al., 2018) and can result in a form of replicated count data that may be used to 89 90 index abundance (Bacheler et al., 2013b; Schonbernd et al., 2014). However, appropriate statistical methods that create indices from data collected with these two sampling gears have 91 92 yet to be developed. Combining data from multiple gears presents the opportunity for 93 improved inference, but in this case, introduces two prominent challenges. Firstly, the paired 94 samples of the chevron trap and video count are not fully independent. Although each gear represents an independent sample of the vulnerable fish community at the survey location, 95 96 they are non-independent at the spatial scale of inference (i.e. the region) because samples are collected from the same locations and thus do not represent two independent measures of 97 stock size at the regional level. Secondly, early research comparing trap catches to video 98 counts revealed substantial variation between the two (Bacheler et al., 2013b), likely due to 99 100 differences in how environmental conditions influenced the catchability of traps and videos 101 for various species of fish (Bacheler et al., 2014; Coggins et al., 2014). Here we develop a novel fishery-independent index of abundance that integrates 102 paired trap catches and video counts into a single index of stock size using a Bayesian 103 104 hierarchical formulation of a state-space model (SSM). The SSM has three key features that

make it potentially useful for this application: (i) The model incorporates the baited trapcatches and video counts into a single index that accounts for dependence between the gears;

107 (ii) the model accommodates changes in catchability due to temporal and spatial variation in the environment through the use of covariates and random effects of the observation 108 processes; and (iii) the model can account for aspects of variable catchability due to shifts in 109 110 the sampling frame by modeling temporal variation at the meta-population scale separate from spatial variation at the sub-population scale. We apply this model to vermilion snapper 111 (Rhomboplites aurorubens) data collected along the southeast U.S. Atlantic coast by the 112 113 Southeast Reef Fish Survey as an example and compare it to an index developed with the current methods (Conn, 2010) taken from the most recent stock assessment for the species 114 115 (SEDAR, 2018). The current method of index development (i.e. Conn, 2010) treats the chevron trap catches and camera counts as independent measures of the stock and does not 116 explicitly account for shifts in the spatial frame of the surveys, thus offering a useful 117 118 comparison for the SSM method. 119 2. Methods 120

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122 2.1 Overview of methods

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We organize our methods in four main parts. First, we describe the sampling design 124 and data treatment in the context of the Southeast Reef Fish Survey sampling of R. 125 126 aurorubens along the southeastern coast of the U.S., which is the motivation behind our model; second, we describe the general model structure, covariate structure, model fit 127 evaluation and model optimization methods used in the example analyses; third we describe 128 129 how we compare our index to the current index used for stock assessment of R. aurorubens; and last we describe validation methods of our model on a set of simplified simulated data 130 sets. 131

133 2.2 Sampling design

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R. aurorubens count data were collected along the southeast United States Atlantic 135 Coast from Florida to North Carolina by the Southeast Reef Fish Survey (Fig. 1a). All baited 136 traps were set on or near hard-bottom reef locations. There were 15,629 chevron trap samples 137 available covering a period of 27 years (1990-2016). The number of locations sampled has 138 varied substantially among years due to program development and funding. In the early 139 140 years, the number of samples collected annually was typically in the range of several hundred; however, this number has expanded several fold to over thirteen hundred in the most 141 recent years. Along with increased sampling intensity, the sampling frame of the program has 142 143 expanded in both the latitudinal and longitudinal directions, thus shifting the sub component 144 of the stock vulnerable to sampling (for a detailed description of the sampling frame shift, see Appendix A). Traps were set no closer than 200 m from one another to maintain spatial 145 146 independence relative to fish movement, and at depths between 13 and 115 m. All trap sites used for this analysis were selected randomly from a defined sampling frame of hard-bottom 147 sampling points (Bacheler et al., 2014). Traps were baited with menhaden and set for 148 approximately 90 min. For the time period of 2011-2016, the chevron traps were fitted with 149 150 an outward-looking video camera (Fig. 1b) resulting in 7,644 41-frame video samples (Fig. 151 1c). The camera (Canon Vixia HFS200 in 2011 - 2014 and GoPro Hero 3 or 4 in 2015 and 2016) recorded at least 20 minutes of video from the bottom, and videos were read according 152 to Schobernd et al. (2014). Specifically, a series of video frames spaced 30 seconds apart 153 154 were read 10 to 30 minutes after the trap landed on the bottom. This resulted in 41 replicate camera samples and one baited trap sample per site. 155

159	For trap data, we analyzed the un-transformed catch and for the video data, the sum of
160	the counts across the 41 camera frames (SumCount). We chose to use the SumCount of the
161	camera data because SumCount changes linearly with the MeanCount (Bacheler and
162	Carmichael, 2014), which is often the preferred camera metric (Conn, 2011; Schobernd et al.,
163	2014; Campbell et al., 2015), and using the SumCount preserves the discrete nature of the
164	camera counts allowing for the use of derivations of the Poisson distribution to describe both
165	the chevron trap and camera observation processes. We applied several data filters to either
166	simplify predictor variables, remove records with missing predictor variables, or to remove
167	unusual values. Detailed methods of the data cleaning process are reported in Appendix B.
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169	2.4 Model development
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171	The model was formulated with three distinct hierarchical layers such that the relative
172	abundance at the meta-population level (representing our index of interest, denoted as I_t) was
173	modeled separately from the relative abundance at the sub-population level (i.e. at sample
174	sites, denoted as $n_{s,t}$) and separately from the observation processes. By modelling the meta-
175	population level abundance separately from the sub-population abundance, we were able to
176	isolate the fishery index of interest from components of spatial variation among sampling
177	locations. This is the key component that separates shifts in spatial sampling frame relative to
178	latitude, longitude, and depth from the changes in the average meta-population abundance.
179	Furthermore, by modeling the abundance processes and observation processes with separate
180	sub-models we were able to separate observation error from process error and account for
181	systematic variation in catchability.

182 The most general version of our model describes the latent meta-population level 183 relative abundance (hereafter referred to simply as abundance, I_t) for each year as an 184 independent, freely estimated parameter represented as:

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$$\log I_t \sim \text{Normal 0,100} \tag{1}$$

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however more constrained formulations that assume that meta-population level abundance is 187 a random effect among years (i.e. log $I_t \sim \text{Normal } \overline{I}, \sigma$), a Markovian random walk (i.e. 188 log $I_t = \log I_{t-1} + r_t$, where $r_t \sim \text{Normal } \bar{r}, \sigma$), or any population dynamics model (e.g. 189 logistic model, age-structured model) could be applied based on the intended use of the 190 191 index. If the index will be used to fit a more complex population dynamics model for stock assessment, it may be desirable to impose as little constraint on the temporal pattern of the 192 index as possible; thus, we present the model that assumes indexes are independence among 193 years to represent this case. 194

195 Spatial variation in abundance across sample sites each year (sub-population level)196 was modeled on the log scale as:

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$$\log(n_{s,t}) = \log I_t + co \, {}^n_{s,t} + \varepsilon^{abun}_{s,t}$$
⁽²⁾

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where the term log I_t is the year specific intercept of the linear model, *co* ${}_{s,t}^n$ is a linear combination of spatial covariates, and $\varepsilon_{s,t}^{abun}$ describes random site-level variation in abundance that is not explained by the covariate structure.

We approximated the baited trap catches $(c_{s,t}^{trap})$ and the camera *SumCounts* $(c_{s,t}^{cam})$ as deviates drawn from Poisson log-Normal distributions, which are similar in character to negative binomial distributions (Ntzoufras, 2009, p. 315-317), but can demonstrate better mixing properties than negative binomial distributions when applied in Bayesian programs
such as JAGS. We specified these models as:

207

$$c_{s,t}^{trap} \sim \operatorname{Poisson}\left(e^{\log(n_{s,t}) + cov_{s,t}^{trap} + \varepsilon_{s,t}^{trap}}\right)$$
(3)

$$c_{s,t}^{cam} \sim \operatorname{Poisson}\left(e^{\log(n_{s,t}) + cov_{s,t}^{cam} + \varepsilon_{s,t}^{cam}}\right)$$
(4)

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where the mean on the log scale is the site-specific abundance $n_{s,t}$ plus a linear combination of environmental and/or sampling covariates (i.e. $co \ t,j^{trap}$ and $co \ t,j^{cam}$) to account for systematic variation in catchability. The parameters $\varepsilon_{s,t}^{trap}$ and $\varepsilon_{s,t}^{cam}$ are gear-specific log-Normal distributed random observation errors modeled as, $\varepsilon_{s,t} \sim \text{Normal } 0, \sigma$, with a mean of zero and an estimated standard deviation specific to each sampling method (i.e. σ^{trap} and σ^{cam}).

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216 2.5 Model covariates

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To account for systematic variation in our count data, we incorporated a suite of 218 covariates into the abundance and observation sub-models. We selected covariates based on 219 220 two key considerations. Our first consideration was to separate covariates that influenced the spatial distribution of fish from those that influenced temporal patterns in fish abundance. 221 This was important because spatial and temporal patterns of abundance are modeled in two 222 separate hierarchical layers (i.e. equation 1 and 2) to create a distinction between the fishery 223 index, i.e. temporal patterns in abundance at the meta-population level (I_t) , from spatial 224 variation in the data due to patterns in the spatial distribution of fish $(n_{s,t})$ and shifts in the 225 sampling frame through time. Thus, we included nonlinear (quadratic) effects of latitude (lat 226

and lat^2), longitude (lon and lon^2) and depth (dep and dep²), as well as the potential 227 interaction between latitude and longitude as covariates of local-scale abundance. We 228 included both main and quadratic effects of these variables to account for any optimal ranges 229 230 in latitude, longitude and depth within our sampling frame that vermilion snapper may prefer. The interaction between latitude and longitude was included to allow any preferred range of 231 one variable to be dependent on the other. For example, if vermilion snapper demonstrated a 232 preferred distance from shore, a positive interaction between latitude and longitude could 233 approximate this spatial distribution. Lastly, we included a measure of bottom relief (*rel*) and 234 235 the percent of the substrate that was hard-bottom (sub) as these habitat features may affect the local density of fish. Spatial covariates of abundance were incorporated into the model as: 236

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$$co \ _{s,t}^{n} = \beta_{1}lat_{s,t} + \beta_{2}lat_{s,t}^{2} + \beta_{3}dep_{s,t} + \beta_{4}dep_{s,t}^{2} + \beta_{5}lon_{s,t} + \beta_{6}lon_{s,t}^{2} +$$
(5)
$$\beta_{7}lat_{s,t}lon_{s,t} + \beta_{8}rel_{s,t} + \beta_{9}sub_{s,t}.$$

238

239 Our second key consideration was to separate covariates of the abundance and observation processes. This was important because our model likely has limited ability to 240 disentangle systematic patterns in abundance from systematic patterns in catchability when 241 242 they are similar. Thus, we do not expect to be able to resolve the effects of covariates that have similar influences on patterns in abundance and catchability (Barker et al., 2017). Given 243 244 this limitation, the most useful covariates for predictive purposes are those that either, (i) only influence abundance or catchability, or (ii) have very different influences on abundance and 245 catchability. Thus, we included main and quadratic effects of trap soak time (E and E^2), and 246 main and quadratic effects of temperature (temp and temp²) as continuous variables; we 247 included water turbidity (*turb*) as a categorical variable with two levels (low as turb = 0 and 248 high as turb = 1; and we included current direction as a categorical variable with three levels 249

(current away from the lens and trap opening indicated by dir1 = 0 and dir2 = 0; current towards the side of camera and trap indicated by dir1 = 1 and dir2 = 0; and current away from the lens and trap mouth indicated by dir1 = 0 and dir2 = 1). We incorporated these covariates into our chevron trap observation model as:

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$$co \ _{s,t}^{trap} = \eta_1 E_{s,t} + \eta_2 E_{s,t}^2 + \eta_3 temp_{s,t} + \eta_4 temp_{s,t}^2 + \eta_5 turb_{s,t} +$$

$$\eta_6 dir 1_{s,t} + \eta_7 dir 2_{s,t}.$$
(6)

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In the camera catchability sub-model, we included turbidity, current direction, and main andquadratic effects of bottom temperature as:

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$$co \ _{s,t}^{cam} = \varphi_1 + \varphi_2 turb_{s,t} + \varphi_3 dir1_{s,t} + \varphi_4 dir2_{s,t} + \varphi_5 temp_{s,t}$$
(7)
$$+ \varphi_6 temp_{s,t}^2 + \nu_t$$

259

where the intercept φ_1 allows for a systematic difference in the catchability of the camera 260 261 relative to the chevron trap. The parameter v_t is a fixed value (i.e. log(1.72), Bacheler and Ballenger, 2018) that accounts for the increased field of view of the video cameras used in 262 2015 and 2016. All continuous covariates were centered on zero and scaled to one standard 263 264 deviation with the exception of the effort covariate. We scaled effort by subtracting 60 and dividing by 60 to ease interpretation (effects are relevant to one hour). The absolute value of 265 the Pearson correlation coefficient between covariates were all < 0.6 with the exception of 266 latitude and longitude ($\rho = 0.87$); however, we chose to retain both covariates as we expected 267 that they would both be important for describing site-level variation in abundance and the 268 269 correlation would not impact adversely on the abundance index after model regularization. All covariate definitions are provided in Table 1, the correlation matrix of all covariates is 270

presented in Table B1 (of Appendix B) and JAGS model code and fitting methods are
provided in Appendix C.

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274 2.6 Model fitting and prior specification

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The posterior distributions of all parameters were estimated using a Gibbs sampler 276 implemented in JAGS (Plummer, 2003). We called JAGS from program R (R Core Team, 277 2015) using the library R2jags (Su and Yajima, 2015). All prior distributions of log-scale 278 covariate effect parameters, including model intercepts and the fisheries index I_t were 279 specified as diffuse normal distributions (N[0,100]). Standard deviation parameters including 280 all random effects were specified as scaled half Student-t distributions with input parameter 281 values chosen to stabilize fit while inducing negligible parameter shrinkage (i.e. $\mu = 0, \tau =$ 282 2.78, k = 2). Inference was drawn from 10,000 posterior samples taken from two chains of 283 10⁶ samples. We discarded the first 500,000 values of each chain to remove the effects of 284 initial values and thinned the chain to every 100th value. Convergence of all models was 285 diagnosed by visual inspection of trace plots and Gelman-Rubin statistic ($\hat{R} \leq 1.1$ indicate 286 model convergence, Gelman et al. 2004). 287

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289 2.6 Model fit evaluation and regularization

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There are two common purposes of models in applied ecology, (i) causal explanation and (ii) empirical prediction, and the same model will often not perform well for both purposes (Shmueli, 2010; Authier et al., 2016). A model used for the purpose of explanation requires that the uncertainty in parameter estimates are appropriately accounted for such that the realized 95% credible interval coverage is equivalent to the *a priori* expectation (i.e. true

parameter value contained within 95% CI 95% of the time). In practice, this requires that the 296 model error structure adequately explains the residual error and, thus, can be determined with 297 model fit tests. Alternatively, the optimal predictive model will often be a model where the 298 299 covariate effect estimates are removed or shrunk towards zero through a process termed regularization (e.g. Reineking and Schroder, 2006; Hooten and Hobbs, 2015). Thus, some 300 level of increased bias is accepted for the predictive advantage of decreased variance. 301 302 Although optimal prediction of our index is our main purpose, we were also interested in the influence of our covariates on abundance and catchability. Thus, we first used a posterior-303 304 predictive check to determine an adequate error structure for our fully parameterized model for the purpose of evaluating covariate relationships (termed 'global model'). Covariates 305 were considered statistically different than zero when the associated 95% Bayesian credible 306 307 intervals (quantile based) did not include zero. Second, for our best error structure, we used a process termed Stochastic Search Variable Selection (SSVS) to induce shrinkage of covariate 308 effects and generate a model with optimal predictive properties to produce the fisheries index 309 (termed 'reduced model'). Using SSVS to produce models with desirable predictive 310 properties was first introduced by George and McCulloch (1993) but has been thoroughly 311 discussed in more recent ecological literature by O'Hara and Sillanpaa (2009), Tenan et al. 312 (2014), and Hooten and Hobbs (2015). 313

We evaluated model fit of the global model for eight general model error structures with Bayesian p-values (Kéry, 2010). The Bayesian p-value is a posterior-predictive check that provides a measure of under- or over-dispersion of the data relative to the model (Kéry, 2010; Hooten and Hobbs, 2015). The eight error structures were models that either included or excluded the random variables ε^{abun} , ε^{trap} , and/or ε^{cam} . We performed our model fit evaluation by simulating our data directly from each model for each Markov Chain Monte Carlo (MCMC) iteration and calculating a Pearson residual between the simulated and

expected values (i.e. predicted χ^2) and observed and expected values (i.e. observed χ^2). The 321 simulated data are considered "perfect" because they are generated directly from the model 322 323 and, thus, the resulting Pearson residual represents the fit of the model when all model assumptions are perfectly met (Kéry, 2010). We then created a fit metric that is equal to zero 324 325 when the Pearson residual was greater for the observed data than the simulated data and is 326 equal to one, otherwise. The Bayesian p-value was then calculated as the mean of the 327 posterior sample of the fit metric for each data type, where a mean of 0.5 indicates perfect model fit to the data and a mean approaching 1 or 0 indicates under- or over-dispersion of the 328 329 data relative to the model, respectively.

We chose the procedure of SSVS to produce the reduced model and optimize 330 prediction because preliminary analysis indicated that processing times in excess of four days 331 may be expected for the example data. Thus, many common approaches to variable selection 332 that either employ iterative model runs such as information theoretic methods (e.g. AIC, 333 WAIC, DIC, etc.) or k-fold cross validation are prohibitive. Therefore, we employed SSVS 334 which took approximately five days to complete two million MCMC iterations. We applied 335 the SSVS method for each covariate effect parameter in Eq. 5, 6, and 8 to invoke parameter 336 337 shrinkage. Specifically, we applied a hierarchical structure for each of our covariate priors that is conditional on a random effect indicator variable as: $P(\beta_i | w_i) \sim \text{Normal}(0, \sigma_i)$, where 338 $\sigma_i = 100w_i + 0.01$. The variable w_i is a random effect for each covariate that has a prior 339 distribution of $P(w_j)$ ~Bernoulli 0.5, such that when $w_j = 1$, $\sigma_j = 100.01$, approximating a 340 standard uninformative prior on the covariate effect parameter β_i . Alternatively, when $w_i =$ 341 0, $\sigma_j = 0.01$ which approximates a highly informative prior for a $\beta_j \cong 0$. Thus, the 342 conditional prior creates a region of high probability around zero similar to ridge regression 343 or a "slab and spike" prior (Tibshirani, 1996; Ishwaran and Rao, 2005). Furthermore, the 344 posterior mean of w_i can be interpreted as the relative support of a non-zero value of β_i 345

similar to the posterior probabilities for different model structures obtained via reversible
jump methods (e.g. Hillary 2011). However, one advantage of the SSVS process is that
model predictions are automatically model averaged, providing a more refined level of
regularization. Thus, we produced the index from the regularized model that included all
covariates as well as the indicator variables and conditional priors.

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- 352 2.7 Comparison of indices
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354 To increase our insight into the value of the SSM index, we compared it to an index developed for use in the most recent stock assessment of *R. aurorubens* (Conn, 2010; 355 356 SEDAR, 2018; hereafter referred to as the "Conn index"). The Conn index utilized a 357 hierarchical analysis to combine multiple indices into a single index for use in stock assessment (Conn, 2010). The method requires prior knowledge of sampling error and 358 constraints on process error, which may be difficult to inform. A detailed description of 359 360 methods is provided in Conn (2010). In brief, the approach treats multiple, independently developed indices of abundance as measurements of the same underlying quantity (the true 361 relative abundance), with each index subject to sampling and process error. For this 362 application toward R. aurorubens, two indices were combined, one developed from video 363 364 gear (Cheshire et al., 2017) and one from chevron traps (Bubley and Smart, 2017). Thus, the 365 data were the same as those used for the SSM index, and the primary difference in methodology is that the Conn (2010) approach operates on previously created indices, 366 whereas the approach presented here operates at the level of the observed data. By doing so, 367 368 our approach more naturally accounts for the lack of independence between the gears that might be expected when sampling co-occurs (i.e., cameras are mounted on traps) and the 369

potential impact of non-independence between the sampling methods on the indexuncertainty.

To simplify comparison of the indices we used a parametric bootstrap method to estimate the linear slope of population change through time for each index. For each year and index, we sampled 10,000 random values drawn from log-Normal distributions with the means specified as the annual index point estimates and the associated standard deviations. For each random sample, we use least square methods to estimate the intercept and slope of the index through time on the log scale. This results in a probability distribution of the logscale linear trend for each index.

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380 2.7 Model validation

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To validate the efficacy of our model, we addressed two questions with a simulation 382 experiment; (i) is our model identifiable and (ii) does it produce unbiased parameter estimates 383 384 when applied to perfect data? Our methods were to define a data-generating model, simulate multiple datasets, and analyze the simulated datasets with the data-generating model. Our 385 data-generating model is presented in Table 2 and was identical to the model described for 386 our R. aurorubens analysis where the temporal abundance process is modeled as an 387 independent variable for each year (Eq. 1, Table 2) drawn from a log Normal distribution 388 389 with a mean and standard deviation set to represent observed variation in the R. aurorubens index. However, we excluded the random variables ε^{abun} , ε^{trap} , and ε^{cam} to reduce the 390 391 limitations of computation time. We simulated nine covariate relationships influencing subpopulation level abundances, trap catchability and camera catchability (θ_{1-9} , Table 2), where 392 the simulated covariates, x1-x9 (Table 2) are nine separate vectors of random draws from 393 normal distributions with mean of zero and standard deviation of one to simulate generic 394

centered and scaled covariates. We chose covariate effect sizes arbitrarily to represents different levels of effects and the absence of effects. The input values for the simulated covariate effects were, $\theta_{1,4,7} = 1$, $\theta_{2,5,8} = -.5$, and $\theta_{3,6,9} = 0$. Simulated data sets were fit with the data generating model. We report the mean absolute error as a measure of bias and, to evaluate if the credible interval coverage was appropriate, we reported when the true parameter value was excluded from the 95% credible intervals for each iteration of the simulation. All simulation code is included in Appendix D.

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403 **3. Results**

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405 3.1 Simulation study
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Our simulation study revealed that the SSM model does indeed return unbiased 407 estimates of meta-population abundance (I_t) and covariate relationships with appropriate 408 credible intervals. The mean absolute error of all covariate effect estimates centered on zero 409 410 (Fig. 2a) and the true value was included in the 95% Bayesian credible intervals between 91.5 and 96.5% of the time. The results for the simulated relative abundance index were similar 411 with little to no systematic bias (Fig. 2b) and 95% credible interval coverage of the true index 412 value for 90.2 to 97.2% of simulation interactions. These results indicate that the model is 413 identifiable and produced unbiased parameter estimates with appropriate levels of 414 uncertainty. 415 416

417 *3.2 Vermilion snapper analysis*

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419 All eight error structures of the global model fit to R. aurorubens count data converged after 10⁶ iterations and each required up to 96 hours of computer processing of 420 two MCMC chains run in parallel. Our posterior-predictive check indicated that three model 421 error structures adequately fit the data (models 1, 2, & 3 in Table 3). All of these models 422 included a site-specific random effect in the abundance sub-model (ε^{abun}) and either a site-423 specific random effect in the camera sub-model (ε^{cam}), the trap sub-model (ε^{trap}) or both. 424 Global model 2 and 3 had the simplest structure of only two random effects, allowing us to 425 exclude global model 1 as the most parsimonious error structure. Global model 3 produced a 426 lower model deviance than global model 2 and the posterior estimates of the standard 427 deviation of the random effect ε^{trap} were near zero when estimated with global model 1 428 offering additional support for global model 3 as the best error structure (See Appendix E). 429 Thus, we used global model 3 for the remaining analyses in this paper. This model included 430 the random effects ε^{abun} and ε^{cam} and excluded the random effect ε^{trap} (Table 3). 431 Most of the covariates evaluated with global model 3 (had a statistically significant 432 433 influence on abundance or catchability (Table 4). We found that the strongest determinants of sub-population abundance $(n_{s,t}, \text{ equation 3})$ were the latitude, longitude, depth, and percent 434 435 hard-bottom substrate at the sample site (Fig. 3, Table 4). However, the interaction between the latitude and longitude of the location was also a strong influencer (Fig. 3, Table 4). The 436 only covariates of abundance that were not statistically different than zero were the main 437 effect of depth (lon^2 , $\beta_6 \approx 0$, Table 4) and the bottom relief at the site (*rel*, $\beta_8 \approx 0$, Table 4). 438 The catchability of the chevron trap was found to be strongly related to the amount of time 439 the trap was set $(E, \eta_1 > 0, \text{ Table 4})$ and its square $(E^2, \eta_2 < 0, \text{ Table 4})$. This relationship 440 suggests that the number of R. aurorubens captured increases with trap soak time to a 441 maximum (at ~110 minutes of soak time), beyond which the catch declines (Fig. 4a). 442 Temperature and its square (temp $\eta_3 \varphi_5$ and temp² $\eta_4 \varphi_6$, Table 4) defined a pattern in 443

catchability for both the chevron trap and camera that stayed fairly constant at lower 444 temperatures and increased rapidly at temperatures greater than ~25° C (Fig. 4b); however, 445 this pattern was less pronounced for the camera (Fig. 5a). Current direction influenced the 446 catchability of both the chevron trap and camera (η_6 , η_7 , φ_2 , and φ_3 , Table 4) but was a 447 stronger effect for the camera (Fig. 4c and 5c). For both gears, the lowest catchability was 448 449 when the current direction was towards the mouth of the trap and camera lens, while it was 450 the highest when the current direction was away from the trap mouth and camera lens (Fig. 451 4c and 5c). Finally, higher levels of turbidity increased the catchability of the camera (Table 452 4, Fig. 5b), but had no influence on chevron trap sampling efficiency (Table 4).

Our model regularization procedure resulted in a reduced model with the effective 453 removal of eight covariates relative to the global model ($w_i \ll 0.05$, Table 4). For example, 454 the three non-statistically significant covariates (i.e. β_6 , β_8 , and η_5 , Table 4) had w_j values 455 equal to zero. Additionally, six statistically significant covariates (i.e. β_5 , η_6 , η_7 , φ_3 , φ_4 , and 456 φ_5) were effectively removed from the model with w_i values ≤ 0.23 . Although statistically 457 458 different than zero in the global model, these covariates tended to have small effects sizes with relatively high levels of uncertainty (Table 4). We found that the value of several 459 covariates with high inclusion probabilities (i.e. $w_i \approx 1.00$) differed between the global and 460 reduced model (i.e. $\beta_1, \beta_3, \beta_4, \varphi_2$, Table 4). This is likely a result of some level of 461 462 multicollinearity among covariates (particularly for latitude and longitude covariates). Our index generated from the reduced model tended to be equally precise as the index generated 463 from the global model with an average coefficient of variation of 0.40 (range across years = 464 (0.35, 0.52) and (0.42) (range across years = (0.36, 0.51)), for the reduced and global model, 465 respectively. The observed different of 0.02 is likely not large enough to be biologically 466 467 relevant.

Our index of *R. aurorubens* suggests high annual variation in abundance (Fig. 6a). For 468 example, our model predicted a nine-fold increase in abundance between 1990 and 1991. 469 After 1991, annual variation in abundance ranges between a 168% increase in 1994 and an 470 471 87% decrease in 2003. This level of variation was fairly consistent across the time series (Fig. 6a). The index also suggests a linear decline in *R. aurorubens* since the 1990s. A 472 bootstrapped slope of this decline on the log scale was statistically negative ($\mu = -0.60, 95\%$ 473 474 CI = -0.69, -0.51, Fig. 6b) and suggests that *R. aurorubens* are currently (2016) at about 16% of their average abundance in the early 1990s (i.e. 1990-1995). 475

476 The SSM index described a very similar pattern in abundance to the index generated from the methods of Conn et al. (2010); however, there were some differences (Fig. 6c). For 477 example, the Conn index had a smaller average coefficient of variation than the SSM index 478 479 (Conn = 0.35, SSM = 0.40) and demonstrated some differences in year-to-year variation in the index, however these differences were subtle (Fig. 6a, and b). Most notably, the SSM 480 index described a stronger pattern of decline across the time frame of the data than the Conn 481 index. The bootstrapped slope of the Conn index was statistically different than zero but 482 nearly half the value of the SSM index ($\mu = -0.36$, 95% CI = -0.49, -0.24, Fig. 6d). This 483 484 decline suggests that *R. aurorubens* in 2016 are at approximately 33% of their mean abundance in 1990-1995, which is over twice the value predicted by the SSM index. 485

486

487 **4. Discussion**

488

We developed a state-space model that integrates data from multiple gears that are non-independent relative to the sampling process into a single fisheries index. We demonstrated its use for indexing *R. aurorubens* abundance from paired count data derived from underwater video cameras and catch data from traditional fisheries-independent baited

493 traps. The method provides a means to account for random and systematic variation in the 494 catchability of both sampling gears and adjusts for aspects of non-proportionality due to changes in the spatial frame of sampling expected when monitoring programs are developing. 495 496 The model produced unbiased estimates of meta-population level relative abundance when 497 the model is correctly specifies and demonstrated good fitting properties. We see this modelling approach as a flexible tool that has the potential to be useful for generating 498 fisheries indices for stock assessment for a variety of fish species sampled with paired non-499 independent gears, particularly traditional gears paired with underwater video cameras. 500

501 One of the key strengths of the SSM model is its ability to account for variation in catchability for both sampling gears. The importance of the covariates of catchability was 502 503 highlighted by our SSVS model regularization procedure that indicated the optimal predictive 504 model included many of these covariates. Furthermore, it is important to note the advantage that multiple sampling gears provide in addition to covariates when estimating parameters of 505 state-space models. The addition of multiple gears, and thus, multiple observation sub-models 506 507 to the SSM provides contrast between the residual error of each gear and the covariates that describe it. This contrast between patterns in residual error provides greater information for 508 509 the model to disentangle process error from observation error. For example, when relative 510 catch rates of the gears deviate from the expected value differently, at least one of these 511 deviations must be due to observation error. Alternatively, when only one observation sub-512 model is included in the SSM, the pattern in the residual and the *a priori* choice of covariates to describe it are the only sources of information that the model has to distinguish observation 513 error from process error. Furthermore, it is the inclusion of multiple sampling methods that 514 515 allows a model that assumes independence of the index among years to be identifiable, which is a desirable option when the index will be further used to fit a stock assessment population 516 dynamics model. With only a single observation model, a more confining structure must be 517

imposed on the index to obtain identifiability, such as a Markovian process commonly
applied in state-space models (e.g. Clark and Bjornstad 2004; Jiao et al. 2008). Furthermore,
greater contrast between the variation in catchability of the gears will provide the most
informative data and likely result in greater index precision. Thus, the inclusion of multiple
gears can be quite advantageous in this context.

In our case, the direction of the covariate effects on the observation sub-models 523 524 tended to be consistent with previous research on the sampling efficiency of these gears (Bacheler et al., 2013b; Bacheler et al., 2013c; Coggins et al., 2014; Shertzer et al., 2015). 525 526 This comes as no surprise because we based our choice of covariates, in part, on these studies. For example, we found a dome shaped relationship between trap soak time and 527 catchability that resulted in a maximum catch at about 110 min of soak time. A similar 528 529 relationship has been found for other reef fish species such as black sea bass (Centropristis striata) and is likely the result of entry and exit rates of fish into and out of the trap that 530 change through time inversely proportional to each other (Bacheler et al., 2013c; Shertzer et 531 al., 2015). Similarly, we found that the effect of temperature on both the trap and camera was 532 positive with the appearance of a threshold-like response at $\sim 25^{\circ}$ C. Bacheler et al. (2014) 533 found a comparable relationship between chevron trap catch of *R. aurorubens*, with a 534 threshold at $\sim 20^{\circ}$ C, but did not detect this relationship for cameras. We observed a positive 535 536 relationship between camera counts of *R. aurorubens* and turbidity which has also been 537 observed for red snapper (Lutjanus campechanus, Coggins et al., 2014). Although this response may be counterintuitive, our data filtering process was similar to Coggins et al. 538 (2014), which removed high turbidity data points that demonstrably impacted the counting of 539 540 fish in video frames; thus, this effect may be a result of fish behavioral changes with variation in water clarity (e.g. McMahon and Holanov, 1995; De Robertis et al., 2003; Andersen et al., 541 2008). 542

Another important benefit of our SSM is that it can account for shifts in the sampling 543 frame from year to year. For example, over the length of time of the Southeast Reef Fish 544 Survey sampling program, the number of chevron traps set each year has systematically 545 increased as the program expanded (particularly since 2011). The expanding of the program 546 has led to changes in the distribution of traps relative to latitude, longitude, and depth (Fig. 547 7a, b, c), resulting in variability in the mean covariate values among years with apparent 548 549 systematic increases in depth and decreases in latitude over the life of the program (Fig. 7). Our model accounts for this shift by modeling the index I_t at a fixed point in space (relative 550 551 to latitude and longitude) and for a fixed depth. The limitation of this method is that it only accounts for the shift in the sampling frame relative to these covariate relationships. Thus, 552 any unaccounted for systematic spatial patterns in abundance that coincide with the 553 expansion of sampling may still result in a biased index. This provides high incentive to 554 determine the important drivers and structure of the spatial distribution when using this 555 method, which could include environmental covariates as well as modeling a spatially 556 autocorrelated residual. In our case, inspection of the residual did not reveal any non-random 557 patterns in the spatial distribution relative to the covariates and the expanding sampling 558 design, nor did calculating the index from only the sample locations contained within a core 559 area that was sampled every year produce an index substantially different from the one 560 presented in Figure 6a. These two diagnostics suggest low risk of a biased index due to 561 shifting sampling frame, in our case (see Appendix F for details about the diagnostics). 562 However, unaccounted for changes in the average abundance due to shifts in the sampling 563 frame or shifts in the species distribution should be carefully considered when applying this 564 method. This is particularly the case if the count data are derived from a fishery-dependent 565 source, where preferential sampling that is often related to fish density is common (Pennino 566 et al. 2018). As accounting for preferential sampling in the analysis of count data can be 567

568	analytically challenging (e.g. Conn et al. 2017, Pennino et al. 2018), we recommend, first,
569	that appropriate spatial designs be used for sampling and, when this is not possible, that
570	appropriate diagnostics be used to evaluate the risk of induced bias.
571	

572

4.1 Model extensions

There are several possible extensions to the SSM that would allow it to accommodate 574 various idiosyncrasies of different data sets worth discussing. One prominent extension is to 575 576 accommodate various levels of zero inflation in the sub-population model. Our example data set was zero inflated with 75% and 70% zeros in the trap catches and camera counts, 577 respectively. We approximated the structural component of these zeros with the log-normal 578 random effect ε^{abun} ; however, this method makes explicit the assumption that these potential 579 zeros are actually very small non-zero values. Our model fit test suggested that this model 580 581 structure provided adequate fit to our example data; however, another option is to model a zero-inflated spatial abundance process by including a shared Bernoulli variable in both (or 582 all) observation models as: 583

584

$$c_{s,t}^{trap} \sim \operatorname{Poisson}\left(z_{s,t} e^{\log(n_{s,t}) + cov_{t,j}^{trap} + \varepsilon_{s,t}^{trap}}\right)$$
(8)

$$c_{s,t}^{cam} \sim \text{Poisson}\left(z_{s,t}e^{\log(n_{s,t}) + cov_{t,j}^{cam} + \varepsilon_{s,t}^{cam}}\right)$$
(9)

585

where $z_{s,t}$ is a latent random variable distributed as, $z_{s,t} \sim \text{Bernoulli}(\psi_{s,t})$. The Bernoulli probability of a non-zero abundance could be modeled independently for each year, as a function of a set of spatial covariates with a logit link, or as a function of *co* $_{s,t}^n$ to create a formal relationship between the spatial abundance and occurrence processes (e.g. Smith et al. 590 2012). Additionally, a zero-inflated observation process could be modelled by specifying591 unique Bernoulli processes for each observation sub-model.

Another prominent extension would be to model spatiotemporal variation in patterns 592 in abundance more explicitly. For example, applying a multivariate normal prior to $\varepsilon_{s,t}^{abun}$ to 593 explicitly model spatial auto-correlation could be used to improve the predictive potential of 594 the model and to better account for changes in the spatial distribution of sampling among 595 years. Furthermore, specifying covariate effects of the spatial abundance process as random 596 effects across years could be used to evaluate and account for non-stationarity in these 597 relationships through time. These are only a few examples of potentially useful extensions to 598 our model that could improve its application to various settings. Thus, we see this model as a 599 600 foundation that could be easily extended to accommodate the nuances of a variety of data structures and contexts. 601

602

603 4.2 Management implications

604

605 The application of our model to R. aurorubens revealed a systematic decline in abundance across the time period of 1990-2016. This decline was similar to, but stronger than 606 the decline described by the Conn index (Conn et al., 2010). This discrepancy between the 607 two indices is in the direction that would be predicted given the systematic expansion of the 608 sampling design into latitudes, longitudes, and depths of greater abundance, and given that 609 the Conn index does not account for this systematic expansion, while the SSM does (Figure 610 7d). The difference also suggests that the R. aurorubens stock may have a lesser ability to 611 compensate for the reductions in density due to harvest (i.e. lower productivity) than would 612 be indicated by the Conn index. It is difficult to predict the effect this would have on 613 management recommendations; however, we may expect the use of the SSM in a formal 614

615	stock assessment to result in more conservative harvest regulations to meet management
616	targets such as Maximum Sustainable Yield (Beverton and Holt, 1957) and maintain
617	acceptable levels of risk of overfishing (Zhou et al. 2016). Although an explicit comparison
618	between the outcomes of formal stock assessments with each index would be necessary to
619	know this for sure.
620	
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622	
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798 Tables

Table 1

801 Covariate descriptions and definitions.

Variable	Abbreviation	Class	Definition
Latitude	lat	continuous	The latitude of the sample location.
Longitude	lon	continuous	The longitude of the sample location.
Depth	dep	continuous	A continuous variable indicating the water
			depth at the trap location.
Soak time	Ε	continuous	A continuous variable indicating the length
			of time the trap was set before retrieval.
Temperature	temp	continuous	The water bottom temperature at the trap
			locations during sampling.
Turbidity	turb	categorical	A dummy variable indicating the level of
			turbidity $(1 = \text{level } 2, 0 = \text{level } 1)$.
Substrate	sub	continuous	The percent of the substrate visible with the
			camera that is hard-bottom.
Relief	rel	categorical	A dummy variable with value of 1 indicating
			that the relief was "high".
Current away	dir1	categorical	A dummy variable that is 1 when the current
			direction is flowing away from the camera
			lens.
Current side	dir2	categorical	A dummy variable that is 1 when the current
			direction is flowing perpendicular to the
			camera lens.

Table 2

- 806 Simulation structure and inputs. The equations represent the structure of the data-generating
- 807 model and the Inputs are the parameter values used in the simulation.

Data-generating model	Description	Inputs
Process model		
log I_t ~Normal μ, σ	Temporal abundance model	$\mu = -3, \sigma = 0.93$
$\log(n_{s,t}) = \log I_t + co n_{s,t}$	Site-level abundance model	
$co \ _{s,t}^{n} = \theta_{1}x1_{s,t} + \theta_{2}x2_{s,t} + \theta_{3}x3_{s,t}$	Spatial covariates	$\theta_1 = 1, \theta_2 = -0.5, \theta_3 = 0$
Trap observation model		
$c_{s,t}^{trap} \sim \operatorname{Poisson}\left(e^{\log(n_{s,t})+cov_{s,t}^{trap}}\right)$	Trap observation model	
$co \ _{s,t}^{trap} = \theta_4 x 4_{s,t} + \theta_5 x 5_{s,t} + \theta_6 x 6_{s,t}$	Trap catchability covariates	$\theta_4 = 1, \theta_5 = -0.5, \theta_6 = 0$
Camera observation model		
$c_{s,t}^{cam} \sim \text{Poisson}(e^{\log(n_{s,t}) + cov_{s,t}^{cam}})$	Camera observation model	
$co \sum_{s,t}^{cam} = \theta_7 x 7_{s,t} + \theta_8 x 8_{s,t} + \theta_9 x 9_{s,t}$	Camera catchability covariates	$\theta_7 = 1, \theta_8 = -0.5, \theta_9 = 0$

812 **Table 3**

Bayesian p-values for model fit evaluation. Each model includes or excludes site level random effects in the abundance (ε^{abun}), trap (ε^{trap}), and camera (ε^{cam}) sub-models. The Bayesian p-value is the output metric of a posterior-predictive check where a value of 0.5 indicates perfect fit of the model to the data and values approaching zero or one indicate under- or over-dispersion of the data relative to model predictions, respectively.

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#	Random effects	Model	Bayesian p-value	
#	included in model	deviance	Camera	Trap
1	$\varepsilon^{abun}, \varepsilon^{trap}, \varepsilon^{cam}$	31511.1	0.33	0.49
2	$\varepsilon^{abun}, \varepsilon^{trap}$	31487.2	0.11	0.67
3	$\varepsilon^{abun}, \varepsilon^{cam}$	31281.3	0.33	0.48
4	$\varepsilon^{trap}, \varepsilon^{cam}$	31741.2	0.99	0.71
5	ε^{abun}	120003.7	0.02	0.67
6	ε^{trap}	3081507.0	1.00	0.64
7	ε^{cam}	183413.1	1.00	1.00
8	None	3218795.0	1.00	1.00

819

822 Covariate parameter posterior summaries. Posterior means and credible intervals are derived 823 from posterior samples of the full model prior to model reduction. The grey text indicates 824 covariates that are not statistically different than zero at $\alpha = 0.05$. Variable definitions are 825 presented in Table 1. The column labeled 'Mean (SSVS)' is the mean of the posterior 826 distribution with induced shrinkage via the Stochastic Search Variable Selection procedure 827 (SSVS) and the column labeled ' I_j ' is the parameter inclusion indicator variable.

Variable	Parameter	Mean	95% Credible	Mean	I _i
<u> </u>			intervals	(55V5)	2
Abundan	<u>ce</u>				
lat	β_1	-1.38	-2.03, -0.71	-1.86	1.00
lat^2	β_2	-1.02	-1.27, -0.76	-1.00	1.00
lon	β_3	0.80	0.24, 1.35	1.24	1.00
lon^2	eta_4	-1.03	-1.33, -0.74	-0.64	1.00
lat:lon	β_5	0.79	0.29, 1.32	0.09	0.12
dep	β_6	0.12	-0.04, 0.29	0.00	0.00
dep^2	β_7	-0.15	-0.19, -0.1	-0.14	1.00
rel	β_8	0.04	-0.33, 0.39	0.00	0.00
sub	β_9	0.61	0.50, 0.73	0.60	1.00
<u>Trap</u>					
Ε	η_1	4.65	2.86, 6.47	4.83	1.00
E^2	η_2	-2.92	-4.28, -1.6	-3.05	1.00
temp	η_3	0.81	0.71, 0.91	0.72	1.00
$temp^2$	η_4	0.11	0.09, 0.13	0.10	1.00
turb	η_5	0.04	-0.21, 0.28	0.00	0.00
dir1	η_6	0.63	0.32, 0.97	0.10	0.23
dir2	η_7	0.35	0.06, 0.64	0.00	0.00
Camera					
turb	$arphi_1$	0.78	0.49, 1.03	0.79	1.00
dir1	φ_2	1.06	0.72, 1.43	0.59	1.00
dir2	$arphi_3$	0.41	0.06, 0.76	0.00	0.00
temp	$arphi_4$	0.28	0.13, 0.42	0.02	0.11
$temp^2$	$arphi_5$	0.05	0.00, 0.11	0.00	0.00

831 Figures

832





Fig. 1. Study area (a), sample video frame (b) and a Chevron fish trap outfitted with an
outward-looking Canon high-definition video camera over the mouth of the trap (c). The
points on panel (a) represent sample locations.



Fig. 2. The bias of simulated covariate effect parameters (a) and fishery index (b) posterior
distributions. Posterior samples were derived by fitting the data-generating model to 200
simulated 20-year data sets.



Fig. 3. The predicted response of sub-population abundance to spatial covariates. The grey
region represents 95% Bayesian credible intervals.





environmental covariates. The grey region represents 95% Bayesian credible intervals.



Fig. 5. The predicted response of video camera sampling efficiency to environmental

857 covariates. The grey region represents 95% Bayesian credible intervals.





861 Fig. 6. The predicted annual relative abundance of the vermilion snapper meta-population using our State-Space Model (a) and the methods of Conn et al. (2010) (c). The grey region 862 represents 95% Bayesian credible intervals. The dashed line represents the estimated linear 863 864 trend. Panels (b) and (d) represent the probability distributions of the bootstrapped linear trend for each index. 865



Year of sampling program

Fig. 7. Impact of changing sampling frame on the predicted relative abundance at the metapopulation level. Panel (a), (b), and (c) represent the mean and range in latitude, longitude, and depth across samples collected each year. Panel (d) is the model predicted increases to the fishery index expected when the spatial changes on panel (a), (b), and (c) are not accounted for. The grey region on panel (d) represents 95% Bayesian credible intervals of the predictions and the dashed line is the log-linear trend of the predictions.