Spatio-Temporal Models of Intermediate Complexity for Ecosystem Assessments: a new tool for spatial fisheries management

James T. Thorson[1*], Grant Adams[2], Kirstin Holsman[3]

[1] Habitat and Ecosystem Process Research program, Alaska Fisheries Science Center, NMFS, NOAA, Seattle, WA, USA

[2] School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA, USA

[3] Resource Ecology and Fisheries Management program, Alaska Fisheries Science Center, NMFS, NOAA, Seattle, WA, USA

* Corresponding author

James.Thorson@noaa.gov

Running header: MICE-in-space models

Abstract

Multispecies models are widely used to evaluate management trade-offs arising from species interactions. However, identifying climate impacts and sensitive habitats requires integrating spatial heterogeneity and environmental impacts into multispecies models at fine spatial scales. We therefore develop a spatio-temporal model of intermediate complexity for ecosystem assessments (a "MICE-in-space"), which is fitted to survey sampling data and time-series of fishing mortality using maximum likelihood techniques. The model is implemented in the *VAST* R package, and it can be configured to range from purely descriptive to including ratio-dependent interactions among species. We demonstrate this model using data for four groundfishes in the Gulf of Alaska using data from 1982-2015. Model selection for this case study shows that models with species interactions are parsimonious, although a model specifying separate density dependence without interactions also has substantial support. The AIC-selected model estimates a significant, negative impact of Alaska pollock (*Gadus chalcogrammus*, Gadidae) on productivity of other species and suggests that recent fishing mortality for Pacific cod (*G. microcephalus*, Gadidae) is above the biological reference point (BRP) resulting in 40% of unfished biomass; other models show similar trends but different scales due to different BRP estimates. A simulation experiment shows that fitting a model with fewer species at a coarse spatial resolution degrades estimation performance, but that interactions and biological reference points can still be estimated accurately. We conclude that MICE-in-space models can simultaneously estimate fishing impacts, species-tradeoffs, biological reference points, and habitat quality. They are therefore suitable to forecast short-term climate impacts, optimize survey designs, and designate protected habitats.

43 Keywords: ecosystem model; models of intermediate complexity for ecosystem assessments;
44 essential fish habitat; spatio-temporal model; VAST
45

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1. Introduction

Fisheries managers use a mix of different management instruments to regulate fishing and other marine impacts (Walther and Möllmann 2014; Dolan *et al.* 2016). Scientific advice to support fisheries management typically includes (but is not limited to): limits on fishery landings and incidental catch for individual species; spatial regulation of activities occurring near sensitive habitats or species; ecosystem-based limits on total landings and fishing gears; and allocation of species quotas to different ports or fleets based on forecasted changes in species distribution or productivity. These four examples are informed, respectively, by analysis of stock status, habitat quality, ecosystem function, and climate linkages, and fisheries science is developing tools to implement these four types of analysis rapidly, transparently, and at low cost. Fisheries managers have benefited from tools that can be used for multiple types of analysis, e.g., by using "models of intermediate complexity for ecosystem assessments" (MICE; Plagányi *et al.* 2014) to simultaneously analyze stock status and multispecies tradeoffs.

The dynamics of marine species is regulated by biological interactions such as predation and competition, and also impacted by technical interactions arising from shared impacts of fishing activities (Gaichas *et al.* 2010; Pikitch *et al.* 2014; Spencer *et al.* 2016). As a result, harvesting can impact target species directly, and also impact interdependent species indirectly through changes in natural mortality and resource availability (Reum *et al.* 2019; Collie and Gislason 2001). The indirect impact of harvesting on non-target species may be counterintuitive, and fisheries management requires information regarding these impacts both to mitigate fishing impacts on unproductive species as well as to identify management strategies that are expected to perform well for a variety of stakeholders (Plagányi *et al.* 2011; Marshall *et al.* 2019).

85 Fisheries managers therefore use ecosystem models to identify potential trade-offs of
86 management decisions that arise from biological and technical interactions (Hollowed 2000;
87 Lassen *et al.* 2013; Plagányi *et al.* 2014). Ecosystem models can vary in complexity from
88 models of intermediate complexity for ecosystem assessments (MICE), which estimate
89 population parameters for a subset of key interacting species from time-series of data, to end-to-
90 end whole ecosystem models that simulate the interactions of multiple oceanographic,
91 ecological, and anthropogenic processes (Plagányi *et al.* 2011; Collie *et al.* 2016; Ortiz *et al.*
92 2016). However, a key aspect of ecosystem models is that they incorporate processes such as
93 predation, competition, and fishing (Plagányi and Butterworth 2012; Ortiz *et al.* 2016;
94 Mackinson *et al.* 2018). These models are typically used to forecast changes in population
95 density, productivity, and fishery catch under alternative management procedures and
96 environmental conditions, and forecasts will likely be improved via explicit inclusion of
97 biological and technical interactions (Howell and Filin 2014; Tommasi *et al.* 2017).
98 Global climate change is causing rapid shifts in the spatial distribution of physical habitat,
99 nutrients, forage species, and predators. These shifts can cause rapid changes in structure and
100 productivity for the ecosystem managed by a given jurisdiction. Models that fail to account for
101 ecosystem changes resulting from spatial shifts are less likely to accurately forecast performance
102 of alternative management procedures, and in some cases will have degraded performance when
103 informing fisheries management (Kempf *et al.* 2010; Spencer *et al.* 2016; Fu *et al.* 2017). One
104 avenue to account for ecosystem changes resulting from spatial distribution shifts is to develop
105 ecosystem models that estimate variation in species density and/or productivity at fine-spatial
106 scales while also accounting for species interactions (see review in Hunsicker *et al.* 2011)

Spatially-explicit ecosystem models are currently used to inform spatial planning, identify tradeoffs for alternative management strategies, and provide annual advice regarding limits on fishery harvest. Spatially-explicit ecosystem models that are widely used include Atlantis (Fulton *et al.* 2011), OSMOSE (Shin and Cury 2001), EwE (Christensen and Walters 2004), and Gadget (Begley and Howell 2004), and these existing models vary in the extent to which users must "tune them by hand" prior to further model usage. Ideally, spatially-explicit ecosystem models would have good statistical properties (e.g., statistical consistency and well-defined forecast intervals; (Magnusson *et al.* 2013)), would assimilate available data (e.g., resource surveys) through probabilistic estimation methods, and could provide biological reference points for harvest recommendations. In parallel, there is a growing literature developing multispecies spatio-temporal models to predict variation in density at fine spatial scales while estimating spatial correlation functions that are used to interpolate and extrapolate population density to unsampled locations (Ovaskainen *et al.* 2017; Thorson *et al.* 2017; Schliep *et al.* 2018). However, these previous approaches have not explicitly included fishing mortality, and therefore have not been capable of estimating biological reference points for regulating fishery catches.

We therefore develop a spatio-temporal multispecies model including species interactions, fishing mortality, and estimating fishing mortality and biomass relative to biological reference points that are commonly used in stock assessment. This spatio-temporal model has structural complexity intermediate between single-species and end-to-end ecosystem models while accounting for spatial variation, so we call it a "Spatial model of intermediate complexity for Ecosystem assessments" (MICE-in-space). It fits directly to survey data using maximum-likelihood techniques, and assumes that biological interactions depend upon local densities of modeled species. To do so, we extend an existing vector-autoregressive spatio-temporal

modelling framework, implemented using package *VAST* (Thorson and Barnett 2017), which has been used previously for stock assessments, ecosystem status reports, and journal articles in many regions worldwide (see Thorson (2019b) for examples). We then demonstrate this MICE-in-space model by application to survey data for four species in the Gulf of Alaska, and use a simulation experiment conditioned on this case study to explore the statistical properties of the model. Through development of generic software, we envision that MICE-in-space models will help further align stock, ecosystem, and habitat assessments, and improve future ecosystem-based management advice.

2. Methods

We seek to develop an approach that combines features of three existing types of models used in marine ecosystems:

1. Spatially explicit models can be broadly categorized as "spatially stratified" or "spatio-temporal" models (Berger *et al.* 2017). Spatially stratified models have a long history in population and ecosystem modelling (Beverton and Holt 1957; Goethel *et al.* 2011), but typically cannot be fitted to data representing dynamics occurring at fine spatial scales because the amount of data per stratum decreases as the number of spatial strata is increased. By contrast, we develop a spatio-temporal model that incorporates a spatial correlation function to approximate dynamics occurring continuously across space (Cressie and Wikle 2011; Kristensen *et al.* 2014), such that the spatial resolution of the model can be manipulated with relatively small changes in model performance. Although there have been previous "spatio-temporal multispecies models" (e.g., Walters and Bonfil 1999), they typically have not been fitted statistically using techniques that estimate uncertainty.

2. Models of Intermediate Complexity (MICE), which represent dynamics for 2-10 species; explicitly consider environmental, ecological, anthropogenic, and management trade-offs; and fit to available data in a probabilistic framework that allows for model validation similar to conventional single-species models (Plagányi 2007). Specifically, our MICE-in-space model can fit a similar number of species while estimating parameters and generating probabilistic forecasts of spatio-temporal dynamics.
3. Joint dynamic species distribution models (JDSDM), which estimate population density including the degree of spatial autocorrelation; account for covariation in density and productivity among multiple species; and incorporate changes in spatial distribution for multiple species over time (Thorson *et al.* 2016). Specifically, the MICE-in-space model identifies the predicted mix of species encountered at any given location, thereby providing an estimate of likely technical interactions (e.g., Dolder *et al.* 2018).

Finally, we seek to combine these elements in a manner that allows ecologists to explore nested changes in model structure that scale in structural complexity from descriptive (i.e., without explicit models for species dynamics and interactions) through stacked single-species models (i.e., independent dynamics for each species) to multi-species models (i.e., explicitly considering species interactions). To accomplish these goals, we develop a model as follows.

2.1 Index-standardization model as starting point

We start by modelling biomass-density $d(s,c,t)$ for each category c (in this case representing different species), location s, and year t while fitting to samples of biomass, where b_i is the i-th sample (of I total samples), and this sample records biomass at location s_i for category c_i and year t_i (of S locations, C categories, and T years total). We first describe the simplest

multispecies spatio-temporal model configuration, which we call an "index standardization" model, and then describe how it is modified to approximate species interactions.

First, we adapt an existing Poisson-link delta model (Thorson 2018) that specifies the probability $\Pr(b_i = B)$ that the i-th sample b_i would yield a biomass of B. This model specifies this probability using numbers-density $n(s,c,t)$ and biomass-per-individual $w(s,c,t)$, where $d(s,c,t) = n(s,c,t) \times w(s,c,t)$:

$$\Pr(b_i = B) = \begin{cases} 1 - p_i & if\ B = 0 \\ p_i \times g\left(B \middle| r_i, \sigma^2(c)\right) & if\ B > 0 \end{cases} \quad (1)$$

where encounter probability $p_i = \exp\left(-a_i \times n(s_i, c_i, t_i)\right)$ follows a Poisson process given numbers density and the area swept a_i by the i-th sample. Similarly, the expected biomass given that a sample encounters the species, r_i, is defined such expected biomass $\mathbb{E}(B) = p_i \times r_i$, which yields $r_i = a_i \times n(s_i, c_i, t_i) \times w(s_i, c_i, t_i)/p(i)$, such that r_i is affected by both numbers density and biomass-per-individual. Finally, $g\left(B \middle| r_i, \sigma^2(c_i)\right)$ is a probability density function for unexplained variation in positive catch rates given residual sampling variance $\sigma^2(c_i)$. This Poisson-link delta model is numerically efficient approximation to the compound Poisson-gamma distribution (Foster and Bravington 2013). We use it in the following because we will later approximate species interactions as a linear model for log-density, and the Poisson-link delta model allows us to predict biomass-sampling data while accounting for spatial and temporal variation in log-density.

Each component of the index-standardization model then has a separate intercept for each species and year ($\beta_n(c,t)$ and $\beta_w(c,t)$), where these intercepts account for differences in average density among species (e.g., due to different equilibrium densities in the community, corresponding to different $\beta_n(c,t)$ for each species c) and over time (e.g., due to different levels

of spatial aggregation, captured via differences in $\beta_w(c,t)$ among years t). Each component also includes "spatial variation," which is constant over time ($\omega_n(s,c)$ and $\omega_w(s,c)$), as well as "spatio-temporal variation," which varies over time ($\varepsilon_n(s,c,t)$ and $\varepsilon_w(s,c,t)$):

$$\log\big(n(s,c,t)\big) = \beta_n(c,t) + \omega_n(s,c) + \varepsilon_n(s,c,t) \quad (2)$$

$$\log\big(w(s,c,t)\big) = \beta_w(c,t) + \omega_w(s,c) + \varepsilon_w(s,c,t)$$

where spatial variation is estimated while specifying a multivariate probability distribution for $\omega_n(s,c)$ and $\omega_w(s,c)$:

$$\boldsymbol{\Omega}_n \sim MVN(\mathbf{0}, \mathbf{R}(\kappa_n, \mathbf{H}) \otimes \mathbf{L}_{\omega n}\mathbf{L}_{\omega n}^T) \quad (3)$$

where $\boldsymbol{\Omega}_n$ is the matrix of spatial variation $\omega_n(s,c)$, and $\mathbf{R}(\kappa_n, \mathbf{H})$ is a matrix of spatial correlations among locations s given estimated decorrelation rate κ_n and a transformation matrix **H.** Estimated matrix **H** represents the tendency for spatial correlations to decline faster in some directions than others, e.g., where ecosystems with a large variation in depth may tend to have to have spatial correlations that decline faster moving perpendicular to depth gradients than along those gradients. We model spatial correlations using a stationary Matérn correlation function although future studies could explore alternative spatial processes, e.g., where correlations vary as a function of local environmental conditions (e.g., Fuglstad *et al.*, 2015). Meanwhile, $\mathbf{L}_{\omega n}$ is a triangular matrix representing species associations with one or more estimated "spatial factors," such that $\mathbf{L}_{\omega n}\mathbf{L}_{\omega n}^T$ is the estimated covariance in spatial distribution (e.g., Pollock *et al.* 2014), and we define an identical distribution for $\boldsymbol{\Omega}_w$, except involving a separate estimate of κ_w and $\mathbf{L}_{\omega w}$.

The index-standardization model specifies that spatio-temporal variation is independent in each year:

$$vec\big(\mathbf{E}_n(t)\big) \sim MVN(\mathbf{0}, \mathbf{R}(\kappa_n) \otimes \mathbf{L}_{\varepsilon n}\mathbf{L}_{\varepsilon n}^T) \quad (4)$$

where $vec\big(\mathbf{E}_n(t)\big)$ is a vector of spatio-temporal variation $\varepsilon_n(s, c, t)$ for all sites s and species c in a given year t, $\mathbf{L}_{\varepsilon n}\mathbf{L}_{\varepsilon n}^T$ represents the covariance in spatio-temporal variation in numbers density, and we again define an identical distribution for $\mathbf{E}_w(t)$, involving a separate estimate of $\mathbf{L}_{\varepsilon w}$. This spatio-temporal index standardization is useful for generating an index of abundance for each species that has little estimation covariance among years (Thorson 2019b). However, it does not define a probability distribution for a year with no available data (due to no information for intercepts in that year).

2.2 Extending the model to account for species interactions

We next extend this model by defining a probability distribution for population density in year t given estimates in the previous years. To do so, we approximate nonlinear dynamics for species interactions via a first-order Taylor series expansion around its equilibrium, which results in a first-order vector autoregressive model (Ives *et al.* 2003; Thorson *et al.* 2017; Certain *et al.* 2018):

$$\log\big(\mathbf{d}(s,t)\big) = \boldsymbol{\alpha}(s) + \mathbf{B}\log\big(\mathbf{d}(s,t-1)\big) + \cdots \quad (5)$$

where $\boldsymbol{\alpha}(s)$ is a vector of spatially varying and time-invariant intercepts, composed of $\alpha(s,c)$ for each species c, which represents spatial variation in carrying capacity. $\mathbf{B}$ is the species interactions matrix where b_{c,c^*} indicates that a 1% change in density for species c^* causes a change of b_{c,c^*} in per-capita productivity for species c. We parameterize the species-interactions matrix as:

$$\mathbf{B} = \mathbf{P} + \boldsymbol{\chi}\boldsymbol{\psi}^{\mathrm{T}} \quad (6)$$

where $\mathbf{P}$ is a diagonal matrix where diagonal element $\rho(c,c) - 1$ represents intra-specific density dependence (the degree that population density for species c decreases per-capita

productivity for that species), and $\boldsymbol{\chi}\boldsymbol{\psi}^{\mathrm{T}}$ represents inter-species density dependence. $\boldsymbol{\chi}$ and $\boldsymbol{\psi}$ are both C by R matrices, where the user specifies rank R and this controls the number of interaction parameters that must be estimated; other identifiability restrictions must be imposed as R approaches the number of species C, and this parameterization is common in cointegration models used in econometrics (Engle and Granger 1987; Thorson *et al.* 2017). Importantly, the user-specified rank of species interactions R can range from 0 to C (i.e., $0 \leq R \leq C$), where the rank represents the number of ratio-dependent axes of community regulation arising from species interactions, and where $\boldsymbol{\chi}\boldsymbol{\psi}^{\mathrm{T}}$ can be defined to have either complex or real eigenvalues (representing dynamics with or without population cycles) depending upon the quality of available data (Thorson *et al.* 2017).

In addition to approximating species interactions via an autoregressive model, we again include spatial variation (e.g., $\omega_n(s,c)$)and spatio-temporal variation (e.g., $\boldsymbol{\varepsilon}_n(s,t)$) and also incorporate the impact of an instantaneous fishing mortality rate $\mathbf{f}(t)$ on population density:

$$\log\big(\mathbf{d}(s,t)\big) = \boldsymbol{\alpha} + \boldsymbol{\omega}(s) + \mathbf{B}\log\big(\mathbf{d}(s,t-1)\big) + \boldsymbol{\varepsilon}(s,t) - \mathbf{f}(t) \tag{7}$$

Solving for $\log\big(\mathbf{d}(s,t)\big)$ and re-writing as a delta-model then yields:

$$\log\big(\mathbf{n}(s,t)\big) = \boldsymbol{\beta}_n + \boldsymbol{\omega}_n(s) + \sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\boldsymbol{\varepsilon}_n(s,t-\Delta) - \xi\sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\mathbf{f}(t-\Delta) \tag{8a}$$

$$\log\big(\mathbf{w}(s,t)\big) = \boldsymbol{\beta}_w + \boldsymbol{\omega}_w(s) + \sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\boldsymbol{\varepsilon}_w(s,t-\Delta) - (1-\xi)\sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\mathbf{f}(t-\Delta) \tag{8b}$$

where species interactions $\mathbf{B}$ are identical between the two components of the delta model, and where ξ determines the degree to which fishing mortality decreases numbers density or biomass-per-individual (we assume $\xi = 1$ in the following, but future research could explore the topic further). Terms summing across lag Δ, $\sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\boldsymbol{\varepsilon}_n(s,t-\Delta)$ and $\sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\mathbf{f}(t-\Delta)$, represent the

252 decaying effect of spatio-temporal variation and fishing mortality, respectively, occurring Δ
253 years previous to year t; the contribution of previous spatio-temporal variation and fishing
254 mortality is additive due to our model specification, and this specification results in fast
255 computation relative to other model structures. Fishing mortality rate $\mathbf{f}(t)$ must be specified as
256 data for every species, although future research could extend the model to estimate this as a
257 parameter by fitting to fishery catches. The model can also be extended to include catchability
258 covariates, density covariates, and vessel effects that can be incorporated into VAST (see
259 Thorson (2019b) for a description). Although we do not explore these features here (and they
260 would require further software development to be used in conjunction with estimates of species
261 interactions), we recommend future research to incorporate covariates so that, e.g., dynamics
262 could be driven by downscaled climate projections (Hollowed *et al.* 2013).
263 Finally, we calculate biological reference points (BRP) for population abundance and fishing
264 intensity. As BRP for population abundance, we calculate average unfished biomass $b_0(c)$ for
265 each species c and envision a scenario in which fisheries managers seek to maintain a population
266 biomass near a proxy for maximum sustainable yield, $b(c) \approx 0.4b_0(c)$, corresponding to 40% of
267 unfished biomass. We use $b_{40\%}$ as it is used as a proxy biomass target for in other US
268 management regions, e.g., for US West Coast rockfishes (Wetzel *et al.* 2017), and future studies
269 could specify a different target or expand the model to accommodate other proxy reference
270 points (e.g., Gabriel and Mace 1999). As BRP for fishing intensity, we calculate the
271 corresponding fishing mortality rate $f_{0.4}(c)$ that would result in 40% of unfished biomass if
272 $f_{0.4}(c)$ were continued indefinitely (sensu Holsman *et al.* 2016b). Given these BRPs, we then
273 calculate stock status as the ratio of fishing mortality or expected biomass in a given year with
274 the associated BRP; see Appendix A for more details regarding computation.

2.3 Parameter estimation

We fit this model using a publicly available package VAST (Thorson and Barnett 2017), release number 3.1.0 (https://github.com/James-Thorson/VAST) within the R statistical environment (R Core Team 2017). This R package has been used in a variety of different stock and ecosystem assessment reports in several marine regions worldwide (Thorson 2019b) but has not previously included features for estimating species interactions **B**, the impact of fishing mortality $\mathbf{f}(t)$, or biological reference points. Species interactions had previously been explored in several recent spatio-temporal models (Ovaskainen *et al.* 2017; Thorson *et al.* 2017; Schliep *et al.* 2018), but this study is the first to our knowledge to incorporate both species interactions and fishing mortality in a multispecies spatio-temporal model. We argue that this combination of features represents the minimum necessary for a MICE-in-space model.

VAST estimates spatial variation $\boldsymbol{\omega}(s)$ and spatio-temporal variation $\boldsymbol{\varepsilon}(s,t)$ for all species, locations, and times as random effects. Users of VAST specify a number of knots n_x, and VAST then uses R package R-INLA (Lindgren and Rue 2013) to generate a triangulated mesh, with vertices at these n_x knots as well as additional boundary vertices, where the total number of knots and boundary vertices is n_s. VAST then estimates spatial variables at all n_s locations, while associating every survey record i with the knot s_i closest to it. Similarly, VAST associates every location in a user-specified extrapolation grid with the knot s_g closest to it. It then uses these predicted values within the extrapolation grid for all plotting and when calculating derived quantities (see the VAST user manual for more details: https://github.com/James-Thorson-NOAA/VAST/blob/master/manual/VAST_model_structure.pdf).

VAST estimates parameters by identifying the values that maximize a log-likelihood function. It estimates several fixed effects as defined previously: species interactions matrix **B**,

298 spatial correlations $\mathbf{L}_{\omega n}$, spatio-temporal correlations $\mathbf{L}_{\varepsilon n}$, spatial decorrelation rate κ_n,
299 geometric anisotropy $\mathbf{H}$, residual sampling variation $\sigma^2(c)$, numbers-density intercepts $\beta_n(c)$
300 and average-weight $\beta_w(c)$ for each species c. To calculate the marginal log-likelihood, it
301 approximates the integral across all random effects using the Laplace approximation (Skaug and
302 Fournier 2006), and specifically integrates across random effects representing spatial variation
303 $\boldsymbol{\omega}(s)$ and spatio-temporal variation $\boldsymbol{\varepsilon}(s,t)$ for all species, locations, and times. The Laplace
304 approximation is implemented using package TMB (Kristensen *et al.* 2016), which uses
305 automatic differentiation to efficiently calculate the matrix of second derivatives (used in the
306 Laplace approximation) and the gradient of the Laplace approximation (used when maximizing
307 fixed effects). TMB predicts all random effects by maximizing the joint likelihood function
308 given maximum likelihood estimates of fixed effects, and we use the epsilon bias-correction
309 estimator to correct for "retransformation bias" when predicting any derived quantity (e.g.,
310 biomass biological reference point $b_{ratio}(c,t)$) that involves a nonlinear transformation of
311 predicted random effects (Thorson and Kristensen 2016). TMB also applies a generalization of
312 the delta-method to calculate standard errors for all fixed and random effects, as well as all
313 derived quantities (Kass and Steffey 1989).

314 We note that this MICE-in-space model involves the assumption that the expected survey
315 catches are proportional to local abundance and sample the entire stock. This assumption is
316 analogous to assuming that the catchability coefficient $q = 1$, and this assumption (or variants
317 involving a tight prior) are common in stock assessments in the Gulf of Alaska. Future
318 developments of the MICE-in-space model may involve estimating a catchability coefficient,
319 presumably by treating the fishery history as a depletion experiment as this is the primary source
320 of information in biomass-dynamic models (Magnusson and Hilborn 2007). We leave this as a

topic of future development and exploration, but note that our assumptions about catchability result in precise estimates of population scale relative to other model assumptions.

2.4 Case study application

We demonstrate this model via application to data for four commercially important species in the US Gulf of Alaska: Alaska pollock, Pacific cod, Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*). We fit the model to biomass-sampling data obtained from a bottom trawl survey data from 1982-2015, conducted every 3rd year from 1982-1999 and every 2nd year from 1999 to present day (Von Szalay and Raring 2016). For fishing mortality, we extract the ratio of fishery catches and stock assessment estimates of total biomass, and define $f(c,t) = -\log(1 - c(c,t)/b(c,t))$.

We compare model performance for one descriptive model, and four nested models that incorporate density dependence:

1. *Index standardization model*: As a descriptive model, we fit a standard "index standardization model" (Eq. 2). We include this model to show estimates of abundance patterns for a "saturated" model that lacks the mechanistic detail of other models.
2. *Complete density dependence*: As a simplified model that includes density dependence and fishing mortality, we specify a model with "complete" density dependence where spatio-temporal variation and fishing mortality in year t has no impact on values in subsequent years.
3. *Same density dependence*: Next, we include a model estimating the same degree of density dependence for all species while including fishing mortality, but without estimating interactions.

4. *Different density dependence*: We also include a more complex version of model #3 but where density-dependence varies among species, while including fishing mortality but still ignoring interactions.
5. *Species interactions*: Finally, we include a model with community-level regulation ($\mathbf{B} = \mathbf{P} + \boldsymbol{\chi}\boldsymbol{\psi}^{\mathrm{T}}$, where $\mathrm{rank}(\boldsymbol{\chi}) = 1$ and intra-specific density dependence is identical across species) and fishing mortality. This model is useful to show whether species interactions improves model fit relative to ignoring interactions among species.

Models 2-5 are nested and all are intended to bridge continuously from description (model #1) to mechanistic (model #5); see Appendix B for more details.

To visualize results, we show log-biomass density at each modeled location and each species:

$$\log\left(\hat{\mathbf{d}}(s,t)\right) = \{\boldsymbol{\beta}_n + \boldsymbol{\omega}_n(s) + \boldsymbol{\varepsilon}_n(s,t)\} + \{\boldsymbol{\beta}_w + \boldsymbol{\omega}_w(s) + \boldsymbol{\varepsilon}_w(s,t)\} - \left\{\sum_{\Delta=0}^{t} \mathbf{B}^{\Delta}\mathbf{f}(t-\Delta)\right\} \quad (12)$$

and where we calculate unfished biomass density $\hat{\mathbf{d}}(s,t_0)$ by fixing $f(c,t_0) = 0$. We recommend future research incorporating dynamic habitat variables (e.g., bottom temperature) as physical drivers of changing productivity, as well as skill-testing for models with and without covariates (Tommasi *et al.* 2017; Thorson 2019b) but do not address the topic further here.

2.5 Simulation experiment

We also explore model performance using a simulation experiment conditioned upon the most parsimonious model fitted to data for these four species in the Gulf of Alaska. To do so, we (1) generate 100 simulated data sets using a "bootstrap simulator" available within the VAST R package, (2) fit a modified model to each simulated data set, and compare estimates from step #2 with known values from step #1. The bootstrap simulator uses the specified model structure and

363 estimated values for all fixed effects, but generates new values for all random effects ($\boldsymbol{\omega}_n(s)$,
364 $\boldsymbol{\varepsilon}_n(s,t)$, $\boldsymbol{\omega}_w(s)$, and $\boldsymbol{\varepsilon}_w(s,t)$) and then generates new values for biomass-sampling data ($\mathbf{b}$)
365 given those simulated values for random effects. In doing so, it generates new data from the
366 same locations, with the same samples sizes and timing as the original data set, and therefore
367 conditions upon both the estimated parameters (fixed effects) and true sample sizes (timing and
368 frequency of sampling) that is available in the real world while generating new spatial
369 configurations (random effects) for the interacting species.

370 For each simulation replicate, we fit a reduced model comprised of data for only two species
371 (arrowtooth and Alaska pollock) and operating at a coarse spatial resolution (50 knots) relative to
372 the resolution used in the bootstrap simulator (100 knots). We do this for two reasons. First,
373 empirical studies in the real-world will always involve fewer interacting species than the "true"
374 number of interacting species operating in nature, and will also involve a reduced spatial
375 resolution relative to the spatial scale operating in nature. Therefore, reducing the number of
376 species and spatial resolution in the estimation model relative to the operating model ensures that
377 both of these potential sources of bias are present in our simulation experiment, although both
378 sources of bias may be stronger or weaker for other data-generating processes. Second, reducing
379 the spatial resolution and number of species increases the speed of parameter estimation, thereby
380 allowing for an efficient simulation experiment. We choose arrowtooth and Alaska pollock
381 because diet analysis has demonstrated strong predation of arrowtooth upon juvenile Alaska
382 pollock (Gaichas *et al.* 2015; Spies *et al.* 2017; Livingston *et al.* 2017). We then evaluate model
383 fit by comparing estimated and true values for the species interaction matrix $\mathbf{B}$ as well as
384 estimates of the fishing mortality biological reference point $\mathbf{f}_{0.4}$. Based on previous research, we

385 expect that the sign of species interactions should be correctly estimated in the majority of
386 simulation replicates (Thorson *et al.* 2017; Certain *et al.* 2018).

387 3. Results

388 Fitting five spatio-temporal models with varying structural complexity to data for four
389 commercial species in the Gulf of Alaska shows that these models estimate similar patterns of
390 biomass (Fig. 1). Specifically, pollock has its highest biomass in 1989 before declining to low
391 biomass in 2001/2007 when fishing mortality rates are relatively high, and Pacific cod similarly
392 reaches its lowest biomass in 2001 before recovering somewhat despite elevated fishing
393 mortality rates. By contrast, arrowtooth flounder attains high biomass in 1989-1992 and again in
394 2003-2005 before declining in recent years. The index-standardization and "perfect density
395 dependence" models only provides estimates of biomass in years with available data, while the
396 other models interpolate biomass between years with sampling data, although uncertainty
397 intervals are wider for years without sampling data (e.g., see the width of uncertainty intervals
398 for arrowtooth flounder in unsampled years 1990/1991 relative to sampled years 1989/1992).
399 Three MICE-in-space models estimate biological reference points, while "index-
400 standardization" and "complete density dependence" models do not. Despite estimating similar
401 patterns in population biomass, these three MICE-in-space models provide different estimates of
402 the fishing mortality rate expected to attain 40% of unfished biomass ($\mathbf{f}_{0.4}$, left column in Fig. 2).
403 The "same density dependence" model by design estimates the same $\mathbf{f}_{0.4}$ for all species, while
404 the "species interactions" model estimates a relatively high $\mathbf{f}_{0.4}$ for pollock and lower $\mathbf{f}_{0.4}$ for
405 other species. The "different density dependence" model also estimates relatively large standard
406 errors for $\mathbf{f}_{0.4}$ (broad distributions in left column Fig. 2). Differences in $\mathbf{b}_{\text{target}}$ estimates for
407 each species are much smaller than differences in $\mathbf{f}_{0.4}$ among models (right column of Fig. 2).

Model selection using the Akaike Information Criterion (AIC) suggests that "species interactions" model is the most parsimonious model (Table 1), although the "different density dependence" model also has strong support ($\Delta AIC = 1.0$). The AIC-selected "species interactions" model includes four interactions among species that are significant based on a two-sided Wald test at $p < 0.05$, representing a negative impact of pollock on per-capita productivity of all other species as well as a positive impact of Pacific halibut on productivity of arrowtooth flounder (see Appendix C for these results for the "different density dependence model"). Inspecting estimates of population density from the AIC-selected model with species interactions (Fig. 3), we see, e.g., that arrowtooth flounder has increased in density primarily inshore from Kodiak Island. Similarly, biomass of pollock in 1984 and 1995 is concentrated offshore from Kodiak Island, and the low biomass in 2005 is due in part to decreased density southwest of Kodiak in that period. All three MICE-in-space models that estimate biological reference points show similar trends in stock status, but differ in scale particularly for Pacific halibut and walleye Pollock, due primarily to differences in estimated biological reference points (Fig. 4). The AIC-selected "species interactions" model shows that fishing mortality is above the estimate of $f_{0.4}$ for Pacific cod from 2011-2015, while the "different density dependence" model (which also has substantial support) shows fishing mortality slightly below $f_{0.4}$ for those same years; both models estimate that Pacific cod biomass was below 40% of b_0 in 2001 and was approaching that level again by 2015 (Fig. 4). However, stock status is not perfectly correlated between fishing mortality and biomass reference points due to short-term environmental variation, interactions, and other effects that can, e.g., allow biomass to remain above 40% of b_0 despite fishing above $f_{0.4}$. These same factors can cause biomass to exceed average unfished biomass

$\mathbf{b}_0$ for several years, and arrowtooth flounder spends nearly half of the modeled years above this biomass due to process errors and a close-to-zero fishing mortality rate (Fig. 4 top-left panel).

Last, we include results from a simulation experiment exploring the ability of a MICE-in-space model to correctly estimate species interactions given plausible forms of model mis-specification, i.e., (1) ignoring species that have non-negligible interactions with modeled species, and (2) modeling dynamics at a coarser spatial resolution than the resolution of biological interactions. To visualize this simulation design, we compare true and estimated population density for a single replicates of the simulation experiment (Fig. 5). This shows that the model can accurately capture spatial variation in unfished population density (i.e., comparing 1st and 2nd rows of Fig. 5), as well as density in the final year (3rd and 4th rows of Fig. 5), despite only fitting biomass for two of the four simulated species and fitting density at a coarser spatial scale than is used when simulating data. When summarizing across all simulation replicates, the MICE-in-space model is able to estimate the negative impact of pollock on arrowtooth productivity (Fig. 6A, top-right panel) and the negative impact of arrowtooth on pollock productivity (Fig. 6A, bottom-left panel) in nearly all simulation replicates, although these estimates appear to be biased towards more negative numbers (stronger interactions). Similarly, the majority of simulation replicates estimate a negative impact of arrowtooth on pollock productivity (Fig. 6A, bottom-left panel), and density-dependence (Fig. 6A diagonal panels) are approximately unbiased. The bias in interactions translates to some bias in estimates of fishing mortality reference point for arrowtooth flounder (Fig. 6B top panel), where the MICE-in-space model exhibits a positive bias in $f_{0.4}$ for arrowtooth flounder. However, the majority of simulation replicates correctly identify that arrowtooth has a lower $f_{0.4}$ than pollock. We therefore conclude that, given the quantity and frequency of available data and conditioning the

simulation experiment upon estimates from the "species interactions" model, the MICE-in-space model is able to estimate broad qualitative differences in productivity among species as well as the likely sign of species interactions. However, caution should be exercised when interpreting the exact value for fishing mortality targets based on this multispecies model.

4. Discussion

In this paper, we have developed the first multispecies spatio-temporal model that includes species interactions, fishing mortality, and statistical estimates of species-specific biological reference points commonly used for fisheries management. We have showed that a MICE-in-space can function as an operating model within a simulation study, and this simulation experiment suggests that the model can accurately estimate species interactions even in the presence of likely forms of model mis-specification (i.e., missing fine-scale dynamics and modeling only a subset of interacting species). Finally, a case-study demonstration involving four species in the Gulf of Alaska has showed that incorporating species interactions is more parsimonious than assuming independent dynamics among species, although an alternative model with separate density dependence for each species but no interactions had similar support ($\Delta AIC = 1.0$). Various configurations of the model estimated similar trends in biomass and biomass reference points but differed more in estimated fishing mortality reference points, and this is in-line with other previous multi-species model comparisons (Kinzey and Punt 2009; Holsman *et al.* 2016b).

The species interactions estimated from MICE-in-space contrast with previous analyses of trophic relationships based on diet analyses in the Gulf of Alaska. Models that include diet data suggest that arrowtooth flounder, cod, and halibut account for the majority of predation upon pollock (Gaichas *et al.* 2015) and therefore predict that these stocks have a negative impact on

476 pollock productivity (A'mar *et al.* 2010; Van Kirk *et al.* 2010). However, the MICE-in-space
477 developed here estimated no significant impact of either arrowtooth flounder, cod, or halibut on
478 pollock productivity. Previous ecosystem models have also suggested that increased pollock
479 production would lead to increased halibut production (Gaichas *et al.* 2015), in contrast with the
480 negative impact of pollock on halibut estimated here.

481 Diet data represent the integrated outcome of behavioral and spatial processes that underlie
482 variation in consumption across habitats, years, species, and individuals. Diet studies therefore
483 provide valuable information regarding trophic interactions that structure marine ecosystems
484 (e.g., Livingston et al. 2017). However, estimates of predation impacts on species productivity
485 will typically depend upon structural modelling assumptions, such that models may differ about
486 the magnitude or sign of species interactions even when fitting to diet data (Kaplan *et al.* 2018;
487 Reum *et al.* 2019). Finally, non-consumptive processes may cause diet analyses to misrepresent
488 the cumulative impact of changing biomass for one species on per-capita productivity for other
489 species. For example, behavioral plasticity can reduce foraging rates in many species (e.g.,
490 Heithaus *et al.* 2007), resulting in a decrease in productivity (due to decreased weight-at-age)
491 that exceeds that predicted due to a direct change in natural mortality measured by predator
492 stomach contents. Comparing results from multiple ecosystem models can help to evaluate the
493 sensitivity of estimated ecosystem properties to structural assumptions and multiple data sources.
494 We therefore support ongoing comparative research using multiple ecological models when
495 evaluating climate or human-mediated changes on marine ecosystems (Olsen *et al.* 2016; Kaplan
496 *et al.* 2018; Spence *et al.* 2018; Tittensor *et al.* 2018; Pope *et al.* 2019), and note that the MICE-
497 in-space model could fill a useful niche in these model portfolios.

Given the differences in estimated interactions between the MICE-in-space model and previous ecosystem models using diet-data, we do not recommend using the MICE-in-space model for analyzing harvest trade-offs between species in the Gulf of Alaska (e.g., Walters *et al.* 2005; Moffitt *et al.* 2016) until these differences have been explained and addressed. However, we note that the MICE-in-space model estimates fine-scaled variation in multispecies density, and also discriminates species interactions from the covariance caused by different responses to shared but unmeasured environmental drivers. We therefore believe that the MICE-in-space model is ready for use for several real-world fisheries management activities including projection of localized climate impacts, optimization of survey designs, designation of essential fish habitat, and multi-model inference regarding fishery status and productivity. We discuss each of these in detail below.

4.1 Projecting climate impacts

Globally, marine heatwaves of anomalously warm conditions are increasing in frequency and strength (Hobday *et al.* 2016a). Climate-driven changes to the survival and distribution of species are have also been well documented (Pinsky *et al.* 2013; Alabia *et al.* 2018; Morley *et al.* 2018). Rapid reorganization of food webs, novel interactions, and shifting spatial distributions confound traditional assessment methods that do not consider unidirectional change or non-stationarity in environmental drivers of mortality, selectivity, and growth (Skern-Mauritzen *et al.* 2015; Pinsky *et al.* 2018). As such, future short-term forecasts and long-term projections of many fish stocks will likely require models that include climate-driven changes to spatial distributions and species interactions (Deyle *et al.* 2016; Hobday *et al.* 2016b, 2018; Tommasi *et al.* 2017). Spatially-explicit MICE models such as the one presented here represent a potential tool for managing fisheries under changing conditions, as they can be used to forecast changes in

521 spatial distribution while accounting for species interactions (Howell and Filin 2014).
522 Presumably, skillful forecasting over longer time-horizons (e.g., >10 years) will require
523 including incorporating physiological and other mechanistic processes (Hollowed *et al.* 2009;
524 Payne *et al.* 2017); we recommend future research to explore including density covariates
525 representing changes in thermal niche, as well as the effect of regional oceanographic variables
526 (Thorson 2019) within MICE-in-space models.

527 **4.2 Optimizing survey designs**

528 In addition to potential conflict between governments (Pinsky *et al.* 2018), changing spatial
529 distributions due to climate change complicates fisheries management because historical survey
530 operations and methods may no longer cover the range of important fish populations (Karp *et al.*
531 In press). For example, walleye pollock and Pacific cod in the Bering Sea are enormously
532 productive and valuable fisheries, and both shifted northward out of the historically surveyed
533 area between 2010 and 2017 (Stevenson and Lauth 2019). Fisheries science and management
534 agencies therefore face a difficult task of funding existing resource surveys versus developing
535 new surveys in response to changes in resource distribution and productivity. Existing fishery-
536 independent surveys are often very expensive (e.g., approximately $1 million US for vessel time
537 alone for the 130 bottom trawl stations in the northern Bering Sea in 2017) and agencies face
538 trade-offs between decreased survey sample sizes or frequency in existing surveys vs. extending
539 surveys to new areas. The trade-off between maintaining existing surveys and developing new
540 ones would ideally be informed by scientific methods that condition upon available data and
541 incorporate known and/or hypothesized forms of spatial, temporal, and sampling variation (e.g.,
542 Reich *et al.* 2018). Similarly, changing ocean use (e.g., offshore energy development) can
543 impact survey design, and it would be helpful to understand likely impacts of these

544 developments on existing survey performance. We therefore recommend future research using a
545 MICE-in-space model for survey evaluation and optimization, whereby a MICE-in-space
546 operating model is fitted to available historical data for interacting species (given their historical
547 fishing mortality rates) to generate simulated sampling data under alternative potential sampling
548 designs. Each simulated data set could then be fitted by each sampling design, and the average
549 performance (e.g., standard error when estimating an index of abundance, or the strength of
550 species interactions) could be calculated across all simulation replicates. This method would
551 represent an objective process to evaluate alternative configurations of limited sampling effort,
552 and could presumably result in more efficient use of limited agency sampling, although it would
553 be unlikely to capture the additional value of sampling data under environmental conditions that
554 have not previously been observed.

555 **4.3 Designation of essential fish habitat**

556 Fisheries managers use a wide array of spatial management tools in addition to regulations on
557 fishery catch, effort, timing, and gear. In the US, fisheries management councils are required to
558 update designations of essential fish habitat (EFH) and habitat areas of particular concern
559 (HAPC) every five years. These designations can be done using species distribution models,
560 SDMs (Rooper *et al.* 2016), and the MICE-in-space is a generalization of these models that
561 additionally includes fishery harvest, species co-occurrence, and biological interactions. We
562 note that the US national EFH program defines four levels of EFH model (NMFS 2010;
563 Lederhouse *et al.* 2017), ranging from low (Levels 1-2: population distribution and density) to
564 high (Levels 3-4: spatial variation in demographic rates and overall productivity). Within this
565 classification, a MICE-in-space reconstructs spatial variation in productivity from survey
566 biomass and fishery removals, and therefore represents the highest-level basis for designating

EFH. Unlike previous EFH models, however, the MICE-in-space estimates temporal variability in species distribution, density, and productivity, driven by both species interactions, fishing, and residual spatio-temporal variation. Temporal variability has not been extensively addressed in EFH models or processes in the US, although we note that EFH-designations are already updated every 5 years and could be designated using five-year forecasts of productivity given forecasted environmental conditions. However, whether this time-varying designation of EFH and HAPC is acceptable to stakeholders and fisheries managers will of course depend upon many local and non-technical considerations including: available human resources; management priorities; and previous regional approaches to EFH designation (Copps *et al.* 2007).

4.4 Multi-model inference regarding status and productivity

Non-spatial climate-enhanced multispecies models (Holsman *et al.* 2016b), and climate-enhanced single-species models (Spencer *et al.* 2016; Barbeaux *et al.* 2017) are increasingly evaluated for Alaskan stocks impacted by anomalously warm conditions in the North Pacific. Balancing model complexity and mechanistic detail with computational demand, data compilation, and ease of interpretation of results is an ongoing challenge, especially for models that require multiple data sources and types (Plagányi *et al.* 2011). Stepwise hierarchical selection approaches for narrowing the focal components for forecasting risk can help balance demands and costs in computing, and identify key attributes to be evaluated in MICE models, which are intermediate in complexity but represent highly quantitative approaches (Hobday *et al.* 2011; Holsman *et al.* 2017). Shifting spatial distributions and changing mortality rates (e.g., through predation or starvation) are often confounded in ecosystem models, and simultaneously addressing these two issues is a key goal in current ecosystem models in regions including the Bering Sea (e.g., Spencer *et al.* 2016). Underlying model structure and implicit versus explicit

590 treatment of environmental or trophic changes to a population becomes extremely important
591 when projecting models for management advice, especially on longer timescales (Lotze *et al.*
592 2019). Forecasting distribution and productivity using a wide range of models with different
593 structural assumptions (a.k.a. multi-model inference) can be used to identify sensitivities in
594 model specification and propagation of error (Kaplan *et al.* 2018; Spence *et al.* 2018; Pope *et al.*
595 2019). Examples of this multi-model approach to forecasting climate impacts include FISH-MIP
596 (Hobday *et al.* 2016b; Tittensor *et al.* 2018) and the Alaska Climate Change Integrated Modeling
597 project (ACLIM; Hollowed et al. submitted). We recommend further research regarding MICE-
598 in-space models when used within an ensemble of other models that have less spatial resolution
599 but more detailed submodels for population demography (e.g., age or size structure) or physical
600 drivers (e.g., linked to regional biophysical models, e.g., Hermann *et al.* (In press)).

601 **4.5 Future research**

602 We recommend several avenues for future research regarding MICE-in-space, including: (1)
603 incorporating prior information regarding species interactions; (2) fitting to fishery catches; (3)
604 incorporating density covariates; and (4) comparison with alternative ecosystem models.

605 1. *Prior information regarding species interactions*: In this paper, we have freely estimated
606 species interactions given information in survey data. However, analysts could seek to
607 incorporate prior information (e.g., from diet data or assumptions about bioenergetics), and
608 we envision two ways to do so. First, analysts could "hardwire" the interaction matrix, either
609 eliminating some interactions a priori (e.g., Rochet *et al.* 2011) or such that it matches
610 specified values for single-species intrinsic growth rates and per-capita consumption rates.
611 Alternatively, analysts might specify a Bayesian prior on these values while using available

612 data. The latter would require additional statistical research, but would allow analysts to
613 integrate diet analyses while retaining the computational flexibility of the current study.
614 2. *Fitting to fishery catches*: In this paper, we have pre-specified a fishing mortality rate for
615 each species that varies among years but is constant across space, and this has driven
616 interannual variation in status relative to estimated biological reference points. We again see
617 two ways to relax this assumption. First, analysts could specify spatial variation in fishing
618 mortality, such that forecasts incorporate historical data regarding the spatial distribution of
619 fishing effort. Alternatively, analysts could specify spatial variation in fishery catch or
620 landings (obtained from fishery observers or other reporting). Specifying fishery catch for
621 each species, location, and year would require estimating fishing mortality rates as a model
622 parameter, but this specification would still be "separable" and previous exploration suggests
623 that this could be done while still being computationally feasible. Neither of these options
624 are currently available in the R package VAST used here, but both could be added during
625 future developments.
626 3. *Incorporating density covariates*: Forecasting climate impacts is a growing concern for
627 identifying suitable management strategies (Miller *et al.* 2010; Holsman *et al.* 2019a).
628 Covariates explaining historical variation in density will improve predictive skill for short-
629 term forecasts in some cases and not others (Hobday *et al.* 2018; Thorson 2019a), so we
630 encourage future skill-testing to measure the potential benefits of incorporating multi-species
631 interactions, density covariates, and species associations for forecasting distribution shifts
632 over short (<3 year) or longer time-horizons.
633 4. *Comparison with alternative ecosystem models*: Perhaps most importantly, we recommend
634 detailed, side-by-side comparison of MICE-in-space and other ecosystem models. These

comparisons are vital to identify the relative computational and human-resource costs of these different models, as well as identify when models provide different advice (Kaplan *et al.* 2018; Pope *et al.* 2019). However, this topic would require substantial additional effort and is an obvious topic for future research.

The MICE-in-space is publicly available in the R package *VAST*, which is already used for stock assessment and ecosystem status reports in the North Pacific (Thorson 2019b). We anticipate that public access and ongoing documentation for this implementation of a "MICE-in-space" model will facilitate future model comparisons. We hope that it will facilitate the use of multispecies models for spatial management including climate forecasts, survey optimization, and EFH designation.

Data Availability Statement

All data used are publicly available and hosted by the Alaska Fisheries Science Center. Survey data can be accessed online at http://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm and records of fishing mortality are online at https://www.afsc.noaa.gov/REFM/Stocks/SARA/sara_access.php. The R package VAST is available at https://github.com/James-Thorson/VAST/.

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References

Alabia, I.D., García Molinos, J., Saitoh, S.-I., Hirawake, T., Hirata, T. and Mueter, F.J. (2018) Distribution shifts of marine taxa in the Pacific Arctic under contemporary climate changes. *Diversity and Distributions*, 1–15. doi:10.1111/ddi.12788.

A'mar, Z.T., Punt, A.E. and Dorn, M.W. (2010) Incorporating ecosystem forcing through predation into a management strategy evaluation for the Gulf of Alaska walleye pollock (Theragra chalcogramma) fishery. *Fisheries Research* **102**, 98–114. doi:10.1016/j.fishres.2009.10.014.

Barbeaux, S., Aydin, K., Fissel, B., et al. (2017) Assessment of the Pacific cod stock in the Gulf of Alaska. *NPFMC Gulf of Alaska SAFE*, 183–326.

Begley, J. and Howell, D. (2004) An overview of Gadget, the globally applicable area-disaggregated general ecosystem toolbox.ICES.

Berger, A.M., Goethel, D.R., Lynch, P.D., Quinn, T., Mormede, S., McKenzie, J. and Dunn, A. (2017) Space oddity: The mission for spatial integration. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 1698–1716. doi:10.1139/cjfas-2017-0150.

Burnham, K.P. and Anderson, D. (2002) *Model Selection and Multi-Model Inference*, 2nd edn. Springer, New York.

Certain, G., Barraquand, F. and Gårdmark, A. (2018) How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution* **9**, 1975–1995. doi:10.1111/2041-210X.13021.

Christensen, V. and Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109–139. doi:10.1016/j.ecolmodel.2003.09.003.

Collie, J.S., Botsford, L.W., Hastings, A., et al. (2016) Ecosystem models for fisheries management: Finding the sweet spot. *Fish and Fisheries* **17**, 101–125. doi:10.1111/faf.12093.

Collie, J.S. and Gislason, H. (2001) Biological reference points for fish stocks in a multispecies context. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2167–2176.

Copps, S.L., Yoklavich, M.M., Parkes, G.B., et al. (2007) Applying marine habitat data to fishery management on the US West Coast: Initiating a policy-science feedback loop. *Mapping the seafloor for habitat characterization. Geol. Assoc. Can. Spec. Pap* **47**, 451–462.

Cressie, N. and Wikle, C.K. (2011) *Statistics for spatio-temporal data*. John Wiley & Sons, Hoboken, New Jersey.

Deyle, E.R., May, R.M., Munch, S.B. and Sugihara, G. (2016) Tracking and forecasting ecosystem interactions in real time. *Proceedings of the Royal Society B: Biological Sciences* **283**. doi:10.1098/rspb.2015.2258.

Dolan, T.E., Patrick, W.S. and Link, J.S. (2016) Delineating the continuum of marine ecosystem-based management: a US fisheries reference point perspective. *ICES Journal of Marine Science: Journal du Conseil* **73**, 1042–1050. doi:10.1093/icesjms/fsv242.

Dolder, P.J., Thorson, J.T. and Minto, C. (2018) Spatial separation of catches in highly mixed fisheries. *Scientific Reports* **8**, 13886. doi:10.1038/s41598-018-31881-w.

Engle, R.F. and Granger, C.W. (1987) Co-integration and error correction: representation, estimation, and testing. *Econometrica: journal of the Econometric Society*, 251–276.

Foster, S.D. and Bravington, M.V. (2013) A Poisson–Gamma model for analysis of ecological non-negative continuous data. *Environmental and Ecological Statistics* **20**, 533–552. doi:10.1007/s10651-012-0233-0.

Fu, C., Olsen, N., Taylor, N., et al. (2017) Spatial and temporal dynamics of predator-prey species interactions off western Canada. *ICES Journal of Marine Science* **74**, 2107–2119. doi:10.1093/icesjms/fsx056.

Fuglstad, G.-A., Lindgren, F., Simpson, D. and Rue, H. avard (2015) Exploring a new class of non-stationary spatial Gaussian random fields with varying local anisotropy. *Statistica Sinica*, 115–133.

Fulton, E.A., Link, J.S., Kaplan, I.C., et al. (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* **12**, 171–188. doi:10.1111/j.1467-2979.2011.00412.x.

Gabriel, W.L. and Mace, P.M. (1999) A review of biological reference points in the context of the precautionary approach. In: *Proceedings of the fifth national NMFS stock assessment workshop: providing scientific advice to implement the precautionary approach under the Magnuson-Stevens fishery conservation and management act. NOAA Tech Memo NMFS-F/SPO-40*. pp 34–45.

Gaichas, Aydin, K. and Francis, R.C. (2015) Wasp waist or beer belly? Modeling food web structure and energetic control in Alaskan marine ecosystems, with implications for fishing and environmental forcing. *Progress in Oceanography* **138**, 1–17. doi:10.1016/j.pocean.2015.09.010.

Gaichas, S.K., Aydin, K.Y. and Francis, R.C. (2010) Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1490–1506. doi:10.1139/F10-071.

Heithaus, M.R., Frid, A., Wirsing, A.J., et al. (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology* **76**, 837–844. doi:10.1111/j.1365-2656.2007.01260.x.

Hermann, A.J., Gibson, G.A., Cheng, W., et al. (In press) Projected biophysical conditions of the Bering Sea to 2100 under multiple emission scenarios. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsz043.

Hobday, A.J., Alexander, L. V., Perkins, S.E., et al. (2016a) A hierarchical approach to defining marine heatwaves. *Progress in Oceanography* **141**, 227–238. doi:10.1016/j.pocean.2015.12.014.

Hobday, A.J., Cochrane, K., Downey-Breedt, N., et al. (2016b) Planning adaptation to climate change in fast-warming marine regions with seafood-dependent coastal communities. *Reviews in Fish Biology and Fisheries* **26**, 249–264. doi:10.1007/s11160-016-9419-0.

Hobday, A.J., Smith, A.D.M., Stobutzki, I.C., et al. (2011) Ecological risk assessment for the effects of fishing. *Fisheries Research* **108**, 372–384. doi:10.1016/j.fishres.2011.01.013.

Hobday, A.J., Spillman, C.M., Eveson, J.P., Hartog, J.R., Zhang, X. and Brodie, S. (2018) A Framework for Combining Seasonal Forecasts and Climate Projections to Aid Risk Management for Fisheries and Aquaculture. *Frontiers in Marine Science* **5**, 1–9. doi:10.3389/fmars.2018.00137.

Hollowed, A. (2000) Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science* **57**, 707–719. doi:10.1006/jmsc.2000.0734.

Hollowed, A.B., Barange, M., Beamish, R.J., et al. (2013) Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science* **70**, 1023–1037. doi:10.1093/icesjms/fst081.

Hollowed, A.B., Bond, N.A., Wilderbuer, T.K., et al. (2009) A framework for modelling fish and shellfish responses to future climate change. *ICES Journal of Marine Science* **66**, 1584–1594. doi:10.1093/icesjms/fsp057.

Holsman, K., Samhouri, J., Cook, G., et al. (2017) An ecosystem-based approach to marine risk assessment. *Ecosystem Health and Sustainability* **3**, e01256. doi:10.1002/ehs2.1256.

Holsman, K.K., Hazen, E.L., Haynie, A., et al. (2019a) Towards climate resiliency in fisheries management. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsz031.

Holsman, K.K., Ianelli, J., Aydin, K., Punt, A.E. and Moffitt, E.A. (2016b) A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species

climate-enhanced stock assessment models. *Deep Sea Research Part II: Topical Studies in Oceanography*. doi:10.1016/j.dsr2.2015.08.001.

Howell, D. and Filin, A.A. (2014) Modelling the likely impacts of climate-driven changes in cod-capelin overlap in the Barents Sea. *ICES Journal of Marine Science* **71**, 72–80. doi:10.1093/icesjms/fst172.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., et al. (2011) Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology Letters* **14**, 1288–1299. doi:10.1111/j.1461-0248.2011.01696.x.

Ives, A.R., Dennis, B., Cottingham, K.L. and Carpenter, S.R. (2003) Estimating community stability and ecological interactions from time-series data. *Ecological monographs* **73**, 301–330.

Kaplan, I.C., Francis, T.B., Punt, A.E., et al. (2018) A multi-model approach to understanding the role of Pacific sardine in the California Current food web. *Marine Ecology Progress Series*.

Karp, M.A., Peterson, J.O., Lynch, P.D., et al. (In press) Accounting for shifting distributions and changing productivity in the development of scientific advice for fishery management. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsz048.

Kass, R.E. and Steffey, D. (1989) Approximate bayesian inference in conditionally independent hierarchical models (parametric empirical bayes models). *Journal of the American Statistical Association* **84**, 717–726. doi:10.2307/2289653.

Kempf, A., Huse, G., Dingsør, G., Floeter, J. and Temming, A. (2010) The importance of overlap – predicting North Sea cod recovery with a multi species fisheries assessment model. *ICES Journal of Marine Science* **67**, 1989–1997.

Kinzey, D. and Punt, A.E. (2009) Multispecies and Single-Species Models of Fish Population Dynamics: Comparing Parameter Estimates. *Natural Resource Modeling* **22**, 67–104. doi:10.1111/j.1939-7445.2008.00030.x.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H. and Bell, B.M. (2016) TMB: Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software* **70**, 1–21. doi:10.18637/jss.v070.i05.

Kristensen, K., Thygesen, U.H., Andersen, K.H. and Beyer, J.E. (2014) Estimating spatio-temporal dynamics of size-structured populations. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 326–336. doi:10.1139/cjfas-2013-0151.

Lassen, H., Pedersen, S.A., Frost, H. and Hoff, A. (2013) Fishery management advice with ecosystem considerations. *ICES Journal of Marine Science* **70**, 471–479. doi:10.1093/icesjms/fss208.

Lindgren, F. and Rue, H. (2013) Bayesian spatial and spatiotemporal modelling with r-inla. *Journal of Statistical Software*.

Livingston, P.A., Aydin, K., Buckley, T.W., Lang, G.M., Yang, M.-S. and Miller, B.S. (2017) Quantifying food web interactions in the North Pacific – a data-based approach. *Environmental Biology of Fishes* **100**, 443–470. doi:10.1007/s10641-017-0587-0.

Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., et al. (2019) Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences* **116**, 12907–12912. doi:10.1073/pnas.1900194116.

Mackinson, S., Platts, M., Garcia, C. and Lynam, C. (2018) Evaluating the fishery and ecological consequences of the proposed North Sea multi-annual plan. *PLOS ONE* **13**, e0190015. doi:10.1371/journal.pone.0190015.

Magnusson, A. and Hilborn, R. (2007) What makes fisheries data informative? *Fish and Fisheries* **8**, 337–358.

Magnusson, A., Punt, A.E. and Hilborn, R. (2013) Measuring uncertainty in fisheries stock assessment: the delta method, bootstrap, and MCMC. *Fish and Fisheries* **14**, 325–342.

Marshall, K.N., Duffy-Anderson, J.T., Ward, E.J., Anderson, S.C., Hunsicker, M.E. and Williams, B.C. (2019) Long-term trends in ichthyoplankton assemblage structure, biodiversity, and synchrony in the

Gulf of Alaska and their relationships to climate. *Progress in Oceanography* **170**, 134–145. doi:10.1016/j.pocean.2018.11.002.
Miller, K., Charles, A., Barange, M., et al. (2010) Climate change, uncertainty, and resilient fisheries: Institutional responses through integrative science. *Progress in Oceanography* **87**, 338–346. doi:10.1016/j.pocean.2010.09.014.
Moffitt, E.A., Punt, A.E., Holsman, K., Aydin, K.Y., Ianelli, J.N. and Ortiz, I. (2016) Moving towards ecosystem-based fisheries management: Options for parameterizing multi-species biological reference points. *Deep Sea Research Part II: Topical Studies in Oceanography* **134**, 350–359. doi:10.1016/j.dsr2.2015.08.002.
Morley, J.W., Selden, R.L., Latour, R.J., Frölicher, T.L., Seagraves, R.J. and Pinsky, M.L. (2018) Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLoS ONE* **13**, 1–28. doi:10.1371/journal.pone.0196127.
Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S. and Link, J.S. (2016) Ecosystem Model Skill Assessment. Yes We Can! *PLOS ONE* **11**, e0146467. doi:10.1371/journal.pone.0146467.
Ortiz, I., Aydin, K., Hermann, A.J., et al. (2016) Climate to fish: Synthesizing field work, data and models in a 39-year retrospective analysis of seasonal processes on the eastern Bering Sea shelf and slope. *Deep-Sea Research Part II: Topical Studies in Oceanography* **134**, 390–412. doi:10.1016/j.dsr2.2016.07.009.
Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B.-E. and Abrego, N. (2017) How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proc. R. Soc. B* **284**, 20170768. doi:10.1098/rspb.2017.0768.
Payne, M.R., Hobday, A.J., MacKenzie, B.R., et al. (2017) Lessons from the First Generation of Marine Ecological Forecast Products. *Frontiers in Marine Science* **4**. doi:10.3389/fmars.2017.00289.
Pikitch, E.K., Rountos, K.J., Essington, T.E., et al. (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* **15**, 43–64. doi:10.1111/faf.12004.
Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. and Levin, S.A. (2013) Marine taxa track local climate velocities. *Science* **341**, 1239–1242. doi:10.1126/science.1239352.
Plagányi, É.E. (2007) *Models for an ecosystem approach to fisheries*. Food & Agriculture Org.
Plagányi, É.E., Bell, J.D., Bustamante, R.H., et al. (2011) Modelling climate-change effects on Australian and Pacific aquatic ecosystems: a review of analytical tools and management implications. *Marine and Freshwater Research* **62**, 1132–1147. doi:10.1071/MF10279.
Plagányi, É.E. and Butterworth, D.S. (2012) The Scotia Sea krill fishery and its possible impacts on dependent predators: Modeling localized depletion of prey. *Ecological Applications* **22**, 748–761. doi:10.1890/11-0441.1.
Plagányi, É.E., Punt, A.E., Hillary, R., et al. (2014) Multispecies fisheries management and conservation: Tactical applications using models of intermediate complexity. *Fish and Fisheries* **15**, 1–22. doi:10.1111/j.1467-2979.2012.00488.x.
Pollock, L.J., Tingley, R., Morris, W.K., et al. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* **5**, 397–406. doi:10.1111/2041-210X.12180.
Pope, J.G., Bartolino, V., Kulatska, N., et al. (2019) Comparing the steady state results of a range of multispecies models between and across geographical areas by the use of the jacobian matrix of yield on fishing mortality rate. *Fisheries Research* **209**, 259–270. doi:10.1016/j.fishres.2018.08.011.
R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, B.J., Pacifici, K. and Stallings, J.W. (2018) Integrating auxiliary data in optimal spatial design for species distribution modelling. *Methods in Ecology and Evolution* **9**, 1626–1637. doi:10.1111/2041-210X.13002.

Reum, J.C.P., Blanchard, J.L., Holsman, K.K., Aydin, K. and Punt, A.E. (2019) Species-specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. *Oikos* **0**. doi:10.1111/oik.05630.

Rochet, M.-J., Collie, J.S., Jennings, S. and Hall, S.J. (2011) Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 469–486. doi:10.1139/F10-159.

Rooper, C.N., Sigler, M.F., Goddard, P., et al. (2016) Validation and improvement of species distribution models for structure-forming invertebrates in the eastern Bering Sea with an independent survey. *Marine Ecology Progress Series* **551**, 117–130. doi:10.3354/meps11703.

Schliep, E.M., Lany, N.K., Zarnetske, P.L., Schaeffer, R.N., Orians, C.M., Orwig, D.A. and Preisser, E.L. (2018) Joint species distribution modelling for spatio-temporal occurrence and ordinal abundance data. *Global Ecology and Biogeography* **27**, 142–155. doi:10.1111/geb.12666.

Shin, Y.-J. and Cury, P. (2001) Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquatic Living Resources* **14**, 65–80. doi:10.1016/S0990-7440(01)01106-8.

Skaug, H. and Fournier, D. (2006) Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. *Computational Statistics & Data Analysis* **51**, 699–709.

Spence, M.A., Blanchard, J.L., Rossberg, A.G., et al. (2018) A general framework for combining ecosystem models. *Fish and Fisheries* **19**, 1031–1042. doi:10.1111/faf.12310.

Spencer, P.D., Holsman, K.K., Zador, S., Bond, N.A., Mueter, F.J., Hollowed, A.B. and Ianelli, J.N. (2016) Modelling spatially dependent predation mortality of eastern Bering Sea walleye pollock, and its implications for stock dynamics under future climate scenarios. *ICES Journal of Marine Science: Journal du Conseil* **73**, 1330–1342. doi:10.1093/icesjms/fsw040.

Spies, I., Aydin, K., Ianelli, J.N. and Palsson, W. (2017) 7. Assessment of the arrowtooth flounder stock in the Gulf of Alaska. In: *Stock assessment and fishery evaluation report for the groundfish fisheries of the Gulf of Alaska.* North Pacific Fishery Management Council, Seattle, WA, pp 743–840.

Stevenson, D.E. and Lauth, R.R. (2019) Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. *Polar Biology* **42**, 407–421. doi:10.1007/s00300-018-2431-1.

Thorson, J.T. (2019a) Forecast skill for predicting distribution shifts: A retrospective experiment for marine fishes in the Eastern Bering Sea. *Fish and Fisheries* **20**, 159–173. doi:10.1111/faf.12330.

Thorson, J.T. (2019b) Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. *Fisheries Research* **210**, 143–161. doi:10.1016/j.fishres.2018.10.013.

Thorson, J.T. (2019) Measuring the impact of oceanographic indices on species distribution shifts: The spatially varying effect of cold-pool extent in the eastern Bering Sea. *Limnology and Oceanography* **0**. doi:10.1002/lno.11238.

Thorson, J.T. (2018) Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1369–1382. doi:10.1139/cjfas-2017-0266.

Thorson, J.T. and Barnett, L.A.K. (2017) Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES Journal of Marine Science* **74**, 1311–1321. doi:10.1093/icesjms/fsw193.

Thorson, J.T., Ianelli, J.N., Larsen, E.A., Ries, L., Scheuerell, M.D., Szuwalski, C. and Zipkin, E.F. (2016) Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring. *Global Ecology and Biogeography* **25**, 1144–1158. doi:10.1111/geb.12464.

Thorson, J.T. and Kristensen, K. (2016) Implementing a generic method for bias correction in statistical models using random effects, with spatial and population dynamics examples. *Fisheries Research* **175**, 66–74. doi:10.1016/j.fishres.2015.11.016.

Thorson, J.T., Munch, S.B. and Swain, D.P. (2017) Estimating partial regulation in spatiotemporal models of community dynamics. *Ecology* **98**, 1277–1289. doi:10.1002/ecy.1760.

Tittensor, D.P., Eddy, T.D., Lotze, H.K., et al. (2018) A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1.0. *Geoscientific Model Development* **11**, 1421–1442. doi:10.5194/gmd-11-1421-2018.

Tommasi, D., Stock, C.A., Hobday, A.J., et al. (2017) Managing living marine resources in a dynamic environment: The role of seasonal to decadal climate forecasts. *Progress in Oceanography* **152**, 15–49. doi:10.1016/j.pocean.2016.12.011.

Van Kirk, K.F., Quinn, T.J. and Collie, J.S. (2010) A multispecies age-structured assessment model for the Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1135–1148. doi:10.1139/F10-053.

Von Szalay, P.G. and Raring, N.W. (2016) Data report: 2015 Gulf of Alaska bottom trawl survey. NMFS-AFSC-325. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA.

Walters, C.J., Christensen, V., Martell, S.J. and Kitchell, J.F. (2005) Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES Journal of Marine Science* **62**, 558–568. doi:10.1016/j.icesjms.2004.12.005.

Walther, Y.M. and Möllmann, C. (2014) Bringing integrated ecosystem assessments to real life: a scientific framework for ICES. *ICES Journal of Marine Science* **71**, 1183–1186. doi:10.1093/icesjms/fst161.

Wetzel, C.R., Cronin-Fine, L. and Johnson, K.F. (2017) Status of Pacific ocean perch (Sebastes alutus) along the US west coast in 2017. Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, WA.

925 Table 1 – Model selection among candidate models, showing the model name (see Section 2.3 in
926 main text for details), the marginal log-likelihood of the maximum likelihood estimate, the
927 number of fixed effects, and the Akaike Information Criterion score for each model (where the
928 most parsimonious model has $\Delta AIC = 0$ and models with $\Delta AIC < 3$ have some statistical
929 support (Burnham and Anderson 2002)

Model	Negative log-likelihood	Number of parameters	ΔAIC
Index standardization	142867.2	160	6.6
Complete density dependence	143019.9	56	103.9
Same density dependence	142971.6	57	9.3
Different density dependence	142964.4	60	1
Species interactions	142959.9	64	0

930

Table 2 – Estimated interactions from the "species interactions" model (listing standard errors in parentheses), specifically listing $\mathbf{B} - \mathbf{I}$ such that the element in the "arrowtooth" column and "Alaska pollock" row shows that a 1% increase in density for arrowtooth is estimated to cause a -0.07 decrease in per-capita productivity for Alaska pollock.

		Impact of a 1% increase in density of …			
		Arrowtooth	Alaska pollock	Pacific cod	Pacific halibut
… on per-capita productivity of …	Arrowtooth	-0.28 (0.06)	-0.05 (0.02)	-0.04 (0.03)	0.12 (0.06)
	Alaska pollock	-0.07 (0.06)	-0.32 (0.04)	0.03 (0.02)	-0.10 (0.07)
	Pacific cod	0.07 (0.04)	-0.05 (0.02)	-0.40 (0.04)	0.10 (0.06)
	Pacific halibut	0.06 (0.04)	-0.04 (0.02)	-0.03 (0.02)	-0.28 (0.07)

Fig. 1 – Total biomass for each species in each of five models (see legend in top-left panel for color codes and Appendix B for detailed model descriptions), as well as fishing mortality rate (black dashed line with scale on right-hand y-axis) for each species. Note that the "index standardization" (black dashed lines) and "complete density dependence" (grey solid lines) models predict biomass only in years with available data and are shown as lines with whiskers (+/- one standard error), while other models predict biomass in years without sampling and are shown as a shaded interval (+/- one standard error)

Fig. 2 – Biological reference points estimated by three MICE-in-space models (i.e., excluding the "index-standardization" and "complete density dependence" models which cannot estimate biological reference points), where b_{targ} is 40% of estimated biomass in the absence of fishing, and f_{targ} is the fishing mortality estimated to result in biomass equal to b_{targ} on average.

Fig. 3 – Estimates of the natural logarithm of biomass density from the AIC-selected "species interactions" model (red: high density; blue: low density) for each species (columns) in several years (rows), where the first year (top row) shows the estimate of unfished biomass. Years are chosen for illustration to be approximately even spaced but only using years with available survey data, and where the density legend is identical among species and years and has units $\ln(kg \cdot km^{-2})$

Fig. 4 – Estimated stock status (y-axis) for each year (x-axis), measured using a fishing intensity ratio (left column: $f_{ratio}(c,t)$) and biomass ratio ($b_{ratio}(c,t)$, see Eq. 11) for each species (rows) and the three MICE-in-space models that estimate biological reference points (see legend in bottom-right panel for color codes). Each panel shows the maximum likelihood estimate (central line) and ± 1 standard error (shaded area and outer lines), as well as the corresponding target (horizontal dotted line); note that y-axes differ between panels.

Fig. 5 – Illustration of simulation experiment, showing natural logarithm of unfished biomass density (1st and 2nd rows) and population density in 2015 (3rd and 4th rows) in units $\ln(kg \cdot km^{-2})$ for the two species included in the estimation model (columns), where the colorbar is shown in the bottom-right panel (red is high density and blue is low density). This illustration allows comparison of true simulated density (1st and 3rd rows) vs. estimated density (2nd and 4th rows) when simulating a new data set conditional on fixed effects estimated from real-world data. Note that the simulation model simulates density for four species at a fine spatial scale (using $n_x = 100$ knots), while the estimation model estimates density for only two species at a coarse spatial scale (using $n_x = 50$ knots). For visual clarity, we do not show

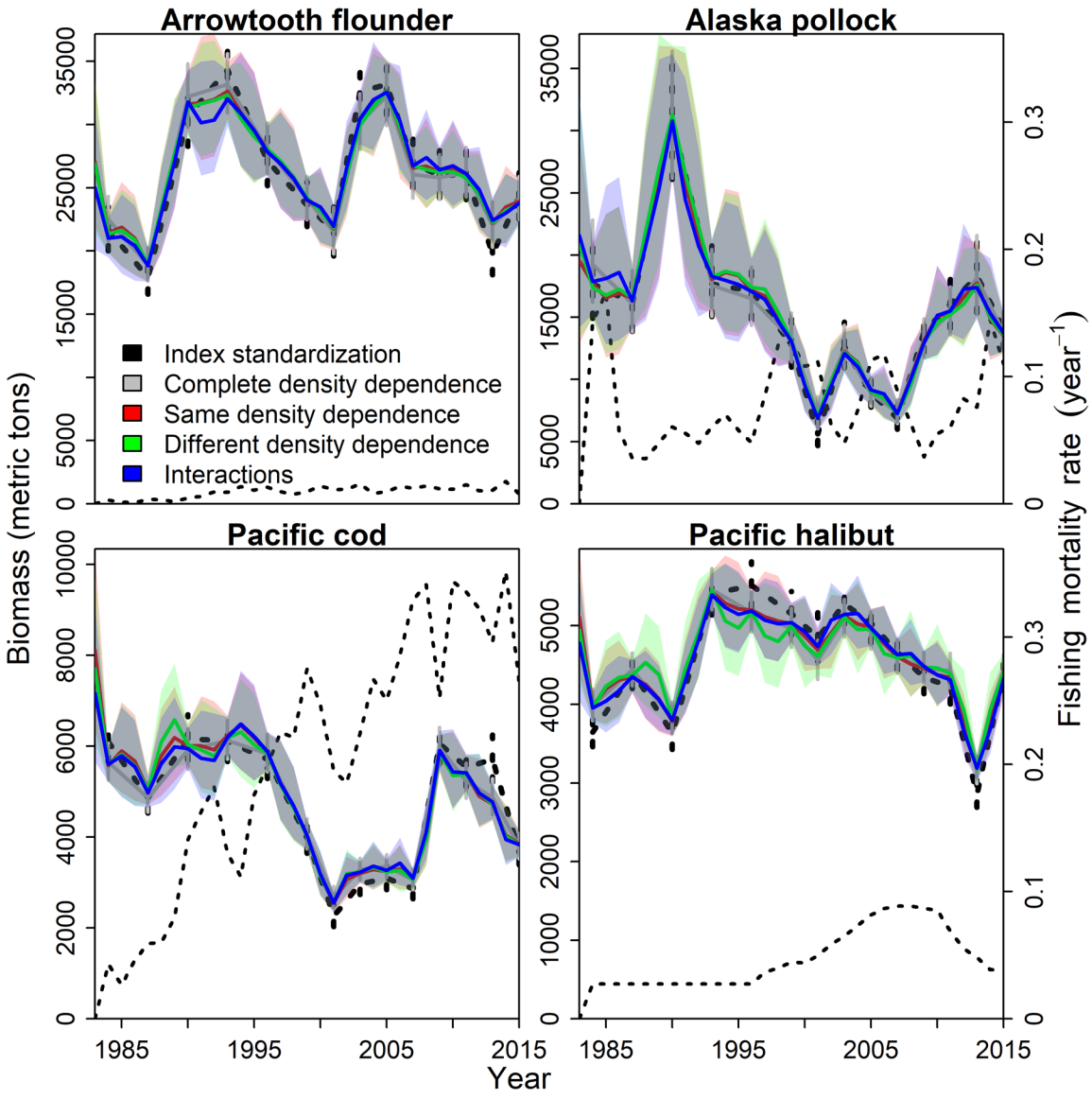
973 simulated density for the two species that are not then included in the estimation model for each
974 simulation replicate.

975

976 Fig. 6 – Illustration of results from a simulation experiment where each panel shows the
977 frequency distribution (y-axis) for different estimated values (x-axis), specifically showing
978 estimates of the interaction matrix **B** (Fig. 6A) or biological reference points including fishing
979 mortality resulting in 40% of average unfished biomass, $\mathbf{f}_{0.4}$ (Fig. 6B left column) or the relative
980 error in estimates of unfished biomass, $\mathbf{b}_{targ}$ (Fig. 6B, right column) from a simulation
981 experiment generating data based on the AIC-selected "species interactions" model, and then
982 restricting data to two species (arrowtooth and Alaska pollock) and fitting at a coarse spatial
983 resolution (50 knots). Each panel in the visualization of the interaction matrix (Fig. 6A) shows a
984 histogram of estimates from each simulation replicate, where the true value is indicated by a
985 vertical dashed line and the mean and standard deviation of estimates is listed (see Table 2 for
986 true values). The visualization of biological reference points (Fig. 6B) similarly shows a
987 histogram of estimates and the true value, and again lists the mean and standard deviation of
988 estimates.

989

990 Fig. 1



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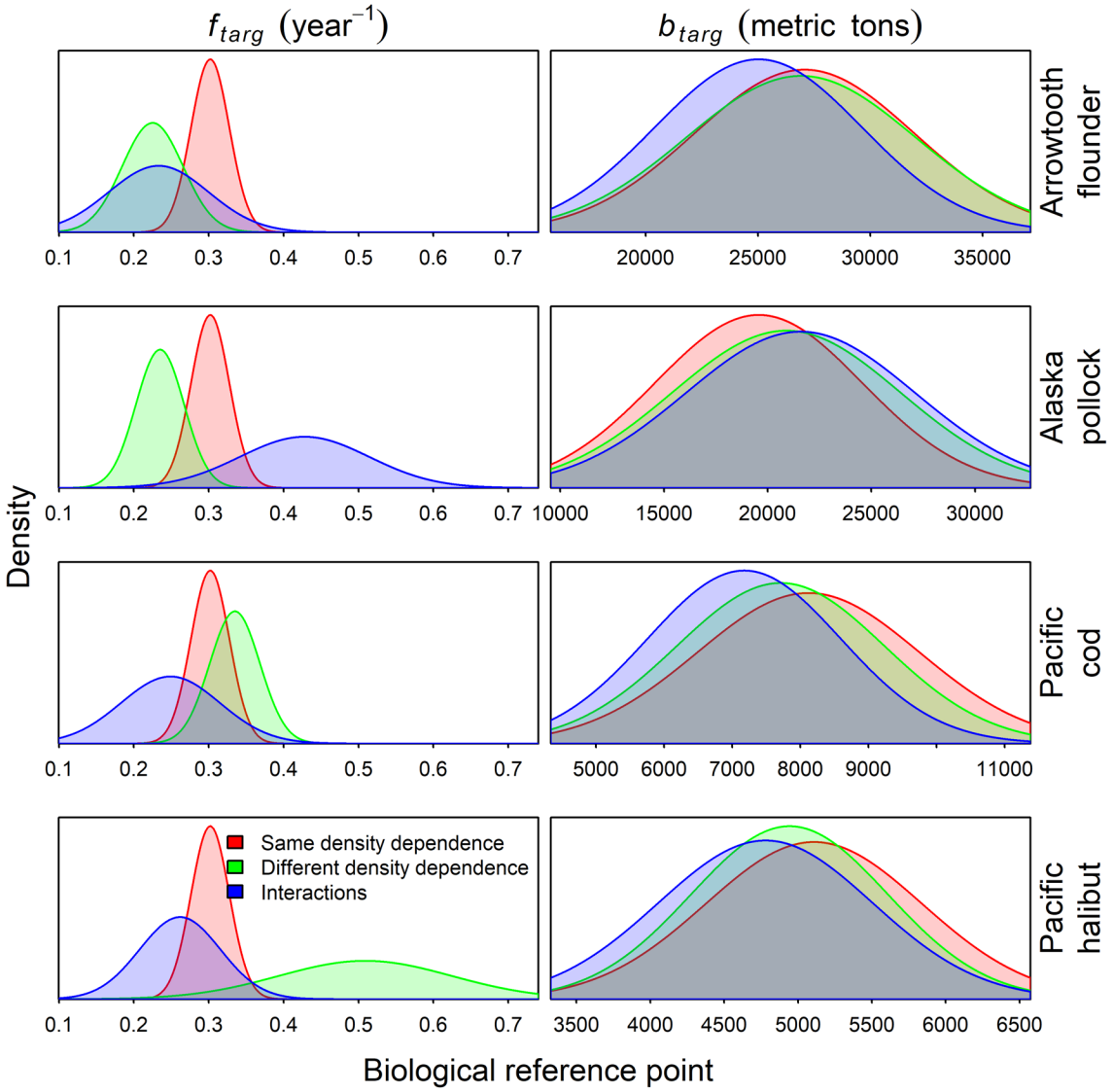
993 Fig. 2



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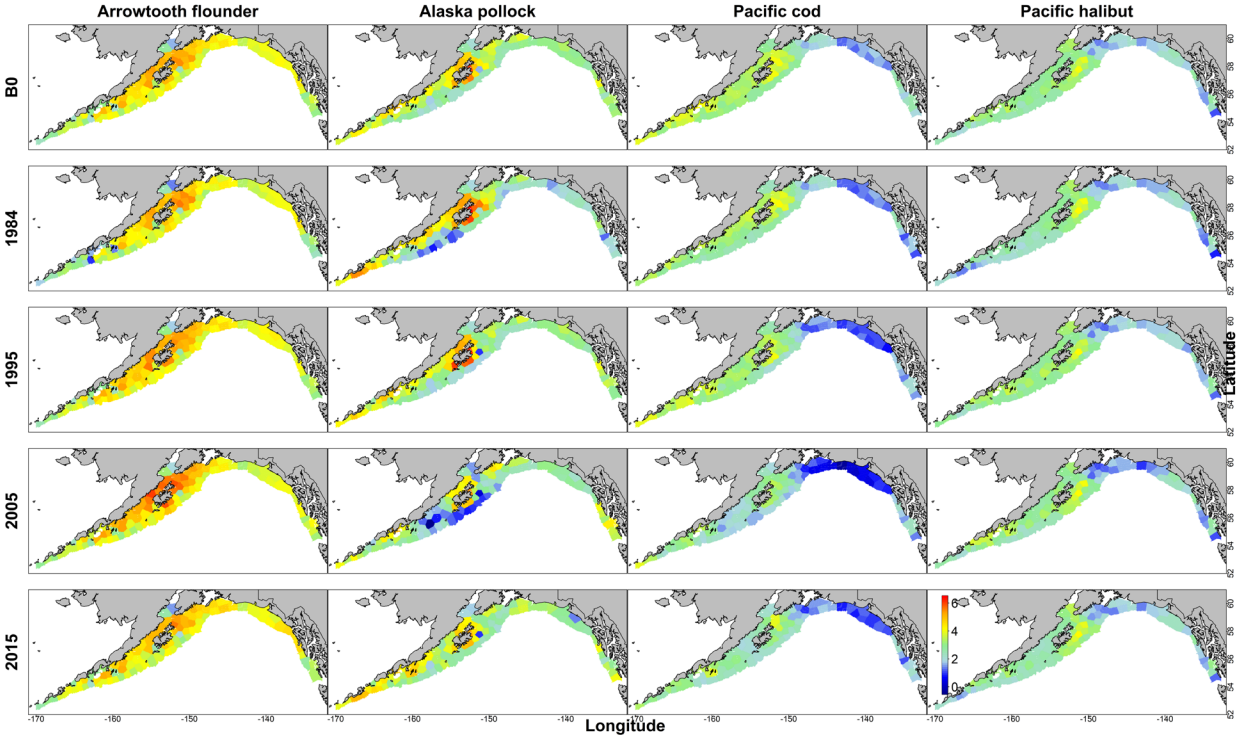
996 Fig. 3



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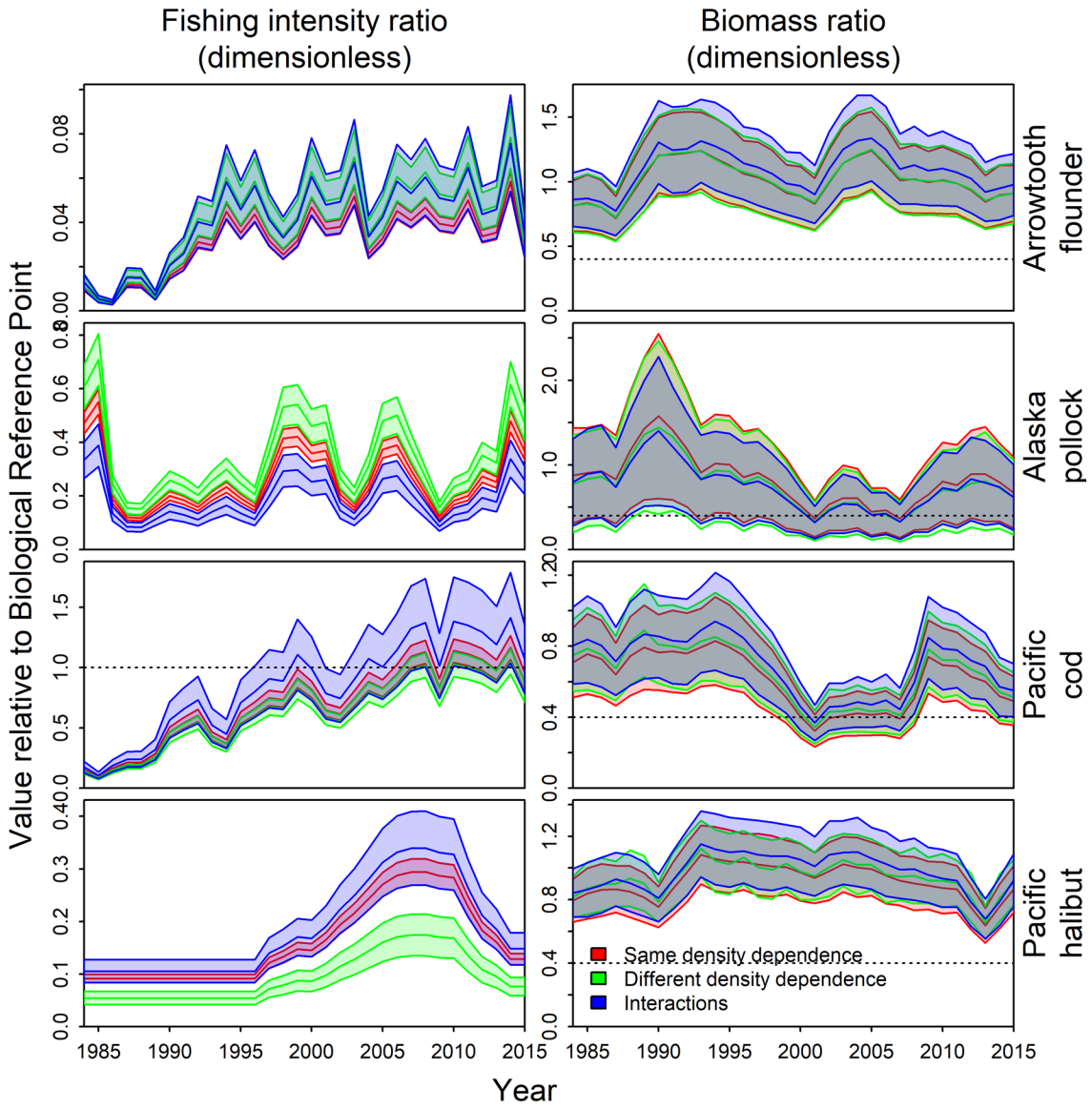
999 Fig. 4



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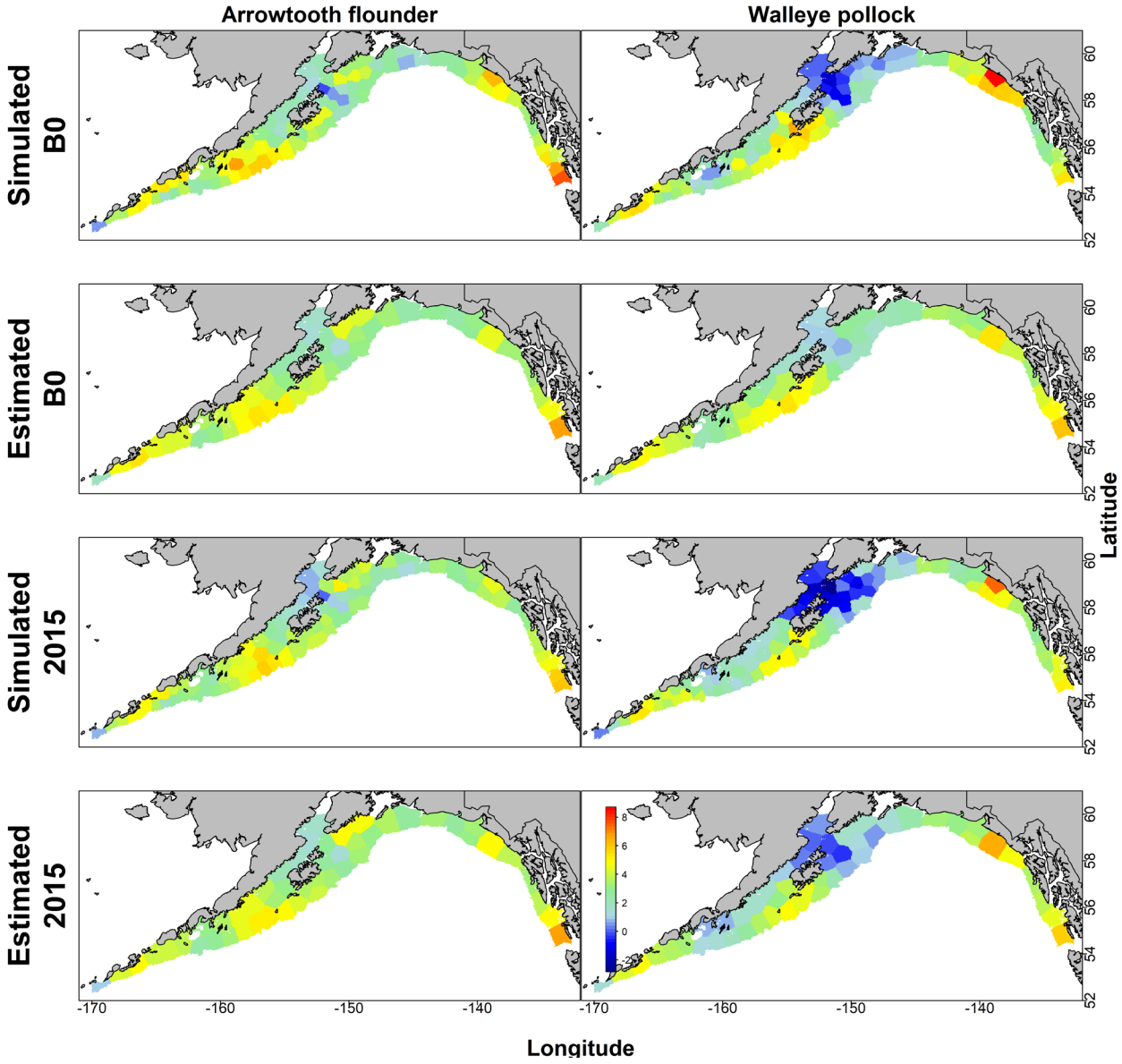
1002 Fig. 5



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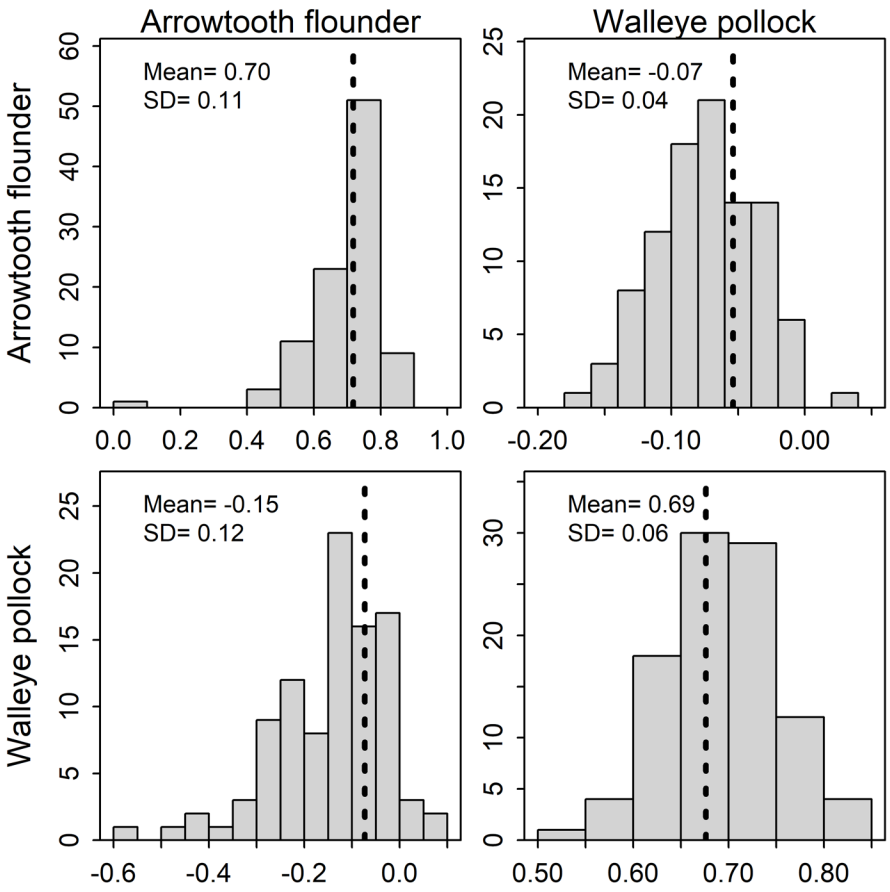
1005 Fig. 6



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