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ACCOUNTING FOR SPATIO-TEMPORAL SAMPLING VARIATION IN JOINT SPECIES DISTRIBUTION MODELS

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Abstract

1: Estimating relative abundance is critical for informing conservation and management efforts and for making inferences about the effects of environmental change on populations. Freshwater fisheries span large geographic regions, occupy diverse habitats, and consist of varying species assemblages. Monitoring schemes used to sample these diverse populations often result in populations being sampled at different times and under different environmental conditions. Varying sampling conditions can bias estimates of abundance when compared across time, location, and species, and properly accounting for these biases is critical for making inferences.

2: We develop a joint species distribution model (JSDM) that accounts for varying sampling conditions due to the environment and time of sampling when estimating relative abundance. The novelty of our JSDM is that we explicitly model sampling effort as the product of known quantities based on time and gear type and an unknown functional relationship to capture seasonal variation in species life history.

3: We use the model to study relative abundance of six freshwater fish species across the state of Minnesota, USA. Our model enables estimates of relative abundance to be compared both within and across species and lakes, and captures the inconsistent sampling present in the data. We discuss how gear type, water temperature, and day of the year impact catchability for each species at the lake level and throughout a year. We compare our estimates of relative abundance to those obtained from a model that assumes constant catchability to highlight important differences within and across lakes and species.

4: *Synthesis and applications.* Our method illustrates that assumptions relating indices of abundance to observed catch data can greatly impact model inferences derived from JSDMs. Specifically, not accounting for varying sampling conditions can bias inference of relative abundance, restricting our ability to detect responses to management interventions and environmental change. While our focus is on freshwater fisheries, this model architecture can be adopted to other systems where catchability may vary as a function of space, time, and species.

Keywords: Bayesian hierarchical model; catch per unit effort; catchability; ecological monitoring; freshwater fish; relative abundance

1 Introduction

Fisheries play an essential role in maintaining ecosystem function and are critical for global food supplies (Tacon & Metian 2013). Monitoring the abundance or relative abundance of fishes is critical for establishing sustainable harvest rates, estimating the effectiveness of management actions, and quantifying the effects of environmental change on fish populations (Hilborn & Walters 1992; Han *et al.* 2021). Monitoring the abundance of inland fisheries is particularly important because they support local economies, provide recreational opportunities, and play a significant role in global food security (Funge-Smith 2018; Radinger *et al.* 2019). Freshwater ecosystems also support high levels of biodiversity (Dudgeon *et al.* 2006) and are disproportionately threatened, compared to terrestrial systems, by anthropogenic activities (Carpenter *et al.* 2011; Reid *et al.* 2019).

Quantifying the abundance of inland freshwater fisheries presents unique challenges. In addition to managing multiple species (Dolder *et al.* 2018; Wagner *et al.* 2020), inland fisheries consist of a large number of managed populations, diverse habitats and species assemblages, and span large geographic regions. Inland freshwater fisheries are frequently managed at the individual lake level, but limited resources for monitoring and evaluation mean that monitoring data for individual lakes are often sparse across space and time. Due to sparse monitoring data and high levels of both process and measurement error, it is often impossible to detect responses of individual systems to management interventions or environmental change within a reasonable time frame (Wagner *et al.* 2013). Such limitations of individual lake management have been previously identified, along with others, resulting in the design and implementation of landscape-level management across a large population of lakes (Lester *et al.* 2003). A key component to such landscape-scale lake fisheries management is the implementation of standardized monitoring in an effort to meet fisheries management and ecological goals (Lester *et al.* 2021).

Ideally, estimates of abundance would be used to inform management decisions. While models such as N-mixture models (Royle 2004) can be used to estimate abundance for different taxa, they require spatially replicated count data from multiple sampling occasions over a relatively short time period for a given location (e.g., removal sampling). Whereas N-mixture

30 models have been used in fisheries contexts (Vine *et al.* 2019; Andres *et al.* 2020), these data
31 do not generally exist when monitoring abundance of multiple species across hundreds to thou-
32 sands of locations. In this context of data sparsity, evaluating the outcomes of management
33 actions or the effects of environmental events on an individual lake is not possible, and only by
34 pooling data from multiple lakes are we able to detect changes in fish populations (Lester *et al.*
35 2003; 2004; 2021).

36 Due to these challenges and data limitations, an index of abundance (e.g., catch per unit
37 effort) is often used for evaluating the status and trends of fish populations. For each survey, ef-
38 fort can be defined as the amount of resources devoted to fishing – a fixed and known quantity.
39 Depending on the gears employed, effort can be measured using various metrics; however, sam-
40 pling time (hrs, minutes) and gear are most common in inland lake fisheries. For active gears
41 (e.g., boat electrofishing), effort would be the amount of time spent electrofishing, whereas for
42 passive gears (e.g. gill nets and trap nets) effort is measured by the number of net nights (i.e.,
43 the number of nets set out over a 24 hour period). Although effort for passive gears is less
44 straightforward, it has been shown that using net nights as the measure of effort is appropriate
45 so long as there is a low variation in soak time (Breen & Ruetz 2006).

46 Dividing total catch by effort creates a relative measure of abundance to compare across
47 time, space, and/or species. Customarily, inland fisheries' relative abundance data are modeled
48 using univariate generalized linear mixed models that either directly model catch per unit effort
49 or model catch and use effort as an offset term in the linear model (Kuparinen *et al.* 2010;
50 Roop *et al.* 2018). More recently, multivariate models have been used in modeling ecological
51 communities (Clark *et al.* 2014). For example, joint species distribution models (JSDM) are
52 able to accommodate a large number of species and account for dependencies across species,
53 space, and time (see Ovaskainen & Abrego 2020, and references therein). These dependencies
54 enable the borrowing of information across data that may be scarce in time or space in order to
55 infer population characteristics. However, JSDMs have rarely been applied to inland fisheries
56 and those that have are limited to investigating patterns and drivers of species occurrence, not
57 abundance (Inoue *et al.* 2017; Wagner *et al.* 2020; Perrin *et al.* 2022).

58 Using indices of abundance to detect changes across time, space, and species requires that

59 we define the relationship between what is caught during routine sampling and true abundance.
60 Let i denote a population of interest. Relative abundance, γ_i , is defined as the ratio of total
61 catch, Y_i , divided by effort, E_i , and equated to the true abundance, N_i , by

$$62 \quad \gamma_i = \frac{Y_i}{E_i} = qN_i. \quad (1)$$

63 Here, q denotes *catchability* – the proportion of the population that is captured per one unit
64 effort (Arreguín-Sánchez 1996). Defining the relationship between γ_i and N_i in this way sug-
65 gests observed differences in γ_i is proportional to differences in true abundance. Catchability is
66 often assumed constant in time and space, which is most likely violated for surveys spanning
67 multiple locations and time points (Tsuboi & Endou 2008; Korman & Yard 2017). In addition,
68 variation in catchability is not accounted for when modeling single species using data from
69 a single gear. Failing to account for differences in catchability can lead to erroneous model
70 inference regarding the changes of a population over time and/or space.

71 Mitigating variation in catchability requires consistent sampling – i.e., sampling each pop-
72 ulation under the same environmental context, such as at the same time of year, using the same
73 gear, and under the same environmental conditions. Unfortunately, even under well-established
74 and long-term sampling programs, consistent sampling is rarely possible due to the large num-
75 ber of populations, limited resources for data collection, heterogeneity of ecosystems, and the
76 rapid pace of environmental change. Accounting for possible differences in catchability is one
77 of the most significant challenges to modeling relative abundance (Wilberg *et al.* 2009; Korman
78 & Yard 2017).

79 Variation in catchability has received significant attention in the marine fisheries literature
80 (Rose & Kulka 1999; Wilberg *et al.* 2009; Zhang *et al.* 2020), yet statistical methods or models
81 that account for differences in catchability for inland freshwater systems are limited (Czeglédi
82 *et al.* 2021). Instead of accounting for catchability during statistical model development, *ad*
83 *hoc* decisions are often made about how to aggregate data across space, time, or gear types, or
84 how to subset data prior to modeling in order to minimize their potential influence on statistical
85 inference (Radomski *et al.* 2020; Rypel 2021; Enders *et al.* 2021; McReynolds *et al.* 2021).
86 These studies commonly rely on datasets compiled from many sources and are composed of

87 observations collected using different sampling methodologies. Fitting models to aggregate or
88 subset data can result in a loss of information (Tehrani *et al.* 2021), and lead to biased parame-
89 ter estimation and underestimates of uncertainty (Calabrese *et al.* 2014). Multi-species studies
90 that span larger spatial extents and multiple systems are particularly impacted by these *ad hoc*
91 approaches given the aforementioned factors affecting catchability. Studies that do account for
92 varying catchability focus on single species with a single gear (Tsuboi & Endou 2008), multi-
93 ple species within one lake (Hosack *et al.* 2014), independent analyses of catch data for each
94 gear (McReynolds *et al.* 2021), or use statistical methods to combine catch rates for differ-
95 ent species collected using multiple gears (Wehrly *et al.* 2012; Rodríguez *et al.* 2021). These
96 approaches fail to properly address the inherent differences in gear selectivity among multi-
97 ple species (Smith *et al.* 2017) or temporal dynamics characteristic of year-to-year variability
98 (Gordoa & Hightower 1991; Gordoa *et al.* 2000; Korman & Yard 2017).

99 The contribution of this work is to develop a JSDM that enables comparison of relative
100 abundance of species sampled under different conditions by explicitly accounting for unequal
101 sampling effectiveness (henceforth, sampling variability). To account for this variation when
102 using γ_i as a proxy for N_i , we replace (1) with

$$103 \quad \gamma_i = \frac{Y_i}{E_i \theta_i} \propto N_i \quad (2)$$

104 where E_i is the fixed and known quantity of the sampling effort (e.g., time or number of gears)
105 and θ_i accounts for variation in catchability due to inconsistent sampling (e.g., variation in en-
106 vironmental conditions, day of the year) that is inherent in ecological monitoring programs. As
107 such, the catchability, θ_i , is indexed in time, space, species, and gear, allowing variation in the
108 utility of one unit of effort. When $\theta_i = 1$, (2) is equivalent to (1). We model θ_i as a function
109 of seasonal and climate variables that are assumed related to fish life history events. For ex-
110 ample, three common families of freshwater fishes include Centrarchidae (sunfishes and black
111 bass), Percidae (walleye and perches), and Esocidae (the pike family) – which we focus on in
112 our study – undertake temperature-dependent seasonal movements for spawning (Hayden *et al.*
113 2014; Hokanson 1977b; Kobler *et al.* 2008). Given the relationship between γ_i and N_i in (2),
114 differences across populations reflect changes in true abundance in the presence of sampling

115 variability. This approach is relevant for monitoring programs in which species are sampled
116 under different environmental conditions over space and time regardless of their sampling de-
117 sign.

118 We apply our model to catch data of six sport fish species collected between the years 2000
119 and 2019 across 1003 lakes in Minnesota. The model enables species-level inference with re-
120 gard to environmental drivers of relative abundance across lakes and accounts for dependence
121 between species. Resultant estimates of relative abundance can be compared both within and
122 across species and lakes. To illustrate how a model accounting for sampling variability could
123 impact inference regarding relative abundance of each species, we also compare our model re-
124 sults to those that would be obtained had catchability been assumed constant over space, time,
125 species, and gear. Importantly, because “true” species abundance is unknown, we cannot for-
126 mally compare the two approaches using measures of model fit or prediction accuracy. Rather,
127 given a specific functional form relating γ_i and N_i , our work aims to identify possible impacts
128 of sampling on model inference that is used to inform management and conservation decisions.
129 We use a simulation study where the true species abundance is known to validate our model
130 and to illustrate how sampling variability could impact inference regarding relative abundance
131 of each species within and across lakes. In our application, we model seasonal patterns of
132 catchability that represent changes in behavior (e.g., movement between habitats) and environ-
133 mental conditions (e.g., water temperature) that vary within year. As such, a more ecologically
134 realistic assumption is that, at a minimum, θ_i varies seasonally.

135 **2 Materials and Methods**

136 **2.1 Catch Data of Sport Fish in Minnesota Freshwater Lakes**

137 Data were collected by the Minnesota Department of Natural Resources (MNDNR) between
138 2000 and 2019 using standard sized experimental gill nets and trap nets as part of their stan-
139 dard sampling program (MNDNR 2017). All data existed prior to the initiation of this study.
140 Fish data were collected by state of Minnesota employees in the course of their fish manage-
141 ment activities and thus were exempt from permit requirements. These gears are designed to

142 index the abundance of sport fishes in the littoral (nearshore) zone, although gill nets are de-
143 ployed in deeper waters. Gill nets and trap nets were selected since they are the main gears
144 used during MNDNR's standard surveys – a survey that uses passive gears and does not tar-
145 get specific species. To account for changes in survey types throughout the time series and to
146 maximize standardization across surveys, we restricted our analysis to a subset of survey types
147 that minimize among-survey variation in survey methodology (MNDNR 2017). Both gill nets
148 and trap nets were deployed at multiple index stations within a lake, where one unit fixed effort
149 consisted of one net (gill net or trap net) deployed for a 24-hour sampling period.

150 Sampling occurred during the ice-free season in Minnesota. Lakes that were considered
151 to be a high priority to fisheries managers were sampled every year, whereas lakes of lower
152 priority were sampled less frequently. The lower priority lakes were sampled on a two to ten
153 year rotation, resulting in lakes having a different number of observations. The data used in our
154 analysis consist of lakes sampled between June 1 and September 30 during the 20 year time
155 period. The median number of surveys per lake was 3, with a minimum and maximum of 1 and
156 19, respectively. For a given lake, monitoring was targeted to occur at approximately the same
157 day of year across surveys, but due to limited gear, personnel, and the large number of lakes,
158 this was not always possible. Fig. S.1 of the Supporting Information shows the median sample
159 day of the year for each lake as well as the range in sample days throughout the study period.
160 Importantly, there doesn't appear to be any spatial pattern in the timing of the sampling nor the
161 variation in the timing of the sampling across years.

162 We considered six ecologically and socioeconomically important species including black
163 crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus*
164 *salmoides*), northern pike (*Esox lucius*), walleye (*Sander vitreus*), and yellow perch (*Perca*
165 *flavescens*). For each species, catch was calculated as the sum of individuals captured in each
166 gear type, and effort was the sum of the number of nets deployed for each gear type from a
167 given survey. Summaries of the total catch and catch per unit effort are shown in Table S.1.

168 Environmental variables associated with fish abundance were included as covariates in
169 our model. Lake area and maximum depth were obtained from MNDNR public databases
170 (<https://gisdata.mn.gov/dataset/water-lake-basin-morphology>). Wa-

171 watershed land use was calculated based on the 2016 National Land Cover Database (Homer
 172 *et al.* 2020), quantified as the proportion of watershed area falling in wetland or urban land
 173 use categories and extracted using the *LAGOSNE* R package (Soranno *et al.* 2017; Stachelek
 174 *et al.* 2019). Water clarity was quantified using annual lake-specific median values of remotely
 175 sensed Secchi depth (Max Gilnes, Rensselaer Polytechnic Institute, Troy, NY, United States,
 176 05/2020, personal communication). Water temperature was included both to account for po-
 177 tential seasonal differences in catchability and to quantify differences in abundances related to
 178 average thermal conditions. In both cases, we used surface water temperatures simulated using
 179 the general lake model (Hipsey *et al.* 2019) for lakes throughout the upper Midwest (Read *et al.*
 180 2021). Specifically, we used a five-year rolling mean of annual degree days with a base of 5°C
 181 as a measure of lake specific temperatures experienced by the fish over their lifetime to capture
 182 annual temperature influence on relative abundance (Chezik *et al.* 2014; Honsey *et al.* 2019). To
 183 quantify the effect of within-year temperature differences on catchability, lake-specific cumu-
 184 lative degree days up to the day of the sample were calculated (base temp of 5°C). Summaries
 185 of the environmental data are shown in Table S.2.

186 2.2 Multi-Species Modeling of Relative Abundance

187 Whereas the goal is to estimate annual relative abundance of each species at each location,
 188 the frequency and timing of sampling events as well as gears used vary across year and lake.
 189 Let y_{ikjdt} denote the number of fish caught in lake $i \in \{1, \dots, I\}$ of species $k \in \{1, \dots, K\}$
 190 using gear type $j \in \{1, \dots, J\}$ during the sampling event on day $d \in \{1, \dots, 365(366)\}$ of year
 191 $t \in \{1, \dots, T\}$. We define the Bayesian hierarchical model for the count data, y_{ikjdt} , as

$$192 \quad y_{ikjdt} \sim \text{Poisson}(\tilde{E}_{ikjdt} \gamma_{ikt}) \quad (3)$$

193 where \tilde{E}_{ikjdt} is the sampling effort and γ_{ikt} is the relative abundance for each lake, species, and
 194 year. Customarily, effort is a fixed and known quantity that is defined by the number of nets
 195 and/or duration of the sampling event. In addition, it is often assumed that effort is equal for
 196 all species and that one unit effort is the same for all days of the year across all years and gear

197 types. Here, we relax these assumptions following (2) and allow effort to vary as a function of
 198 species, day, year, and gear in order to account for seasonal impacts of sampling variability on
 199 estimates of relative abundance.

200 Let E_{ijdt} denote the fixed and known quantity of effort that is defined by the sampling
 201 event at lake i using gear j on day d of year t (e.g., number of net days for the sampling
 202 event). To account for sampling variability across species and through time, we incorporate a
 203 multiplicative scaling, $\theta_{ikjdt} > 0$. Specifically, we model sampling effort as

$$204 \quad \tilde{E}_{ikjdt} = E_{ijdt} \theta_{ikjdt} \quad (4)$$

205 where θ_{ikjdt} captures the variation in catchability across lakes as a function of day, year, and
 206 gear type, as well as important characteristics of the lake. Note that if $\theta_{ikjdt} \equiv 1$, this model
 207 reduces to the customary model of catch per unit effort introduced in (1). Values of $\theta_{ikjdt} > 1$
 208 indicate that the conditions of the sampling event were above average for a given lake, species,
 209 and year, leading to disproportionately high catch relative to true abundance. Conversely, values
 210 of $\theta_{ikjdt} < 1$ indicate the conditions were below average and catch was less than expected
 211 relative to true abundance. These multiplicative catchabilities adjust effort in order to mitigate
 212 the impacts of sampling variability on estimates of relative abundance. Importantly, within
 213 the Bayesian framework, the uncertainty in the model for catchability propagates through to
 214 uncertainty in our estimates of relative abundance.

215 **2.2.1 Modeling Catchability**

216 We model θ_{ikjdt} using a log-linear function capturing lake and time variables that may impact
 217 catchability. Specifically, we define the log-linear function

$$218 \quad \log(\theta_{ikjdt}) = \mathbf{z}'_{idt} \boldsymbol{\psi}_{kj}, \quad (5)$$

219 where \mathbf{z}_{idt} is a length r vector of variables describing the sampling conditions of lake i for
 220 sample day d in year t and $\boldsymbol{\psi}_{kj}$ is a vector of coefficients for each species and gear.

221 The freshwater fish surveys considered in this analysis were conducted between June 1 and

222 September 30, which we term the “fishing season” for Minnesota. Many important fish life
 223 history events that affect foraging, growth, survival, and reproduction throughout the fishing
 224 season follows a seasonal cycle (Hokanson 1977a). Water temperature is known to be one
 225 such driver of fish life history (Beitinger *et al.* 2000). Therefore, water surface temperature,
 226 W_{idt} , on the day of the sample is included as a covariate in z_{idt} the model for catchability. To
 227 capture additional seasonal variation in catchability during the fishing season within a lake, we
 228 constructed two covariates based on the fishing season cycle. For day of the year d , we define

$$229 \quad a_d = \sin\left(\frac{4\pi \times d}{121}\right) \quad \text{and} \quad b_d = \cos\left(\frac{4\pi \times d}{121}\right),$$

230 where 121 corresponds to the number of days between June 1st and September 30th. These two
 231 terms, a_d and b_d , capture any periodic behavior in catchability where the period is set to half
 232 the length of the fishing season. We also include the interaction between W_{idt} and both a_d and
 233 b_d , recognizing that water temperature cycles may vary across the spatial domain. The length
 234 $r = 6$ vector of variables included in the model are

$$235 \quad z_{idt} = [1, W_{idt}, a_d, b_d, W_{idt}a_d, W_{idt}b_d]'. \quad (6)$$

236 Model inference of the coefficient parameters, ψ_{kj} , enables direct comparison of the utility of
 237 one unit effort across species and gear as a function of day of the year and water temperature.
 238 Whereas other variables could be considered, these, at a minimum, are assumed to capture the
 239 variation in fish life history for these species. See Section 4 for further discussion.

240 **2.2.2 Modeling Relative Abundance**

241 The parameter γ_{ikt} is of primary focus of this analysis as it defines the relative abundance of
 242 species k in lake i and year t and is used as a proxy for true abundance. We model species
 243 relative abundance as

$$244 \quad \log(\gamma_{ikt}) = v_i' \beta_k + x_{it}' \alpha_k + \omega_{ik} \quad (7)$$

245 where \mathbf{v}_i is a length p vector of static lake variables, including intercept, \mathbf{x}_{it} is a length q vector
 246 of lake and year specific variables, and β_k and α_k are vectors of species-specific coefficients.
 247 Lastly, ω_{ik} is a lake- and species-specific random effect to capture any remaining variation not
 248 explained by the covariates.

249 The static lake variables in vector \mathbf{v}_i include lake area, lake depth, and land use character-
 250 istics in the lake watershed. The variables in vector \mathbf{x}_{it} include Secchi disk depth (an index of
 251 water clarity) and cumulative growing degree days (GDD), which are assumed to vary across
 252 years and influence species abundance. The cumulative GDD for each lake and year captures
 253 the annual variation in temperature throughout the period of study. Variables were transformed
 254 to be approximately normal and on the same scale. Specifically, lake area, lake depth, and GDD
 255 were log transformed and centered and the land use characteristics were logit transformed. Let-
 256 ting $\omega_i = [\omega_{i1}, \dots, \omega_{iK}]'$, we model the random effect as

$$257 \quad \omega_i \stackrel{iid}{\sim} MVN(\mathbf{0}, \Sigma), \quad (8)$$

258 where Σ is a $K \times K$ covariance matrix to allow for possible dependence between species.

259 **2.2.3 Model Comparison**

260 To explore the assumptions relating what is caught during routine sampling and true abundance,
 261 we also consider a base model with catchability assumed constant (i.e., (1)). This model is
 262 analogous to that outlined above except θ_{ijkdt} is fixed to 1 for all i, j, k, d, t . We investigate
 263 the differences in estimates of relative abundance obtained from the models with and without
 264 varying catchability by comparing estimates across lakes for a given species as well as across
 265 species for a given lake.

266 For the across-lake comparison, we first rank each lake from 1 to I (number of lakes) based
 267 on their estimates of relative abundance for each species. For example, the lake with the largest
 268 estimate of relative abundance for a given species is assigned the value 1, the lake with the
 269 second largest estimate is assigned 2, and so on. We do this ranking using the estimates of
 270 relative abundance obtained from each model and make comparisons based on the difference
 271 in rankings between the two models. For the within lake comparison, we compare our estimates

272 of relative abundance across species for a given lake in order to investigate possible impacts
273 of sampling variability on estimates of community structure or species composition. For each
274 lake, we first scale our estimates of relative abundance across the six species such that they sum
275 to one. Using these scaled estimates, we compute the difference in community percentage of
276 each species between the two models.

277 **2.2.4 Bayesian Model Specification and Inference**

278 The JSDM for multi-species catch data with and without varying catchability are fitted in a
279 Bayesian framework. Model inference is obtained using Hamiltonian Monte Carlo within
280 the Stan computing software (Carpenter *et al.* 2017). To complete the model specification,
281 we assign diffuse prior distributions to the model parameters. For each of the model coeffi-
282 cient parameters in ψ_k , α_k , β_k , for $k = 1, \dots, K$, we assign independent $N(0, 1)$ priors, ex-
283 cept for the intercept terms, which we assign independent $N(0, 10^2)$ priors. Given the scale
284 of each covariate and the models for abundance and effort being specified on the log scale,
285 these priors are relatively diffuse. To model the covariance matrix Σ , we first decompose it as
286 $\Sigma = \text{diag}(\tau_1, \dots, \tau_K) \Omega \text{diag}(\tau_1, \dots, \tau_K)$ where each τ_k is a standard deviation and Ω is a $K \times K$
287 correlation matrix (Barnard *et al.* 2000). Then, we specify priors on the standard deviation
288 and correlation matrix. We specify independent $\tau_k \sim \text{Half-Cauchy}(0, 2.5)$ for all $k = 1, \dots, K$
289 and $\Omega \sim \text{LKJ}(1)$ (see Lewandowski *et al.* 2009, for detail on the LKJ prior). Lastly, to ensure
290 model parameters are identifiable, the random effects, ω_{ik} , are forced to be mean zero and the
291 catchability, θ_{ijkl} , are forced to have a mean of 1 (i.e., both are “hard” constraints).

292 **2.2.5 Simulation Study**

293 To understand the impact on inference of relative abundance from our proposed model with
294 varying catchability compared to the naive model with constant catchability, we conducted two
295 simulation studies. For the first study, we simulated data according to our model with varying
296 catchability and fit both our model and the naive model to the data. For the second study, we
297 simulated data according to the naive model with constant catchability and fit both our model
298 and the naive model to the data. For both simulated datasets, we withhold one year of the

299 simulated data for model validation (see Supplementary material for complete data generating
300 details).

301 For both data sets, we obtained 6000 samples from the joint posterior distribution, discard-
302 ing the first 4500 as burn-in, from both our model and the naive model. We then compared
303 posterior estimates of relative abundance between our model and the naive model for each
304 data simulation on the withheld year of data. Under the assumption the data exhibit varying
305 catchability, we found our model better captures the relative abundance for the validation year
306 (Figures S.6 and S.7). In addition, under the assumption the data exhibit constant catchability,
307 we found our model and the naive model have similar performance for the validation year (Fig-
308 ures S.12 and S.13. Therefore, our model is appropriate under either the assumption the data
309 do or do not exhibit varying catchability, while the naive model is appropriate only under the
310 assumption the data have constant catchability. Specific details to the data generating mecha-
311 nisms for the simulation studies and the compassion's based on inference of relative abundance
312 are shown the Supplemental material.

313 **3 Results**

314 We applied the model to the catch data of sport fish in Minnesota freshwater lakes discussed
315 in section. We obtained 2000 samples from the joint posterior distribution, discarding the first
316 1000 as burn-in. Convergence was assessed both graphically and using the Geweke diagnostic
317 for all parameters and no issues were detected.

318 **3.1 Posterior Estimation of Catchability**

319 Posterior inference for catchability is shown graphically to identify important variation across
320 species, time, lakes, and gear types. Formal inference, including posterior mean estimates and
321 95% credible intervals of the parameters, ψ , are shown in Table S.3. Recall from Section
322 2.2.1 that values of θ_{ikjdt} greater (less than) 1 indicate more (less) favorable conditions for the
323 sampling event, meaning more (less) fish are expected to be observed per unit effort than is
324 representative of the true population. The posterior mean estimates of catchability for each

325 species and gear on each day throughout the fishing season in 2016 are shown in Fig. 1. Sim-
 326 ilar patterns were detected for the other years in the study period (results not shown). These
 327 estimates elucidate variation in sampling effectiveness both within and across species and gear
 328 as a function of water temperature and day within the fishing season.

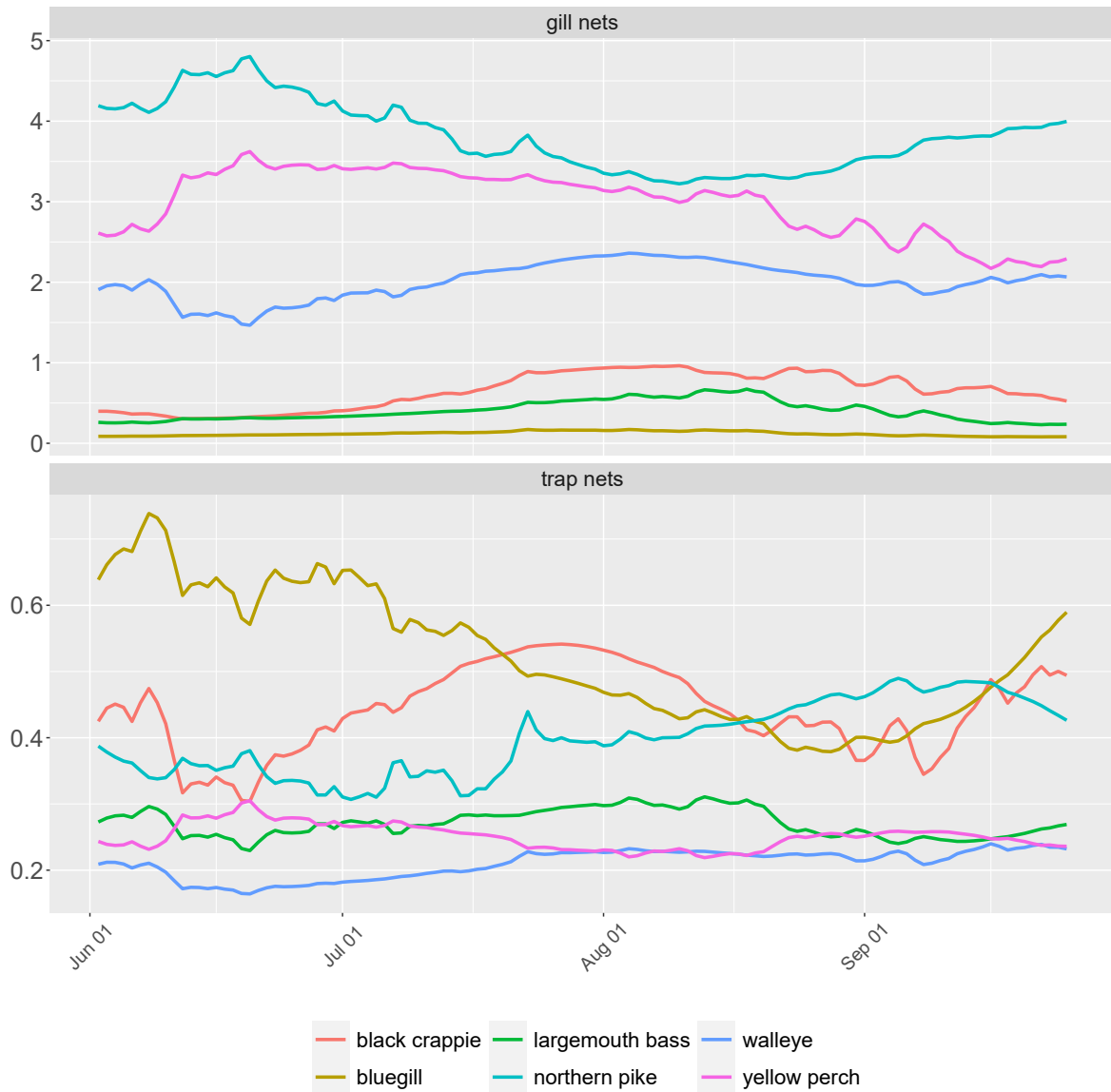


Figure 1: Posterior mean estimate of catchability (θ) for 2016 for each species and gear, averaged across all lakes. Each line corresponds to the catchability for a given species during the fishing season, ranging from June 2 to September 25.

329 In general, gill nets (Fig. 1 top) are more favorable for sampling northern pike, yellow
 330 perch, and walleye compared to nearshore species, like bluegill and black crappie, which are
 331 more favored by trap nets (Fig. 1 bottom). Seasonal variation in sampling effectiveness for

332 black crappie is similar for gill nets and trap nets, where the mid-summer (July 15 - August
333 15) yields proportionally higher catches than early or late summer. No seasonal differences in
334 the sampling effectiveness of bluegill are detected using gill nets, but trap nets show favorable
335 sampling during the early part (June - July) of the fishing season. Gill nets are more effec-
336 tive for sampling largemouth bass during mid to late summer (August - September), while trap
337 nets have no seasonable patterns in effectiveness for this species. Using gill nets, the sampling
338 conditions for northern pike, walleye, and yellow perch experience seasonal patterns, where
339 sampling is more favorable for northern pike and yellow perch in early summer than late sum-
340 mer, and walleye are most favorable in the middle to late summer (August-September). Trap
341 nets are more favorable for northern pike in the late summer than early summer, but no seasonal
342 patterns are exhibited for walleye or yellow perch.

343 To further explore the impacts of sampling variability across gear type and day of the year
344 of sampling, we computed the posterior mean estimate of the expected number of fish that
345 would be caught in each lake on each day given one unit of effort for each gear (i.e., $E_{ijdt} \equiv 1$).
346 Figs 2 and 3 show the difference between expected catch per one unit effort for each species
347 on June 15, 2016 and August 15, 2016 across all lakes. For each lake, species, and gear, these
348 differences are scaled by the average expected number of fish caught per day given one unit
349 effort throughout the entire fishing season of 2016. Values of zero represent no difference
350 in expected catch for the two dates. Positive values indicate a greater expected catch per unit
351 effort in August relative to June, whereas negative values indicate greater expected catch in June
352 relative to August. From Fig. 2, we expect to catch more black crappie, bluegill, largemouth
353 bass, and walleye and catch fewer northern pike and yellow perch with one unit effort using
354 gill nets on August 15 compared to June 15. As a result of the water temperature differences
355 among lakes across the state, a slight north-south spatial gradient also exists in these seasonal
356 difference estimates of expected catch per one unit effort. Similarly, Fig. 3 suggests fewer
357 bluegill and yellow perch to be caught per one unit effort using trap nets on August 15 compared
358 to June 15, whereas we expect more black crappie, largemouth bass, northern pike, and walleye
359 to be caught on August 15 than June 15. Similar to gill nets, there is a north-south gradient in
360 the seasonal differences in expected catch using trap nets.

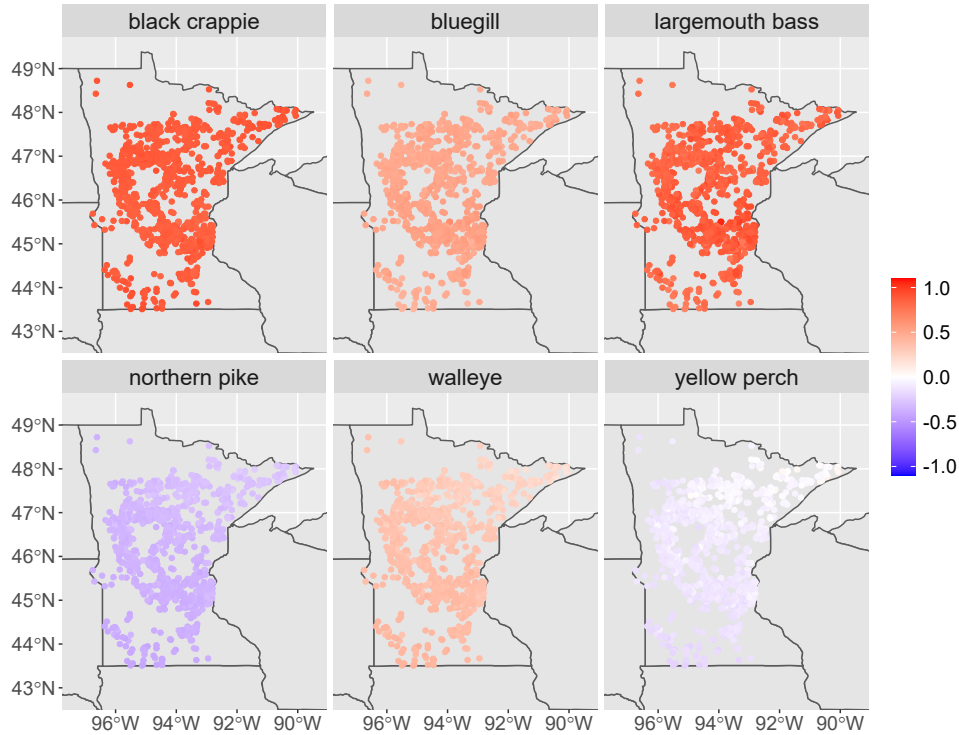


Figure 2: Posterior mean estimates of the difference in expected catch per unit effort between August 15, 2016 and June 15, 2016 using gill nets. Differences are scaled by the average expected number of fish caught per day given one unit effort throughout the entire fishing season of 2016 such that values of ± 1 indicate the difference is equal to the average expected catch for that gear, species, and year by lake. Positive values indicate a greater expected catch per unit effort in August.

361 **3.2 Impacts of varying catchability on model inference**

362 Our modeling approach contributes to inference by modeling variation in catchability due to
 363 sampling variability. In general, our model for catchability attempts to decompose the variation
 364 in expected catch per unit effort that is due to differences in relative abundance from that which
 365 could be the result of more or less favorable sampling conditions for some species, gears, and
 366 lakes. While we recognize the results shown above are specific to our choice of model for θ , we
 367 compare our model inference to that from the model that assumes constant catchability to high-
 368 light possible impacts of sampling designs on (i) estimates of relative abundance across species
 369 and lakes, (ii) inference on environmental drivers of abundance, and (iii) future studies that
 370 investigate the impacts of changes in environmental conditions (e.g., climate) on abundance.

371 The posterior mean estimates and 95% credible intervals for the parameters in the relative

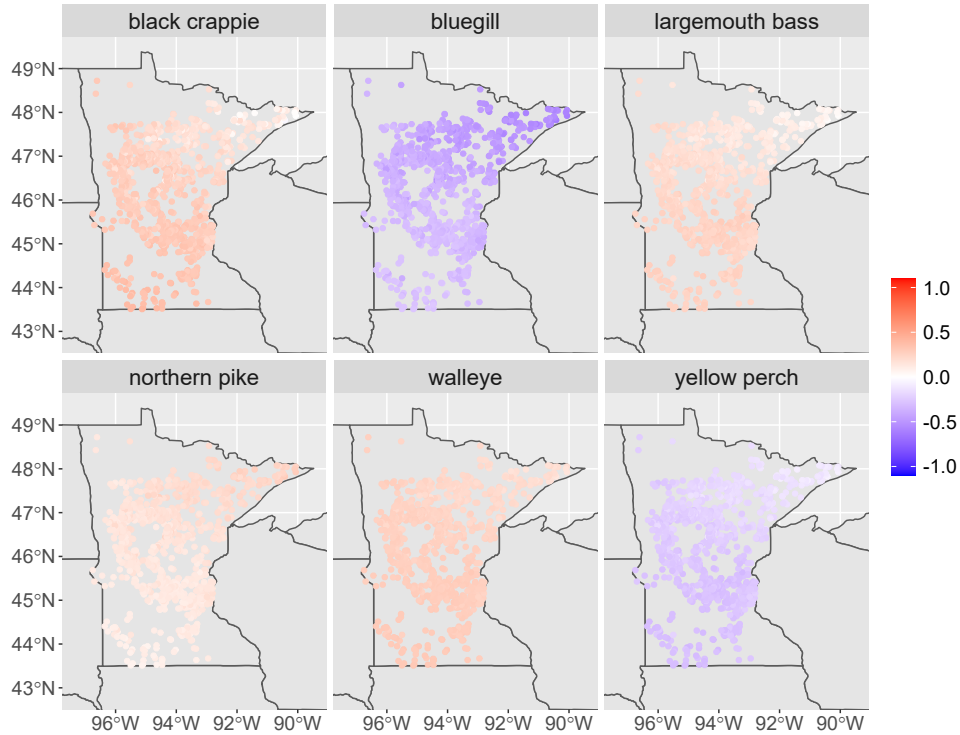


Figure 3: Posterior mean estimates of the difference in expected catch per unit effort between August 15, 2016 and June 15, 2016 using trap nets. Differences are scaled by the average expected number of fish caught per day given one unit effort throughout the entire fishing season of 2016 such that values of ± 1 indicate the difference is equal to the average expected catch for that gear, species, and year by lake. Positive values indicate a greater expected catch per unit effort in August.

372 abundance model, α and β , are shown by the blue points (mean) and bars (credible interval)
 373 in Fig. 4. The red points and bars show posterior estimates for the same parameters when
 374 catchability is assumed constant (i.e., $\theta_i = 1$ in (2)). Parameters are deemed significant if
 375 their credible interval does not contain zero. As expected, the relationship between the envi-
 376 ronmental covariates and relative abundance varied among species. For example, the relative
 377 abundance of walleye – a species that prefers cool-water (Magnuson *et al.* 1990) and thrives
 378 in larger lakes (Nate *et al.* 2000) – has a negative coefficient for growing degree days and
 379 positive coefficient for lake area, regardless of model specification. Contrary to expectations,
 380 bluegill were associated with cooler temperatures (negative growing degree days). Bluegill are
 381 a warmwater species (Magnuson *et al.* 1979), although the influence of water temperature in
 382 our data may be masked by the strong positive influence of urban landcover. Black crappie,
 383 largemouth bass, and yellow perch had a strong relationship with water clarity, where large-

384 mouth bass and yellow perch were more abundant in clear water and black crappie were less
385 abundant in clear water. There are no instances where the sign differs between the two models.
386 The effect of degree days on largemouth bass is positive with varying catchability and overlaps
387 zero when catchability is assumed constant – suggesting that modeling catchability allowed us
388 to capture the positive influence of water temperature on warmwater largemouth bass. As noted
389 previously, the negative effect of growing degree days on bluegill estimated by both models is
390 confusing but might be a result of the strong positive effect of percent urban (which is zero for
391 largemouth bass).

392 A few notable differences exist between parameter estimates from the two models. Some
393 coefficients were significantly different from 0 in our model but are no longer significant in the
394 model with constant catchability (e.g, lake area for largemouth bass), whereas other parame-
395 ters that were not significant in our model are significant in the model with constant catchability
396 (e.g., percent urban for yellow perch). Credible intervals for the two models that don't overlap
397 are deemed significantly different. For yellow perch, the magnitude of the coefficient estimates
398 of growing degree days and percent wetlands were much larger under our model than the model
399 with constant catchability. The coefficient estimates of lake area for northern pike were also
400 significantly different, where our model showed a negative relationship and the model with
401 constant catchability showed a positive relationship. While some of these differences in coef-
402 ficient estimates appear seemingly minor, they culminate in significant differences in estimates
403 of relative abundance for each species as well as subsequent inference regarding community
404 structure across the region. Additional inference from our model with varying catchability is
405 included in the supplementary material. The posterior mean estimate of the species covariance
406 matrix, Σ , is shown in Fig. S.2 and the posterior estimates of relative abundance, γ_{ikt} , by species
407 for all lakes for the year 2016 is shown in Fig. S.3.

408 Fig. 5 shows the difference in ranked relative abundance between the two models across
409 lakes for each species, where the difference is scaled by the number of lakes and can be in-
410 terpreted as a percentile. That is, a value of 30 or (-30) indicates that the lake is ranked 30%
411 higher (lower) in terms of relative abundance for the species using our model compared to the
412 model with constant catchability. Differences between the two models are less pronounced for

413 black crappie, bluegill, and largemouth bass compared to northern pike, walleye, and yellow
414 perch. Spatially, we again detect a north-south gradient due to water temperature differences
415 across the state. Our model produces lower rankings of relative abundance of northern pike,
416 walleye, and yellow perch in much of central and northern Minnesota and higher rankings in
417 southern Minnesota. Additionally, our model produces lower rankings of relative abundance
418 for bluegill in northern and southern Minnesota and higher rankings in central Minnesota.

419 Differences in estimated relative abundance of species within lakes between the two models
420 are shown in Fig. 6. Positive (negative) values indicate that our model produced larger (smaller)
421 estimates of relative abundance than the model with constant catchability for that species com-
422 pared to the other species within the lake. The most pronounced positive difference between the
423 two models is for bluegill, which are estimated to be much more abundant within lakes com-
424 pared to the other species when assuming sampling variability (with varying catchability). We
425 also estimate fish communities to contain a higher percentage of black crappie, particularly in
426 lakes throughout southern and northern Minnesota. Northern pike, walleye, and yellow perch
427 have the most pronounced negative differences, where all three are estimated to be less abun-
428 dant across the state compared to the other species when accounting for sampling variability.
429 That is, our approach estimates fish communities with higher percentages of bluegill and black
430 crappie and lower percentage of northern pike, walleye, and yellow perch.

431 **4 Discussion**

432 We developed a JSMD to study the relative abundance of freshwater fish species monitored
433 throughout the open water season. The model addressed the important challenge of sampling
434 variability across ecological contexts by allowing sampling effectiveness to vary among gears,
435 species, and season. Our results demonstrate that the gear type and time of sampling that
436 maximizes catchability varies among species. Seasonal variation in catchability was detected
437 across species and gear. Notably, important seasonable differences in catchability were detected
438 between higher and lower trophic levels. For example, northern pike catchability is highest for
439 gillnets set in June, while black crappie catchability is high using both gear types in mid-late

440 summer. These differences in catchability are likely a result of fish behavior and life history
441 as influenced by environmental cues throughout the season (e.g., Villegas-Ríos *et al.* 2014).
442 For example, our focal fish species are members of the Centrarchidae (black crappie, bluegill,
443 largemouth bass), Percidae (walleye, yellow perch), and Esocidae (northern pike) families.
444 Seasonal movements of these fishes, as with other fish species, is largely driven by thermal
445 cues (Johnson & Charlton 1960; Schneider *et al.* 2010; Starzynski & Lauer 2015). Temperature
446 plays a critical role in growth and performance of poikilotherms, affecting vital rates and the
447 timing and duration phenological events (Scranton & Amarasekare 2017). Therefore, because
448 of the seasonality in north-temperate ecosystems, it is likely that seasonal thermal cues play a
449 role in the patterns of catchability observed in our study.

450 When compared to the model with constant catchability, significant differences in species
451 community structure and relative abundance estimates were identified. Additionally, as exem-
452 plified by the simulation study, if the true catchability varies in time, relative abundance param-
453 eter estimates from a model where catchability is assumed constant will be biased. While the
454 methods developed here are aimed at monitoring programs of freshwater fish, these approaches
455 can be adapted for other systems, such as birds or plants, where catchability or detection prob-
456 abilities may vary as a function of time, space, or species. For example, the abundance of small
457 mammals is often indexed by catch per unit effort data (e.g., catches per trap night) and the
458 methods developed here could help account for changes in catchability that may arise from
459 environmental factors such as temperature and precipitation (Yarnell *et al.* 2007; Rowe *et al.*
460 2010).

461 We informed our choice of model for effort based on the dominant influence of water tem-
462 perature on fish behavior and population-level processes (Magnuson *et al.* 1979). Recognizing
463 that other choices of functional forms are possible, future work consists of using additional data
464 to inform our estimates of sampling variability across species, gear, and environment. Future
465 data collection programs could be tailored to address the knowledge gap relating catchability
466 of species across time of the year due to life history and gear types. Such an approach would
467 require repeated sampling of fish communities under a variety of conditions. A critical next
468 step will be incorporating time-varying components that influence catchability such as ice off

469 date, water clarity, dissolved oxygen, and thermal structure of lakes (Stoner 2004; Fischer &
470 Quist 2019). Time-varying components will help reduce uncertainty in relative abundance es-
471 timates and allow for a more accurate estimate of varying catchability. Properly addressing the
472 impact of catchability on monitoring species abundance across space and time would lead to a
473 better understanding of the environmental drivers of each species and more accurate estimates
474 of relative abundance that can be compared and combined across lakes to inform management
475 decisions.

476 Currently, lake-rich states such as Minnesota and Wisconsin use lake classification sys-
477 tems to enable comparison of catch rates of fish across similar lake types (Schupp 1992; Rypel
478 *et al.* 2019). Such classification systems implicitly account for environmental differences in
479 lakes that might affect catchability and/or actual abundance, but do not explicitly separate the
480 two. Additionally, lake classification systems do not account for seasonal variation in catch-
481 ability, which is critical for comparing catch rates from surveys conducted at various times
482 throughout the open water season. By explicitly including variables that influence both catch-
483 ability and true abundance, we provide a method that enables comparison of catch rates across
484 a broad range of lake types. A potential direction for future work is to build on the ability to
485 compare across lakes and extend the spatial domain to include surveys from multiple states.
486 However, care will have to be taken to account for methodological differences as there are not
487 universal standards for gear type or survey methods between states. Additionally, there is inter-
488 est in predicting relative abundance under future climate scenarios, with particular interest in
489 joint predictions across multiple states. While our framework has the ability to predict relative
490 abundance at lakes within the observed time domain, as shown by the simulation study in the
491 supplementary material, we do not have constraints that would allow it to produce reasonable
492 predictions at future times. Incorporating a mechanism, such as a temporal dynamic frame-
493 work, into the model to enable predictions under future climate scenarios could provide insight
494 into how fish populations might change.

495 Monitoring of species abundances serves several purposes in the conservation and man-
496 agement of natural resources (Radinger *et al.* 2019). Conservation and management decisions
497 are frequently based on estimates of species abundance or relative abundance, and how they

498 differ among locations or over time (Lyons *et al.* 2008). Actions designed to either increase
499 or decrease the abundance of a species are predicated on information about the relative abun-
500 dance of that species in a given location. For example, the location of protected areas in both
501 terrestrial and aquatic habitats may be based on where certain species are estimated to be most
502 abundant (e.g., Johnston *et al.* 2015; García-Barón *et al.* 2019). Implementation and evalua-
503 tion of management interventions rely on estimates of relative abundance changes over time,
504 and how they are impacted by disturbance or management actions. For example, the allowable
505 harvest of fish and wildlife species may be based on estimates of abundance that vary over
506 time (e.g., Nielson *et al.* 2014), and the impact of interventions, such as habitat improvement
507 relies on comparisons of species abundances over space and time (e.g., Scarcella *et al.* 2015).
508 Accounting for the effects of sampling variability on these abundance estimates could improve
509 the implementation and evaluation of such efforts.

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521 **Conflict of Interest**

522 The authors declare no conflicts of interest.

523 **Author' Contribution**

524 Authors Gretchen Hansen, Tyler Wagner, and Erin Schliep formulated the idea and contributed
525 to the theoretical development of the research. Gretchen Hansen and Holly Kundel collated
526 the data and conducted exploratory data analysis to motivate the modeling. Joshua North and
527 Erin Schliep led the development of the statistical model and North implemented the statistical
528 analysis. Joshua North, Erin Schliep, Gretchen Hansen, Holly Kundel, Christopher Custer,
529 Paul McLaughlin, and Tyler Wagner contributed to the writing of the manuscript.

530 **Data Availability**

531 The fish catch and effort data as well as the environmental data associated with this manuscript
532 are available on the Data Repository for University of Minnesota [https://doi.org/10.](https://doi.org/10.13020/p4rw-z926)
533 [13020/p4rw-z926](https://doi.org/10.13020/p4rw-z926) (Point of contact is GJAH; North *et al.* 2022). The code for Bayesian
534 model fitting and posterior inference are publicly available on GitLab at [https://doi.](https://doi.org/10.5066/P9DALGBL)
535 [org/10.5066/P9DALGBL](https://doi.org/10.5066/P9DALGBL) (North *et al.* 2023).

536 **References**

- 537 Andres, K.J., Sethi, S.A., Duskey, E., Lepak, J.M., Rice, A.N., Estabrook, B.J., Fitz-
538 patrick, K.B., George, E., Marcy-Quay, B., Pauflve, M.R., Perkins, K. & Scofield,
539 A.E. (2020) Seasonal habitat use indicates that depth may mediate the potential for
540 invasive round goby impacts in inland lakes. *Freshwater Biology*, **65**, 1337–1347.
541 <https://dx.doi.org/10.1111/fwb.13502>.
- 542 Arreguín-Sánchez, F. (1996) Catchability: A key parameter for fish stock assessment. *Reviews*
543 *in fish biology and fisheries*, **6**, 221–242.
- 544 Barnard, J., McCulloch, R. & Meng, X.L. (2000) Modeling covariance matrices in terms of
545 standard deviations and correlations, with application to shrinkage. *Statistica Sinica*, **10**,
546 1281–1311.
- 547 Beitinger, T.L., Bennett, W.A. & McCauley, R.W. (2000) Temperature tolerances of North
548 American freshwater fishes exposed to dynamic changes in temperature. *Environmental*
549 *Biology of Fishes*, **58**, 237–275. <https://dx.doi.org/10.1023/A:1007676325825>.
- 550 Breen, M.J. & Ruetz, C.R. (2006) Gear Bias in Fyke Netting: Evaluating Soak Time, Fish
551 Density, and Predators. *North American Journal of Fisheries Management*, **26**, 32–41.
552 <https://dx.doi.org/10.1577/M05-013.1>.

- 553 Calabrese, J.M., Certain, G., Kraan, C. & Dormann, C.F. (2014) Stacking species distribution
554 models and adjusting bias by linking them to macroecological models. *Global Ecology and*
555 *Biogeography*, **23**, 99–112. <https://dx.doi.org/10.1111/geb.12102>.
- 556 Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker,
557 M.A., Guo, J., Li, P. & Riddell, A. (2017) Stan: A probabilistic programming language.
558 *Journal of Statistical Software*, **76**. <https://dx.doi.org/10.18637/jss.v076.i01>.
- 559 Carpenter, S.R., Stanley, E.H. & Vander Zanden, M.J. (2011) State of the World's freshwater
560 ecosystems: Physical, chemical, and biological changes. *Annual Review of Environment and*
561 *Resources*, **36**, 75–99. <https://dx.doi.org/10.1146/annurev-environ-021810-094524>.
- 562 Chezik, K.A., Lester, N.P. & Venturelli, P.A. (2014) Fish growth and degree-days II: selecting a
563 base temperature for an among-population study. *Canadian Journal of Fisheries and Aquatic*
564 *Sciences*, **71**, 1303–1311. <https://dx.doi.org/10.1139/cjfas-2013-0615>.
- 565 Clark, J.S., Gelfand, A.E., Woodall, C.W. & Zhu, K. (2014) More than the sum of the parts:
566 Forest climate response from joint species distribution models. *Ecological Applications*, **24**,
567 990–999. <https://dx.doi.org/10.1890/13-1015.1>.
- 568 Czeglédi, I., Specziár, A. & Erős, T. (2021) Temporal dynamics of freshwater fish assemblages,
569 their background and methods of quantifications—A synthesis. *Fish and Fisheries*, **00**, 1–16.
570 <https://dx.doi.org/10.1111/faf.12601>.
- 571 Dolder, P.J., Thorson, J.T. & Minto, C. (2018) Spatial separation of catches in highly mixed
572 fisheries. *Scientific Reports*, **8**, 13886. <https://dx.doi.org/10.1038/s41598-018-31881-w>.
- 573 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C.,
574 Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006)
575 Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biologi-*
576 *cal Reviews*, **81**, 163. <https://dx.doi.org/10.1017/S1464793105006950>.
- 577 Enders, E.C., Charles, C., van der Lee, A.S. & Lumb, C.E. (2021) Temporal variations in
578 the pelagic fish community of Lake Winnipeg from 2002 to 2019. *Journal of Great Lakes*
579 *Research*, **47**, 626–634. <https://dx.doi.org/10.1016/j.jglr.2021.01.004>.
- 580 Fischer, J.R. & Quist, M.C. (2019) Understanding Fish Assemblage Structure in Lentic Ecosys-
581 tems: Relative Effects of Abiotic Factors and Management Legacies. *North American Jour-*
582 *nal of Fisheries Management*, **39**, 607–624. <https://dx.doi.org/10.1002/nafm.10304>.
- 583 Funge-Smith, S. (2018) Review of the state of the world fishery resources: Inland fisheries.
584 *FAO Fisheries and Aquaculture Circular*, p. 397.
- 585 García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Murcia, J.L.
586 & Louzao, M. (2019) Modelling the spatial abundance of a migratory predator: A call
587 for transboundary marine protected areas. *Diversity and Distributions*, **25**, 346–360.
588 <https://dx.doi.org/10.1111/ddi.12877>.
- 589 Gordo, A. & Hightower, J.E. (1991) Changes in catchability in a bottom-trawl fishery for
590 Cape Hake (*Merluccius capensis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **48**,
591 1887–1895. <https://dx.doi.org/10.1139/f91-224>.

- 592 Gordoa, A., Masó, M. & Voges, L. (2000) Monthly variability in the catchability of Namibian
593 hake and its relationship with environmental seasonality. *Fisheries Research*, **48**, 185–195.
594 [https://dx.doi.org/10.1016/S0165-7836\(00\)00160-0](https://dx.doi.org/10.1016/S0165-7836(00)00160-0).
- 595 Han, Q., Grüss, A., Shan, X., Jin, X. & Thorson, J.T. (2021) Understanding pat-
596 terns of distribution shifts and range expansion/contraction for small yellow croaker
597 (*Larimichthys polyactis*) in the Yellow Sea. *Fisheries Oceanography*, **30**, 69–84.
598 <https://dx.doi.org/10.1111/fog.12503>.
- 599 Hayden, T.A., Holbrook, C.M., Fielder, D.G., Vandergoot, C.S., Bergstedt, R.A., Dettmers,
600 J.M., Krueger, C.C. & Cooke, S.J. (2014) Acoustic telemetry reveals large-scale migration
601 patterns of walleye in lake huron. *PLoS One*, **9**, e114833.
- 602 Hilborn, R. & Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment*. Springer US,
603 Boston, MA.
- 604 Hipsey, M.R., Bruce, L.C., Boon, C., Busch, B., Carey, C.C., Hamilton, D.P., Hanson, P.C.,
605 Read, J.S., de Sousa, E., Weber, M. & Winslow, L.A. (2019) A General Lake Model
606 (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecolog-
607 ical Observatory Network (GLEON). *Geoscientific Model Development*, **12**, 473–523.
608 <https://dx.doi.org/10.5194/gmd-12-473-2019>.
- 609 Hokanson, K.E.F. (1977a) Temperature requirements of some Percids and adaptations to the
610 seasonal temperature cycle. *Journal of the Fisheries Research Board of Canada*, **34**, 1524–
611 1550. <https://dx.doi.org/10.1139/f77-217>.
- 612 Hokanson, K.E. (1977b) Temperature requirements of some percids and adaptations to the
613 seasonal temperature cycle. *Journal of the Fisheries Board of Canada*, **34**, 1524–1550.
- 614 Homer, C., Dewitz, J., Jin, S., Xian, G., Costello, C., Danielson, P., Gass, L., Funk,
615 M., Wickham, J., Stehman, S., Auch, R. & Riitters, K. (2020) Conterminous United
616 States land cover change patterns 2001–2016 from the 2016 National Land Cover
617 Database. *ISPRS Journal of Photogrammetry and Remote Sensing*, **162**, 184–199.
618 <https://dx.doi.org/10.1016/j.isprsjprs.2020.02.019>.
- 619 Honsey, A.E., Venturelli, P.A. & Lester, N.P. (2019) Bioenergetic and limnological founda-
620 tions for using degree-days derived from air temperatures to describe fish growth. *Canadian*
621 *Journal of Fisheries and Aquatic Sciences*, **76**, 657–669. [https://dx.doi.org/10.1139/cjfas-](https://dx.doi.org/10.1139/cjfas-2018-0051)
622 [2018-0051](https://dx.doi.org/10.1139/cjfas-2018-0051).
- 623 Hosack, G.R., Peters, G.W. & Ludsin, S.A. (2014) Interspecific relationships and environmen-
624 tally driven catchabilities estimated from fisheries data. *Canadian Journal of Fisheries and*
625 *Aquatic Sciences*, **71**, 447–463. [https://dx.doi.org/10.1139/cjfas-](https://dx.doi.org/10.1139/cjfas-2013-0236)
[2013-0236](https://dx.doi.org/10.1139/cjfas-2013-0236).
- 626 Inoue, K., Stoeckl, K. & Geist, J. (2017) Joint species models reveal the effects of environment
627 on community assemblage of freshwater mussels and fishes in European rivers. *Diversity*
628 *and Distributions*, **23**, 284–296. <https://dx.doi.org/10.1111/ddi.12520>.
- 629 Johnson, M. & Charlton, W. (1960) Some effects of temperature on the metabolism and activity
630 of the large-mouth bass, *micropterus salmoides* lacepede. *The Progressive Fish-Culturist*, **22**,
631 155–163.

- 632 Johnston, A., Fink, D., Reynolds, M.D., Hochachka, W.M., Sullivan, B.L., Bruns, N.E., Hall-
633 stein, E., Merrifield, M.S., Matsumoto, S. & Kelling, S. (2015) Abundance models improve
634 spatial and temporal prioritization of conservation resources. *Ecological Applications*, **25**,
635 1749–1756. <https://dx.doi.org/10.1890/14-1826.1>.
- 636 Kobler, A., Klefoth, T., Wolter, C., Fredrich, F. & Arlinghaus, R. (2008) Contrasting pike
637 (*esox lucius* l.) movement and habitat choice between summer and winter in a small lake.
638 *Hydrobiologia*, **601**, 17–27.
- 639 Korman, J. & Yard, M.D. (2017) Effects of environmental covariates and density on the catcha-
640 bility of fish populations and interpretation of catch per unit effort trends. *Fisheries Research*,
641 **189**, 18–34. <https://dx.doi.org/10.1016/j.fishres.2017.01.005>.
- 642 Kuparinen, A., Klefoth, T. & Arlinghaus, R. (2010) Abiotic and fishing-related corre-
643 lates of angling catch rates in pike (*Esox lucius*). *Fisheries Research*, **105**, 111–117.
644 <https://dx.doi.org/10.1016/j.fishres.2010.03.011>.
- 645 Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R. & Ryan, P.A. (2004) Light and
646 temperature: Key factors affecting walleye abundance and production. *Transactions of the*
647 *American Fisheries Society*, **133**, 588–605. <https://dx.doi.org/10.1577/T02-111.1>.
- 648 Lester, N.P., Marshall, T.R., Armstrong, K., Dunlop, W.I. & Ritchie, B. (2003) A Broad-Scale
649 Approach to Management of Ontario’s Recreational Fisheries. *North American Journal of*
650 *Fisheries Management*, **23**, 1312–1328. <https://dx.doi.org/10.1577/m01-230am>.
- 651 Lester, N.P., Sandstrom, S., Kerckhove, D.T., Armstrong, K., Ball, H., Amos, J., Dunkley, T.,
652 Rawson, M., Addison, P., Dextrase, A., Taillon, D., Wasylenko, B., Lennox, P., Giacomini,
653 H.C. & Chu, C. (2021) Standardized broad-scale management and monitoring of inland
654 lake recreational fisheries: An overview of the Ontario experience. *Fisheries*, **46**, 107–118.
655 <https://dx.doi.org/10.1002/fsh.10534>.
- 656 Lewandowski, D., Kurowicka, D. & Joe, H. (2009) Generating random correlation matrices
657 based on vines and extended onion method. *Journal of Multivariate Analysis*, **100**, 1989–
658 2001. <https://dx.doi.org/10.1016/j.jmva.2009.04.008>.
- 659 Lyons, J.E., Runge, M.C., Laskowski, H.P. & Kendall, W.L. (2008) Monitoring in the context
660 of structured decision-making and adaptive management. *Journal of Wildlife Management*,
661 **72**, 1683–1692. <https://dx.doi.org/10.2193/2008-141>.
- 662 Magnuson, J.J., Crowder, L.B. & Medvick, P.A. (1979) Temperature as an ecological resource.
663 *American Zoologist*, **19**, 331–343. <https://dx.doi.org/10.1093/icb/19.1.331>.
- 664 Magnuson, J.J., Meisner, J.D. & Hill, D.K. (1990) Potential changes in the ther-
665 mal habitat of Great Lakes fish after global climate warming. *Transactions of*
666 *the American Fisheries Society*, **119**, 254–264. [https://dx.doi.org/10.1577/1548-8659\(1990\)119;0254:PCITTH;2.3.CO;2](https://dx.doi.org/10.1577/1548-8659(1990)119;0254:PCITTH;2.3.CO;2).
- 668 McReynolds, A., Hoff, M., Sikora, A., Nau, C., Pietraszek, M., Bartelme, C., Christie, M.,
669 Hoffman, S., Hayer, C. & Forsythe, P. (2021) Adult and larval fish assemblages vary among
670 small tributary mouths of Green Bay, Lake Michigan. *Canadian Journal of Zoology*, **99**,
671 319–329. <https://dx.doi.org/10.1139/cjz-2020-0143>.

- 672 Minnesota Department of Natural Resources (MNDNR) (2017) Manual of instructions for lake
673 survey. *Minnesota Department of Natural Resources, Special Publication No 180, St Paul,*
674 *Minnesota (version 104, released January 2019).*
- 675 Nate, N.A., Bozek, M.A., Hansen, M.J. & Hewett, S.W. (2000) Variation in walleye abundance
676 with lake size and recruitment source. *North American Journal of Fisheries Management,*
677 **20**, 119–126. [https://dx.doi.org/10.1577/1548-8675\(2000\)020;0119:viwawl;2.0.co;2](https://dx.doi.org/10.1577/1548-8675(2000)020;0119:viwawl;2.0.co;2).
- 678 Nielson, R.M., Mcmanus, L., Rintz, T., McDonald, L.L., Murphy, R.K., Howe, W.H. & Good,
679 R.E. (2014) Monitoring abundance of golden eagles in the western United States. *The Jour-*
680 *nal of Wildlife Management,* **78**, 721–730. <https://dx.doi.org/10.1002/jwmg.704>.
- 681 North, J.S., Schliep, E.M., Hansen, G.J., Kundel, H., Custer, C.A., McLaughlin, P. & Wagner,
682 T. (2022) Data in support of accounting for spatio-temporal variation in catchability in
683 joint species distribution models. *Retrieved from the Data Repository for the University of*
684 *Minnesota.* <https://dx.doi.org/10.13020/p4rw-z926>.
- 685 North, J.S., Schliep, E.M., Hansen, G.J., Kundel, H., Custer, C.A., McLaughlin, P.
686 & Wagner, T. (2023) Software in support of accounting for spatio-temporal variation
687 in catchability in joint species distribution models. *US Geological Software release.*
688 <https://dx.doi.org/10.5066/P9DALGBL>.
- 689 Ovaskainen, O. & Abrego, N. (2020) *Joint species distribution modelling: with applications in*
690 *R.* Cambridge University Press.
- 691 Perrin, S.W., Veen, B., Golding, N. & Finstad, A.G. (2022) Modelling temperature-driven
692 changes in species associations across freshwater communities. *Global Change Biology,* **28**,
693 86–97. <https://dx.doi.org/10.1111/gcb.15888>.
- 694 Radinger, J., Britton, J.R., Carlson, S.M., Magurran, A.E., Alcaraz-Hernandez, J.D., Almod-
695 ovar, A., Benejam, L., Fernandez-Delgado, C., Nicola, G.G., Oliva-Paterna, F.J., Torralva,
696 M. & Garcia-Berthou, E. (2019) Effective monitoring of freshwater fish. *Fish and Fisheries,*
697 **20**, faf.12373. <https://dx.doi.org/10.1111/faf.12373>.
- 698 Radomski, P., Anderson, C.S., Bruesewitz, R.E., Carlson, A.J. & Borkholder, B.D. (2020)
699 An assessment model for a standard fill net incorporating direct and indirect selectiv-
700 ity applied to walleye. *North American Journal of Fisheries Management,* **40**, 105–124.
701 <https://dx.doi.org/10.1002/nafm.10384>.
- 702 Read, J., Appling, A., Oliver, S., Platt, L., Zwart, J., Vitense, K., Hansen, G., Corson-Dosch,
703 H. & Kundel, H. (2021) Data release: Process-based predictions of lake water temperature
704 in the Midwest US: U.S. Geological Survey data release.
- 705 Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd,
706 K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tock-
707 ner, K., Vermaire, J.C., Dudgeon, D. & Cooke, S.J. (2019) Emerging threats and persis-
708 tent conservation challenges for freshwater biodiversity. *Biological Reviews,* **94**, 849–873.
709 <https://dx.doi.org/10.1111/brv.12480>.
- 710 Rodríguez, M.A., Marselli, G. & Mandrak, N.E. (2021) Responses of vulnerable fishes to
711 environmental stressors in the Canadian Great Lakes basin. *Canadian Journal of Fisheries*
712 *and Aquatic Sciences,* **78**, 1278–1292. <https://dx.doi.org/10.1139/cjfas-2020-0314>.

- 713 Roop, H.J., Poudyal, N.C. & Jennings, C.A. (2018) Assessing angler effort, catch, and harvest
714 on a spatially complex, multi-lake fishery in middle Georgia. *North American Journal of*
715 *Fisheries Management*, **38**, 833–841. <https://dx.doi.org/10.1002/nafm.10179>.
- 716 Rose, G. & Kulka, D. (1999) Hyperaggregation of fish and fisheries: how catch-per-unit-effort
717 increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and*
718 *Aquatic Sciences*, **56**, 118–127. <https://dx.doi.org/10.1139/cjfas-56-S1-118>.
- 719 Rowe, R.J., Finarelli, J.A. & Rickart, E.A. (2010) Range dynamics of small mammals along an
720 elevational gradient over an 80-year interval. *Global Change Biology*, **16**, 2930–2943.
- 721 Royle, J.A. (2004) N-Mixture models for estimating population size from spatially replicated
722 counts. *Biometrics*, **60**, 108–115. <https://dx.doi.org/10.1111/j.0006-341X.2004.00142.x>.
- 723 Rypel, A.L. (2021) Spatial versus temporal heterogeneity in abundance of fishes
724 in north-temperate lakes. *Fundamental and Applied Limnology*, **195**, 173–185.
725 <https://dx.doi.org/10.1127/fal/2021/1405>.
- 726 Rypel, A.L., Simonson, T.D., Oele, D.L., Griffin, J.D.T., Parks, T.P., Seibel, D., Roberts,
727 C.M., Toshner, S., Tate, L.S. & Lyons, J. (2019) Flexible Classification of Wisconsin
728 Lakes for Improved Fisheries Conservation and Management. *Fisheries*, **44**, 225–238.
729 <https://dx.doi.org/10.1002/fsh.10228>.
- 730 Scarcella, G., Grati, F., Bolognini, L., Domenichetti, F., Malaspina, S., Manoukian, S., Polidori,
731 P., Spagnolo, A. & Fabi, G. (2015) Time-series analyses of fish abundance from an artificial
732 reef and a reference area in the central-Adriatic Sea. *Journal of Applied Ichthyology*, **31**,
733 74–85. <https://dx.doi.org/10.1111/jai.12952>.
- 734 Schneider, K.N., Newman, R.M., Card, V., Weisberg, S. & Pereira, D.L. (2010) Timing of
735 walleye spawning as an indicator of climate change. *Transactions of the American Fisheries*
736 *Society*, **139**, 1198–1210.
- 737 Schupp, D.H. (1992) An ecological classification of Minnesota lakes with associated fish com-
738 munities.
- 739 Scranton, K. & Amarasekare, P. (2017) Predicting phenological shifts in a changing climate.
740 *Proceedings of the National Academy of Sciences*, **114**, 13212–13217.
- 741 Smith, B.J., Blackwell, B.G., Wuellner, M.R., Graeb, B.D.S. & Willis, D.W.
742 (2017) Contact selectivity for four fish species sampled with North American stan-
743 dard gill nets. *North American Journal of Fisheries Management*, **37**, 149–161.
744 <https://dx.doi.org/10.1080/02755947.2016.1254129>.
- 745 Soranno, P.A., Bacon, L.C., Beauchene, M., Bednar, K.E., Bissell, E.G., Boudreau, C.K.,
746 Boyer, M.G., Bremigan, M.T., Carpenter, S.R., Carr, J.W., Cheruvelil, K.S., Christel, S.T.,
747 Claucherty, M., Collins, S.M., Conroy, J.D., Downing, J.A., Dukett, J., Fergus, C.E., Fil-
748 strup, C.T., Funk, C., Gonzalez, M.J., Green, L.T., Gries, C., Halfman, J.D., Hamilton, S.K.,
749 Hanson, P.C., Henry, E.N., Herron, E.M., Hockings, C., Jackson, J.R., Jacobson-Hedin, K.,
750 Janus, L.L., Jones, W.W., Jones, J.R., Keson, C.M., King, K.B.S., Kishbaugh, S.A., Lapierre,
751 J.F., Lathrop, B., Latimore, J.A., Lee, Y., Lottig, N.R., Lynch, J.A., Matthews, L.J., McDow-
752 ell, W.H., Moore, K.E.B., Neff, B.P., Nelson, S.J., Oliver, S.K., Pace, M.L., Pierson, D.C.,

- 753 Poisson, A.C., Pollard, A.I., Post, D.M., Reyes, P.O., Rosenberry, D.O., Roy, K.M., Rud-
754 stam, L.G., Sarnelle, O., Schuldt, N.J., Scott, C.E., Skaff, N.K., Smith, N.J., Spinelli, N.R.,
755 Stachelek, J., Stanley, E.H., Stoddard, J.L., Stopyak, S.B., Stow, C.A., Tallant, J.M., Tan,
756 P.N., Thorpe, A.P., Vanni, M.J., Wagner, T., Watkins, G., Weathers, K.C., Webster, K.E.,
757 White, J.D., Wilmes, M.K. & Yuan, S. (2017) LAGOS-NE: a multi-scaled geospatial and
758 temporal database of lake ecological context and water quality for thousands of US lakes.
759 *GigaScience*, **6**, 1–22. <https://dx.doi.org/10.1093/gigascience/gix101>.
- 760 Stachelek, J., Oliver, S. & Masrour, F. (2019) LAGOSNE: Interface to the lake multi-scaled
761 geospatial and temporal database. *R package version 202*.
- 762 Starzynski, D. & Lauer, T.E. (2015) How temperature affects timing and duration of yellow
763 perch spawning in the indiana waters of lake michigan. *Journal of Freshwater Ecology*, **30**,
764 445–453.
- 765 Stoner, A.W. (2004) Effects of environmental variables on fish feeding ecology: implications
766 for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology*,
767 **65**, 1445–1471. <https://dx.doi.org/10.1111/j.0022-1112.2004.00593.x>.
- 768 Tacon, A.G.J. & Metian, M. (2013) Fish matters: Importance of aquatic foods in hu-
769 man nutrition and global food supply. *Reviews in Fisheries Science*, **21**, 22–38.
770 <https://dx.doi.org/10.1080/10641262.2012.753405>.
- 771 Tehrani, N.A., Naimi, B. & Jaboyedoff, M. (2021) A data-integration approach
772 to correct sampling bias in species distribution models using multiple datasets
773 of breeding birds in the Swiss Alps. *Ecological Informatics*, p. 101501.
774 <https://dx.doi.org/10.1016/j.ecoinf.2021.101501>.
- 775 Tsuboi, J. & Endou, S. (2008) Relationships between catch per unit effort, catchability, and
776 abundance based on actual measurements of salmonids in a mountain stream. *Transactions*
777 *of the American Fisheries Society*, **137**, 496–502. <https://dx.doi.org/10.1577/T06-259.1>.
- 778 Villegas-Ríos, D., Alós, J., Palmer, M., Lowerre-Barbieri, S., Bañón, R., Alonso-Fernández,
779 A. & Saborido-Rey, F. (2014) Life-history and activity shape catchability in a sedentary fish.
780 *Marine Ecology Progress Series*, **515**, 239–250. <https://dx.doi.org/10.3354/meps11018>.
- 781 Vine, J.R., Kanno, Y., Holbrook, S.C., Post, W.C. & Peoples, B.K. (2019) Using side-
782 scan sonar and N-Mixture modeling to estimate Atlantic sturgeon spawning migra-
783 tion Abundance. *North American Journal of Fisheries Management*, **39**, 939–950.
784 <https://dx.doi.org/10.1002/nafm.10326>.
- 785 Wagner, T., Hansen, G.J., Schliep, E.M., Bethke, B.J., Honsey, A.E., Jacobson, P.C., Kline,
786 B.C. & White, S.L. (2020) Improved understanding and prediction of freshwater fish com-
787 munities through the use of joint species distribution models. *Canadian Journal of Fisheries*
788 *and Aquatic Sciences*, **77**, 1540–1551. <https://dx.doi.org/10.1139/cjfas-2019-0348>.
- 789 Wagner, T., Irwin, B.J., Bence, J.R. & Hayes, D.B. (2013) Detecting temporal trends
790 in freshwater fisheries surveys: Statistical power and the important linkages be-
791 tween management questions and monitoring objectives. *Fisheries*, **38**, 309–319.
792 <https://dx.doi.org/10.1080/03632415.2013.799466>.

- 793 Wehrly, K.E., Breck, J.E., Wang, L. & Szabo-Kraft, L. (2012) A landscape-based classification
794 of fish assemblages in sampled and unsampled lakes. *Transactions of the American Fisheries*
795 *Society*, **141**, 414–425. <https://dx.doi.org/10.1080/00028487.2012.667046>.
- 796 Wilberg, M.J., Thorson, J.T., Linton, B.C. & Berkson, J. (2009) Incorporating time-varying
797 catchability into population dynamic stock assessment models. *Reviews in Fisheries Science*,
798 **18**, 7–24. <https://dx.doi.org/10.1080/10641260903294647>.
- 799 Yarnell, R., Scott, D., Chimimba, C. & Metcalfe, D. (2007) Untangling the roles of fire, grazing
800 and rainfall on small mammal communities in grassland ecosystems. *Oecologia*, **154**, 387–
801 402.
- 802 Zhang, C., Chen, Y., Xu, B., Xue, Y. & Ren, Y. (2020) Evaluating the influence of spatially
803 varying catchability on multispecies distribution modelling. *ICES Journal of Marine Science*.
804 <https://dx.doi.org/10.1093/icesjms/fsaa068>.

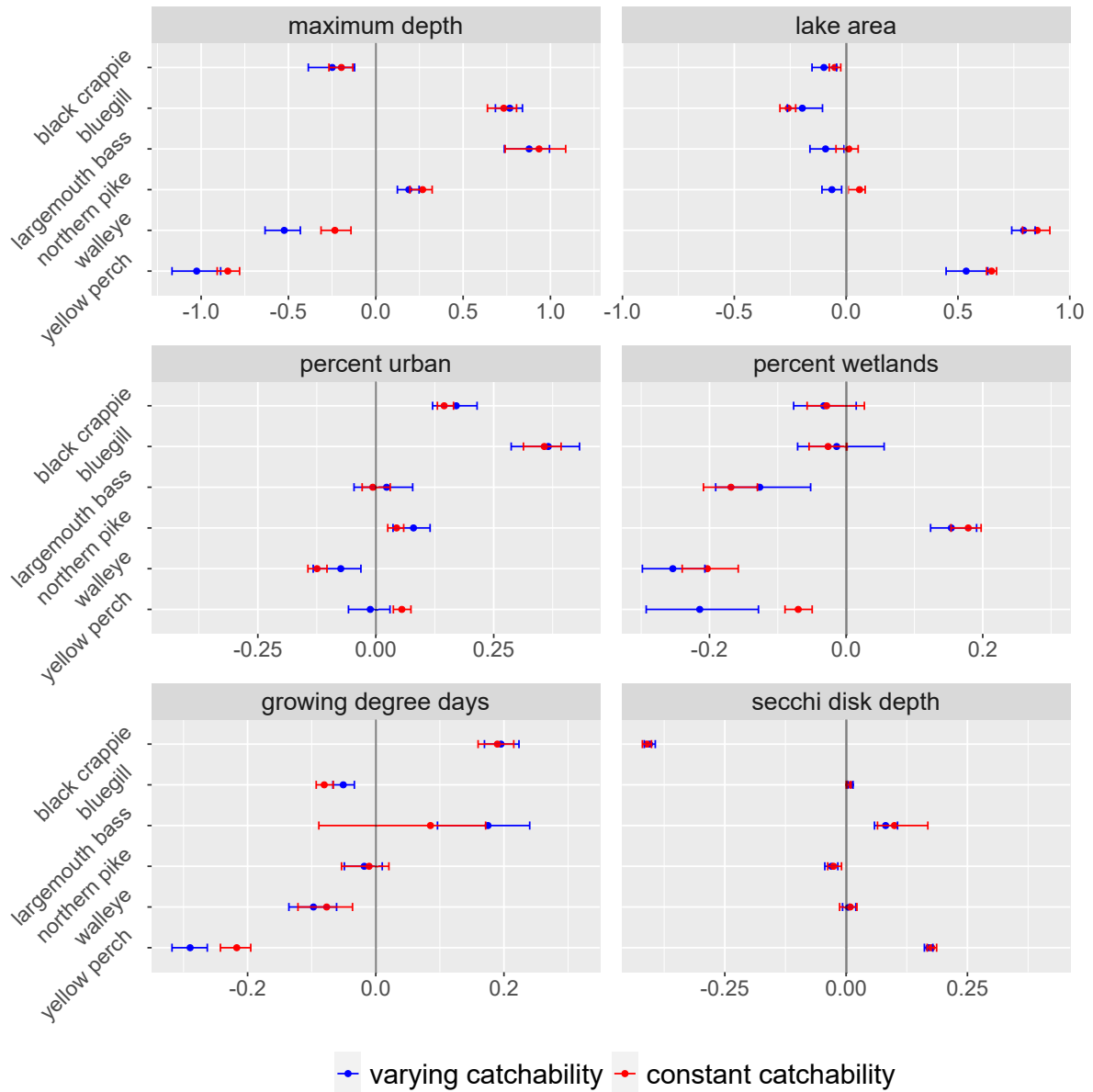


Figure 4: Estimates of the abundance parameters, α and β , for each species from our model with varying catchability (blue) and with constant catchability (red). The posterior mean is shown by the point and the 95% credible intervals are shown by the horizontal bars. A vertical line at zero is used to visually identify parameters that are significantly different from zero.

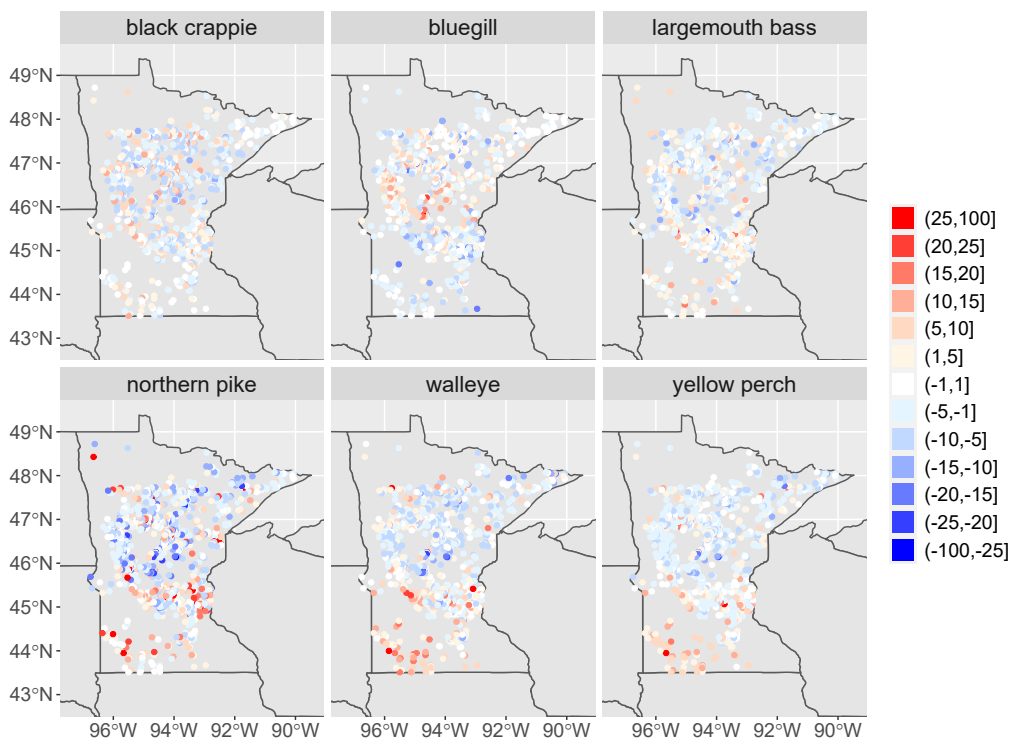


Figure 5: Difference in rank of relative abundance by species between our model with varying catchability and the model with constant catchability.

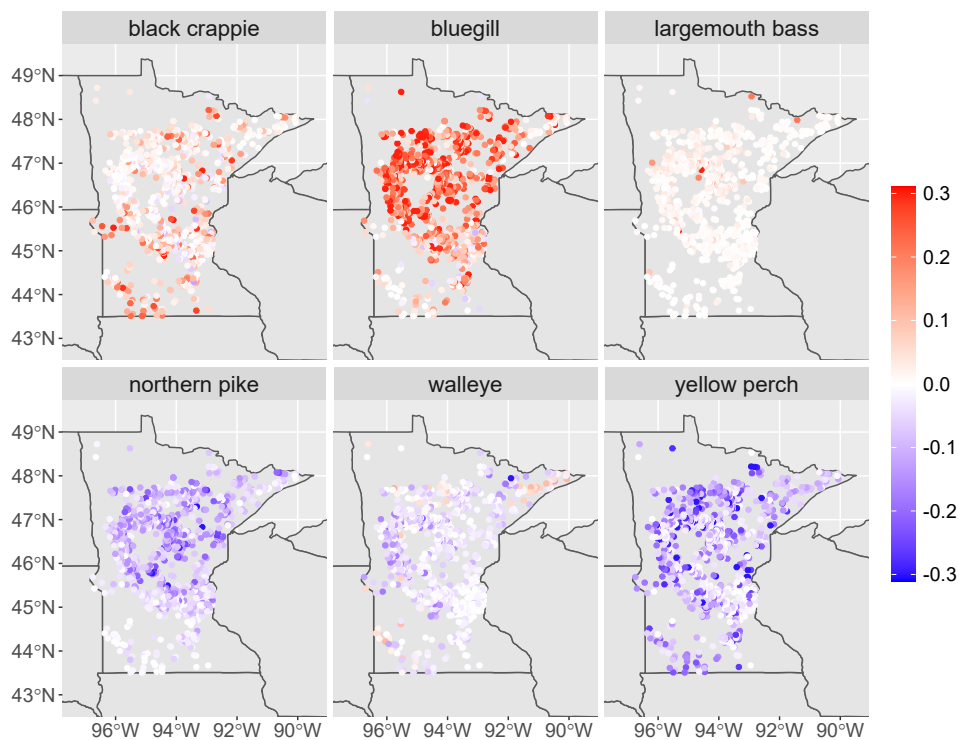


Figure 6: Difference in species community structure by lake between our model with varying catchability and the model with constant catchability. Positive values (red colors) indicate higher species abundance relative to other species within the lake when accounting for varying catchability. Negative values (blue colors) indicate lower species abundance relative to other species within the lake when accounting for varying catchability.