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**Spatial delay-difference models for estimating spatiotemporal variation in
juvenile production and population abundance**

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Abstract

Many important ecological questions require accounting for spatial variation in demographic rates (e.g., survival) and population variables (e.g., abundance per unit area). However, ecologists have few spatial modelling approaches that (1) fit directly to spatially referenced data, (2) represent population dynamics explicitly and mechanistically, and (3) estimate parameters using rigorous statistical methods. We therefore demonstrate a new and computationally efficient approach to spatial modelling, which uses random fields in place of the random variables typically used in spatially aggregated models. We adapt this approach to delay-difference dynamics to estimate the impact of fishing and natural mortality, recruitment, and somatic growth on spatial population dynamics for a fish population. In particular, we develop this approach to estimate spatial variation in expected production of juvenile fishes (termed recruitment), as well as annual variation in the spatial distribution of recruitment. We first use a simulation experiment to demonstrate that the spatial delay-difference model can in some cases explain over 50% of spatial variance in recruitment. We also apply the spatial delay-difference model to data for rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska from 1991 to 2011 and show that expected recruitment (across all years) is greatest near Kodiak Island, but that some years show greatest recruitment in southeast Alaska or the western Gulf of Alaska. Using model developments and software advances presented here, we argue that future research can develop models to approximate adult movement, incorporate spatial covariates to explain annual variation in recruitment, and evaluate management procedures that use spatially explicit estimates of population abundance.

Keywords: Gaussian random field; spatial variability; recruitment; Gulf of Alaska; delay-difference model; random function; spatial modelling; rex sole

Introduction

Ecologists are increasingly tasked with understanding how population and community dynamics vary spatially. Understanding spatial processes is necessary to predict many important phenomena, including the impact of global climate change on population distributions and productivity (Cheung et al. 2009), the impact of marine protected areas on population management and assessment (Field et al. 2006), and the role of dispersal in structuring life history trade-offs (Buoro and Carlson 2014). However, many classic ecological models (and associated ecological theories) are spatially aggregated, e.g., classical Lotka-Volterra predator-prey models, demonstrations of deterministic chaos (Sugihara and May 1990), and tests of density dependence (Pimm and Redfearn 1988). Research over at least twenty years has shown that spatial models often have radically different properties regarding community dynamics and species co-existence compared to aggregated models (Kareiva et al. 1990, Levin and Pacala 1997). Recent research has also shown that estimates of ecological processes (e.g., density dependence) can differ substantially between spatial and nonspatial models (Thorson et al. In press-b). Consequently, spatially aggregated modelling tools and ecological theories are unlikely to be sufficient for understanding and predicting many spatially motivated ecological questions (Ray and Hastings 1996).

As one example, marine ecologists have known for almost a century that fish population dynamics are marked by high variability in cohort strength, such that a population may be composed primarily of individuals born in a few "high productivity" years (Hjort 1926, Thorson et al. 2014). Cohort strength could arise from differences in the high daily mortality rates for young individuals, caused in turn from the spatial match or mismatch between juvenile fish, their prey, and their predators (Cushing 1990). In at least a few cases, cohort strength appears to vary

spatially at smaller spatial scales than the total population or meta-population range (Mueter et al. 2002, Field and Ralston 2005, Minto et al. 2014), and this has important implications for tests to detect or estimate density dependence (Hastings 1993, Ray and Hastings 1996). However, studies correlating cohort strength with environmental drivers generally relate spatially aggregated estimates of recruitment to average environmental measures through the population's range (e.g., Bailey et al. 2005).

Given the increasing emphasis on estimating and predicting spatial variation in dynamics (e.g., fish recruitment), ecologists have responded in several different ways. Many research projects have used spatial data to extract a time series (e.g., center of gravity for species distribution, or indices of total abundance) and then correlated the series with environmental signals to infer an environmental driver of population dynamics (Lehodey et al. 1997, Lindegren et al. 2013). Other projects have developed increasingly sophisticated agent-based models (Jørgensen et al. 2006), which generate predictions about spatial population and community dynamics given assumptions about individual rates and spatial data regarding environmental drivers. These models are generally parameterized using individual demographic rates, but rarely are parameters updated via the fit to spatially referenced survey data (although see Hartig et al. [2011] for suitable methods). Alternatively, ecologists have used sophisticated geographical analysis tools (e.g., in ArcGIS) to estimate single- or multi-species distributions, which can then used for management decisions that require spatial detail (Royle and Wikle 2005, Goetz et al. 2014). However, existing geostatistical modelling tools have relatively little capacity to include the demographic dynamics (i.e. length-based mortality rates, age-structured dynamics, individual growth rates, etc.) that are typically included in nonspatial models of marine populations.

In summary, there are, to our knowledge, few modelling approaches that can simultaneously: (#1) fit to spatially referenced survey data, while (#2) using explicit and mechanistic models for population dynamics, and (#3) using rigorous statistical machinery to estimate the parameters governing dynamics. For examples, a geostatistical approach to estimating species and community distributions will fit to spatial data (#1) using robust statistical methods (#3), but rarely has any detail regarding how dynamics will change over time due to mortality, individual growth, and recruitment rates (#2). Alternatively, stock assessment models with multiple spatial strata will have explicit dynamics (#2) and sophisticated parameter estimation (#3), but rarely fit directly to spatially referenced data (instead using derived summaries of spatial data like indices of abundance for each stratum). Finally, individual and agent-based models are developed using realistic mechanisms (#2), and tuned to fit available data (#1), but are rarely fitted to broad-scale data in a statistically robust manner.

We therefore seek to demonstrate a statistical approach that can satisfy all three expectations, i.e., fitting explicit and mechanistic models for population dynamics to spatially referenced data using rigorous statistical methods. We start by describing “random fields”, which provide a multivariate analogue to the “random variables” that are commonly used in nonspatial models. We then proceed by demonstrating how a delay-difference model (Schnute 1985) can be modified to include spatial variation in recruitment and resulting population densities. We use the delay-difference model because (1) it is a conventional model for approximating population dynamics of fishes, (2) it represents the simplest approach to age-structured population models, and hence shows that these concepts can be adapted to complicated model settings, and (3) it has relatively simple motivation and transparent assumptions. We conduct a short simulation-study to demonstrate that the spatial delay-difference model can provide accurate and precise estimates

of spatial variation in recruitment. Finally, we apply the model to a 21-year time series of spatially-referenced survey data for rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. This method may provide a way to improve on catch recommendations based on aggregate survey biomass estimates and assumptions about natural mortality and implicitly, fishery selectivity (Restrepo 1998, Anon. 2013).

Methods

Random fields: the bridge to spatial dynamical models

Two sources of variance are typically considered when fitting modern population models to data (Buckland et al. 2004, Royle and Dorazio 2008): process variation (i.e., variations in the underlying population dynamics) and observation errors (i.e., sampling and measurement errors). In some cases, only observation errors are considered in fitting models to data, such that the underlying state variables (i.e., population abundance) evolve deterministically over time. In contrast, state-space models account for both the process errors and the observation errors, and are increasingly used in marine and terrestrial ecology in recognition of the fact that we never perfectly understand the factors that contribute to ecological dynamics, nor can we perfectly measure the ecological state (i.e., abundance) at any time. State-space ecological models were developed over twenty years ago (Schnute 1991, Meyer and Millar 1999), and generally outperform deterministic models (which omit either process variability or measurement errors) when reconstructing historical states (i.e., abundance) or dynamical properties (de Valpine and Hastings 2002, Punt 2003, Ono et al. 2012). State-space models are derived by assuming that dynamics include a process error term:

$$x_{t+1} = f(x_t) + \varepsilon_t$$

where x_t is a population statistic (e.g., the logarithm of population abundance), $f(x_t)$ is a function that represents density-dependent and density-independent processes affecting expected change in the population statistic (e.g., survival, individual growth, and production of juveniles), and ε_t is a random variable representing the net contribution of unknown and nonstationary effects on dynamics:

$$\varepsilon_t \sim \text{Gaussian}(0, \sigma_\varepsilon^2)$$

where process variability is specified to have mean of zero and some estimated variance σ_ε^2 .

Spatial state-space models proceed by envisioning that, instead of summarizing the population statistic x_t as constant across space (e.g., total abundance in numbers), we instead track a population statistic \mathbf{X}_t (e.g., density defined as numbers per unit area) at every point in space $\langle x, y \rangle$ (where x and y could be latitude and longitude, eastings and northings, along and perpendicular to a coastline, etc.). Abundance again follows dynamics that includes deterministic and random components:

$$\mathbf{X}_{t+1} = f(\mathbf{X}_t) + \mathcal{E}_t$$

where $f(\mathbf{X}_t)$ is some deterministic model for population dynamics (potentially including movement, growth, reproduction, mortality), and \mathcal{E}_t is a random field, a multivariate analogue to a random variable:

$$\mathcal{E}_t \sim \text{GRF}(0, C_\mathcal{E})$$

where $\text{GRF}(0, C_\mathcal{E})$ is a Gaussian random field distribution with mean zero and covariance function $C_\mathcal{E}$ that only depends on spatial proximity of the data points. This statement specifies the joint distribution for every possible point within a given (spatial) domain, and means that, for any given finite set of points $\mathbf{s} = \{x_1, y_1, x_2, y_2, \dots, x_n, y_n\}$:

$$\mathbf{E}_t[\mathbf{s}] \sim \text{Multi.Normal}(0, \Sigma_E[\mathbf{s}])$$

i.e., that the value of the random field at any set of points is multivariate normal with covariance $\Sigma_E[\mathbf{s}]$. However, the more general notation $GRF(0, C_E)$ recognizes that \mathcal{E}_t is a random function that is continuous (i.e. defined at any possible point in space and not just at the points in \mathbf{s}). If dynamics $f(\mathbf{X}_t)$ are represented using a linear function, the state variable \mathbf{X}_t will follow a Gaussian random field as long as \mathcal{E}_t is also a Gaussian random field (because a linear function of multivariate Gaussian random variables is also Gaussian). However, if dynamics $f(\mathbf{X}_t)$ are nonlinear (as they will be in the subsequent delay-difference model), the state variable is a random field but not necessarily Gaussian.

The covariance among points $\Sigma_E[\mathbf{s}]$ requires two parameters (at least): the marginal variance (i.e. what is the variance at a given point between two realizations of the same random field distribution?), and the range (i.e., how does covariance decline as a function of distance?). As example, we show two random fields (Fig. 1) that differ in terms of their marginal variance and range. The first random field has small marginal variance ($\sigma_E^2 = 0.5$; i.e., where the curve in the upper-right panel intersects with the y-axis) and a large range ($\kappa = 0.25$), while the second has larger variance ($\sigma_E^2 = 1.0$) and a shorter range ($\kappa = 0.10$). This can be seen in the realized value for these random fields, where the first has less variance (lower contrast in colors) and less variability over space than the second.

Background on delay-difference dynamics

We next seek to demonstrate how random fields can be incorporated into nonlinear dynamical models to account for variation in states (abundance) and dynamics (productivity) continuously over space. We proceed by modifying the delay-difference model, a widely known approximation to dynamics for marine species. This model uses annual information regarding relative abundance and average weight to account for the basic demographic processes typically

176 included in age-structured population dynamics models, i.e., somatic growth, recruitment, natural
 177 mortality, and fishing mortality. Specifically, it assumes that total abundance n (in units
 178 numbers) decreases between years $t-1$ and t due to instantaneous fishing F_{t-1} and natural
 179 mortality M rates, and increases due to recruitment r_t :

$$180 \quad n_t = n_{t-1} \exp[-M - F_{t-1}] + r_t$$

181 The Deriso-Schnute delay-difference model (Schnute 1985) then involves the assumption that
 182 individual weight w_a at age a follows an autoregressive model:

$$183 \quad \begin{aligned} w_a &= w_k && \text{if } a = k \\ w_a &= \alpha_g + \rho_g w_{a-1} && \text{if } a > k \end{aligned}$$

184 where w_k is weight (in kilograms) at age at recruitment k , ρ_g is the growth coefficient from a
 185 Ford-Walford plot, and α_g controls the asymptotic weight. Given this assumption, population
 186 biomass b_t in year t can be expressed as:

$$187 \quad b_t = \exp[-M - F_{t-1}] (\alpha_g n_{t-1} + \rho_g b_{t-1}) + w_k r_t$$

188 where the first summand on the right-hand side represents growth of surviving individuals, and
 189 the second summand represents the weight of recruiting individuals. Given dynamic equations
 190 for abundance (numbers) and biomass, average weight is calculated as their ratio:

$$191 \quad \bar{w}_t = \frac{b_t}{n_t}$$

192 and total expected catch biomass can be calculated from the Baranov catch equation:

$$193 \quad c_t = \frac{F_t}{M + F_t} (1 - \exp[-M - F_t]) b_t$$

194 For simplicity, this approach assumes that only mature individuals are vulnerable to the fishery.

195 **Adapting the delay-difference model for spatial variation**

We next replace random variables in the delay-difference model (e.g., total recruitment r_t in year t) with random fields (e.g., spatial densities of recruits $\mathbf{R}_t[\mathbf{s}]$ at locations $\mathbf{s} = \langle s_1, s_2, \dots, s_N \rangle^T$ in year t , where each location $s = \langle x, y \rangle$ has a fixed eastings x and northings y). This results in the following spatial delay-difference model:

$$\begin{aligned} \mathbf{N}_t[\mathbf{s}] &= \mathbf{N}_{t-1}[\mathbf{s}] \exp(-M - F_{t-1}) + \mathbf{R}_t[\mathbf{s}] \\ \mathbf{B}_t[\mathbf{s}] &= \exp[-M - F_{t-1}] (\alpha_g \mathbf{N}_{t-1}[\mathbf{s}] + \rho_g \mathbf{B}_{t-1}[\mathbf{s}]) + w_k \mathbf{R}_t[\mathbf{s}] \\ \bar{\mathbf{W}}_t[\mathbf{s}] &= \frac{\mathbf{B}_t[\mathbf{s}]}{\mathbf{N}_t[\mathbf{s}]} \end{aligned}$$

where $\mathbf{N}_t[\mathbf{s}]$, $\bar{\mathbf{W}}_t[\mathbf{s}]$, \mathbf{B}_t , and $\mathbf{R}_t[\mathbf{s}]$ are, respectively, random fields representing density (numbers per unit area), average weight (mass per individual), biomass density (mass per unit area), and density of recruits (numbers per unit area) in year t at locations \mathbf{s} . These fields represent variation in numbers, average weight, biomass, and recruitment across continuous space but in discrete years.

In the following, we assume that fishing mortality is constant for all spatial locations but varies among years. The assumptions of spatially constant fishing mortality could be explored in future research given spatial data regarding fishing effort (i.e. vessel monitoring or spatial logbook data). Given the assumption of a spatially constant value for fishing mortality F_t and that adult movement rates occur a fine spatial scale relative to the distance between sampled locations, spatial variation in density is driven by spatial variation in recruitment. We assume that recruitment has stochastic variation that is correlated spatially, where the expected value of recruitment also varies spatially. Specifically,

$$\mathbf{R}_t[\mathbf{s}] = \exp(\beta + \mathbf{A}[\mathbf{s}] + \mathbf{E}_t[\mathbf{s}])$$

where β the median expected density of recruits (in numbers), \mathbf{A} represents spatial variation in productivity, and \mathbf{E}_t is annual variation in the spatial distribution of recruitment. We note that

recruitment is not a function of spawning biomass in this formulation (i.e., expected recruitment is independent of population density), which avoids the need for estimating population age at maturity. \mathbf{A} and \mathbf{E}_t are estimated as Gaussian random fields such that their values $\mathbf{A}[\mathbf{s}]$ and $\mathbf{E}_t[\mathbf{s}]$ at fixed locations \mathbf{s} follow multivariate normal distributions:

$$\begin{aligned} \mathbf{A}[\mathbf{s}] &\sim \text{Multi.Normal}(0, \boldsymbol{\Sigma}_A[\mathbf{s}]) \\ \mathbf{E}_t[\mathbf{s}] &\sim \text{Multi.Normal}(0, \boldsymbol{\Sigma}_E[\mathbf{s}]) \end{aligned}$$

where $\boldsymbol{\Sigma}_A[s_1, s_2]$ is the covariance of \mathbf{A} random field between locations $s_1 = \langle x_1, y_1 \rangle$ and $s_2 = \langle x_2, y_2 \rangle$. This covariance is a function of the Euclidean distances $d(s_1, s_2)$ between these locations:

$$d(s_1, s_2) = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$$

where the decay over distance follows one of many common covariance functions, and we use the Matérn function (see Fig. 1 for two examples) in the following:

$$\boldsymbol{\Sigma}_A[s_1, s_2] = \sigma_A^2 \frac{1}{\Gamma(\nu) 2^{\nu-1}} (\kappa d(s_1, s_2))^\nu K_\nu(\kappa d(s_1, s_2))$$

where σ_A^2 is the spatial variance of expected recruitment \mathbf{A} , κ is the parameter governing the rate at which correlations decline over distance, $\Gamma(\bullet)$ is the gamma function, $K(\bullet)$ is the Bessel function of the second kind (covariance $\boldsymbol{\Sigma}_E[s_1, s_2]$ is defined similarly). The spatial variance σ_A^2 of expected recruitment \mathbf{A} and the spatial variance σ_E^2 of annual variation in recruitment are each estimated while sharing a common range parameter κ .

These dynamics imply that the population equilibrium for a given fishing mortality rate F (and assuming deterministic dynamics) is given by:

$$\mathbf{N}_F[\mathbf{s}] = \frac{\exp[\beta + \mathbf{A}[\mathbf{s}]]}{1 - \exp[-F - M]}$$

$$\mathbf{B}_F[\mathbf{s}] = \frac{\exp[\beta + \mathbf{A}[\mathbf{s}]](w_k - (w_k - \alpha_g)\exp[-F - M])}{1 - \exp[-F - M] - \rho \exp[-F - M] + \rho \exp[-2F - 2M]}$$

$$\bar{\mathbf{W}}_F[\mathbf{s}] = \frac{\mathbf{B}_F[\mathbf{s}]}{\mathbf{N}_F[\mathbf{s}]}$$

where $\mathbf{N}_F[\mathbf{s}]$, $\bar{\mathbf{W}}_F[\mathbf{s}]$, and $\mathbf{B}_F[\mathbf{s}]$ are, respectively, random fields representing equilibrium abundance, average weight, and biomass given fishing mortality rate F .

As in the simple model, catch in each year is assumed to follow the Baranov catch equation:

$$c_t = \frac{F_t}{M + F_t} (1 - \exp[-M - F_t]) \int_y \mathbf{B}_t[s] ds$$

where it is necessary to integrate across the random field for spawning biomass \mathbf{B}_t when calculating a population-wide value such as total catch. In future studies, this equation could be replaced with spatially varying fishing intensity \mathbf{F}_t , which would presumably be estimable given auxiliary information regarding the spatial distribution of fishery catches or fishing effort.

Model estimation

We next present how this model can be estimated by fitting directly to survey data that are commonly available for marine populations. Following standard practice for the conventional delay-difference model, we assume that the analyst has information regarding survey catch rates (to form an index of abundance) and average weight. However, rather than having to “standardize” survey data to estimate annual indices of abundance and average weight (Maunder and Punt 2004), we include the raw spatially-referenced survey data directly within the spatial delay difference model. Thorson et al. (In press-b) show that this can be done using spatially explicit dynamical models. However, their approach requires tracking abundance in every year at every spatial location that is sampled, and hence becomes computationally intractable for large

numbers of samples and/or years. We therefore propose a predictive-process modelling approach (Cressie and Wikle 2011), where demographics are only tracked at K “knots”, and where each sampling location is assumed to have densities, biomass, and average weight equal to that at the nearest knot (i.e., densities are spatially constant over fine-scale areas). This predictive approach loses information regarding variation at a fine spatial scale (i.e., below the average minimum distance between knots), but is computationally faster than the alternative, especially as the amount of data (and hence the number of unique sampling locations) increases. The accuracy of the predictive approach can be controlled by varying the number of knots K to achieve a balance between fine-scale spatial detail and computational speed.

Expected catch rates and average weight for sample i can be calculated from model predictions of local densities, biomass, and average weight at the nearest knot $k(i)$. Specifically, survey catches are assumed to arise as a function of local densities:

$$p_i \sim \text{Neg.Bin}(qe_i\mathbf{N}_{t(i)}[k(i)], \boldsymbol{\theta})$$

where e_i is the effective area swept (in square-kilometers) for sample i , q is the probability that a fish within this area swept will be captured by the fishing gear (the “catchability coefficient”), $k(i)$ is the location of the closest knot to sample i , $t(i)$ is the year for sample i , and $\mathbf{N}_{t(i)}[k(i)]$ is the density (in numbers) at the closest knot. We use a negative binomial distribution to account for overdispersed counts, representing local-scale heterogeneity in densities, such that variance is a power-function of local densities:

$$\text{Var}[p_i] = \theta_1\mathbf{N}_{t(i)}[k(i)] + \theta_2\mathbf{N}_{t(i)}[k(i)]^2$$

where θ_1 and θ_2 are linear and quadratic terms for overdispersion (Lindén and Mäntyniemi 2011). Similarly, average weight for each sample is normally distributed:

$$w_i \sim \text{Normal}(\bar{W}_{t(i)}[k(i)], \bar{W}_{t(i)}[k(i)](\sigma_w^2 + \sigma_{extra}^2))$$

where the variance of this measurement process represents the sum of sampling variance σ_w^2 and estimated variance σ_{extra}^2 , which accounts for unexplained variation (“overdispersion”) in average weight data. We assume that average weight follows a normal distribution because average weight represents the sum of individual weights, and hence the central limit theorem applies. Catch in each year is assumed to arise from the Baranov catch equation:

$$\hat{c}_t = \frac{F_t}{M + F_t} (1 - \exp[-M - F_t]) \sum_{k=1}^K \mathbf{B}_t[k] l_k$$

where we compute the sum of biomass over all knots $k=\{1,2,...K\}$, and areas l_k (in square-kilometers) for each knot corresponds to the area of a Voronoi diagram for the population domain given this set of knots. This approximation again assumes that densities (in this case, spawning biomass) at each point are equal to that at the nearest knot. Observed harvest for the entire population c_t in year t (in kilograms) is assumed to follow a lognormal distribution

$$c_t \sim \text{Lognormal}(\log(\hat{c}_t), \sigma_c^2)$$

where σ_c^2 is the variance of measurement error in total harvest. When σ_c^2 is fixed *a priori* at a small value (e.g., 0.01), as we do in the following, then parameter estimates will approach those that would be obtained when assuming that catch is known without error.

These equations involve estimating annual fishing mortality rates F_1 through F_b , the proportion of individuals within survey area swept that are captured (catchability q), the spatial variation of expected recruitment σ_A^2 and annual variation in recruitment σ_E^2 , the geographic range for spatial correlations κ , the median expected recruitment β , overdispersion for average-weight data σ_{extra}^2 , and variance inflation parameters for the negative binomial overdispersion parameters θ . These equations also require treating $\mathbf{A}[x(k),y(k)]$ and $\mathbf{E}_t[x(k),y(k)]$ at each knot k as random effects. We chose to use maximum marginal likelihood for this estimation task,

which involves integrating across random effects when calculating the marginal likelihood. Computing the marginal likelihood is accomplished using the Laplace approximation within Template Model Builder (TMB; Kristensen et al. 2014) and this marginal likelihood is then maximized using conventional optimizers within the R statistical platform (R Core Development Team 2013). Given this maximum likelihood estimate, TMB estimates standard errors for parameters using the information matrix, and calculates standard errors for derived parameters via the delta method.

To improve computational speed during parameter estimation, we use the stochastic partial differential equation (SPDE) approach (Lindgren et al. 2011) to approximate the matrix inverses of Σ_A and Σ_E , as calculated using the R-INLA software (Illian et al. 2012). This SPDE approximation stipulates that random fields \mathbf{A} and \mathbf{E}_t have spatial correlations that decline over distance following a Matérn correlation function (and assuming that smoothness $\nu=1$), where the Matérn correlation function is a simple approximation to more-complicated forms of spatial correlation (Simpson et al. 2012). Further details regarding the use of the SPDE approximation in TMB can be found in Thorson et al. (In press-b).

Simulation testing

We first seek to demonstrate that the spatial delay-difference model provides precise estimates of spatial variation in expected recruitment \mathbf{A} and annual variation in recruitment \mathbf{E}_t . We do this by simulating dynamics for a short-lived species, where instantaneous natural mortality rate $M=0.3$, age at maturity $k=3$ yr., and a Ford-Walford growth coefficient $\rho=0.8$, where $w_k=0.488$ kg. and $w_\infty=1$ kg., such that $\alpha_g=0.2$. We simulate a 1000 km. by 1000 km. square spatial domain, where median unfished recruitment is 1 billion individuals; maximum spawning biomass per recruit is 0.384 kg. per individual, so median unfished biomass is approximately 384 thousand tonnes.

Spatial variation in expected recruitment was simulated using a Matérn function with a standard deviation $\sigma_A = 0.5$, and annual variation in recruitment also has a standard deviation of $\sigma_E = 0.5$, where the spatial range is such that correlations fall to 10% at a distance of 425 km. Random fields are simulated using the *RandomFields* package (Schlather 2009) in R.

We simulate 30 years of dynamics, where fishing mortality starts at 0.05 (with the population in equilibrium given this level of fishing), and subsequently changes following a basic effort-dynamics model (Thorson et al. 2013):

$$F_{t+1} = F_t \left(\frac{\sum_{k=1}^K \mathbf{B}_t[x(k), y(k)] \mathbb{V}_k}{a \sum_{k=1}^K \mathbf{B}_{F=0}[x(k), y(k)] \mathbb{V}_k} \right)^x \exp[\varepsilon_t]$$

$$\varepsilon_t \sim \text{Gaussian}(0, \sigma_F^2)$$

where $a = 0.4$ is the biomass at bioeconomic equilibrium (i.e., where fishing mortality neither increases nor decreases on average), $x = 0.2$ is the rate at which effort either enters or leaves the fishery given a doubling/halving of available biomass, $\mathbf{B}_{F=0}$ is the biomass when $F=0$, and $\sigma_F = 0.2$ is the standard deviation of stochastic variation in fishing mortality.

By default, we simulate a scenario in which there are 100 samples per year from a survey where selectivity is knife-edged at age at maturity (as assumed by both conventional and spatial delay-difference models). Each sample has an area swept of 2500 meters-squared and catches all individuals within this area, such that the expected unfished catch rate is approximately 8.7 individuals per tow. Catch rates are Poisson-distributed, and average-weight measurements have a 20% coefficient of variation around true average weight. Finally, fishery catches are known without error, although the estimation model specifies a penalty with a 1% coefficient of variation: this approach is similar to specifying the “explicit-F” parameterization in many age-structured fishery assessment models (Methot and Wetzel 2013). We additionally specify a

number of knots $K = 25$, such that we are smoothing over fine-scale spatial variability. The location of these 25 knots is calculated by applying a k-means clustering algorithm to the location of all available survey data, and the areas for each knot (l_k) is calculated using the Voronoi tool in the *PBSmapping* package (Schnute et al. 2013). This choice of knots is done to achieve fast model convergence, and real-world applications could explore greater numbers of knots. This number of knots allows us to run 200 simulation replicates, and we summarize results by comparing true and estimated spatial variation in productivity \mathbf{A} and annual variation in recruitment \mathbf{E} .

Case study application: rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska

As a case study, we also apply the spatial delay-difference model to data for rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. Rex sole has been assessed in recent years by using a population model to estimate current biomass, and determining an overfishing limit (OFL) as the product of the estimated biomass and an exploitation rate F_{OFL} that is set to the estimate of M . Recent assessments have used the same survey data used here, and have also assumed a known and constant value for natural mortality M . The spatial delay-difference model differs from recent assessments by assuming that fishery selectivity is knife-edged at the age at maturity, and that recruitment and densities vary spatially.

We use 7344 survey observations from 1993-2013, where each survey tow includes catch (in numbers), average weight, latitude, longitude, and area swept. These observations are derived from a bottom trawl survey that samples marine waters in the Gulf of Alaska <1000 m. deep, where 2-3 commercial trawlers are contracted in each year to adhere to a randomized design and standardized sampling methods (Von Szalay et al. 2010). Data are available every third year 1993-1999, and every other year 1999-2013. We also perform a preliminary data analysis of age

and weight data for female individuals throughout the Gulf of Alaska, to estimate parameters for the Ford-Walford growth model. This analysis indicates that weight-at-age for rex sole during these years can be approximated as $\rho = 0.95$, $w_k = 0.13$ kg., and $w_\infty = 0.9$ kg. Finally, we use values for natural mortality $M = 0.17$ yr.⁻¹ and age at maturity $k = 5$ yr. from the 2011 assessment from the Alaska Fisheries Science Center (Stockhausen et al. 2011).

Exploratory model building demonstrated convergence problems for the spatial delay-difference model given unconstrained estimation of fishing mortality F in years without survey data. We therefore stipulate that fishing mortality follows a random walk process:

$$\log(F_{t+1}) \sim \text{Gaussian}(\log(F_t), \sigma_F^2)$$

where σ_F^2 is an estimated parameter representing variation in fishing mortality rates over time, and F is estimated as a random effect for all years (1993-2013). We also follow standard practice for stock assessments in the Gulf of Alaska (including the most recent rex sole assessment), and assume that the survey captures all mature individuals within the survey's area swept (i.e. that catchability $q=1$). Finally, we configure R-INLA to compute distances in the SPDE approximation using three-dimensional coordinates, thus eliminating any distortions induced by projecting spherical distances onto a two-dimensional surface prior to computing distances.

Results

Simulation testing

A randomly chosen simulation replicate using 25 knots shows how the spatial delay-difference model is able to reconstruct variation in recruitment spatially and over time (Fig. 2). The median expected recruitment ($\beta + \Omega$) is highest along the southeast and northern borders of the population's range, while expected recruitment is lowest in the southwest. This general pattern

is recovered by the spatial model, although the spatial model integrates over fine-scale variation (i.e. using large polygons that have constant expected recruitment within). The estimate of spatial variation also has less contrast in color, representing lower total variation: this occurs due to shrinkage, where the model for this simulation replicate estimates lower variance in expected recruitment than the true value. Similarly, recruitment is higher (i.e. more red) in year 2 (third row of Fig. 2) than years 1 or 3 (second and fourth rows), and this pattern is also evident in the spatial-model estimates.

Similar qualitative patterns are obtained when summarizing results across all 200 simulation replicates for the simulation experiment (Fig. 3) rather than inspecting just the first replicate. The correlation between true and estimated values of spatial variation **A** is >0.8 in all replicates, and >0.6 for annual recruitment variation **E**. However, the variance explained is lower than the correlation, because variance-explained measures both (1) whether relative patterns are recovered (does location A have higher expected recruitment than area B?) and (2) whether the correct scale is recovered (how much higher is expected recruitment at location A than location B?). In this latter case, the spatial delay-difference model generally penalizes estimated variation towards zero, and therefore generally leaves some variance unexplained.

Case study: rex sole

We next show the application of the spatial delay-difference model to data for rex sole when using a finer-scale approximation using 100 knots. The k-means algorithm for determining knot locations (Fig. 4) generates a dense cluster of knots around Kodiak Island, where there are nearly four knots from shore to the 1000 m. isobath that demarcates the offshore limit of the survey. By contrast, the shoreline along southeast Alaska generally has only one knot from shore to 1000 m., so there is less capacity for the model to capture differences in recruitment between inshore and

offshore areas in Southeast Alaska. These differences can be seen in estimates of median expected recruitment (Fig. 5a), where Southeast Alaska has little variation between inshore and offshore values, while the area around Kodiak Island shows distinctly greater expected recruitment offshore than inshore. Notably, the area east and southwest of Kodiak Island also have the greatest expected recruitment of the survey domain, while southeast Alaska and the far Aleutian Islands have relatively lowest recruitment. Annual estimates of recruitment (Fig. 5b) show considerable variation in which regions contribute to production in any given year. Several years (1993, 1996, 2003, 2005, 2011 and 2013) have greatest recruitment in central and Southeast Alaska, while other years (1999, 2000, 2002, 2008, 2009 and 2012) have high recruitment coastwide. The model also distinguishes several years (1994, 1995, 1997, 1998, and 2010) when recruitment is uniformly low throughout stock's range. These years with low recruitment can also be distinguished in the coast-wide summary of recruitment (Fig. 6, bottom-left panel), although the coast-wide summary obscures any information about the allocation of recruitment between Southeast Alaska, the central coast, and the Aleutian Islands. Derived quantities, including densities in numbers and biomass can also be tracked (Fig. 6, other panels), and show a decline in population abundance in the early and mid-90s, followed by a stable population size throughout the 2000s. This stability is unsurprising, given that fishing mortality is <0.05 for all years and is largely stable over time.

Discussion

We have introduced a new modelling approach to approximate spatial variation in population abundance and productivity over large spatial ranges, which allows for spatial variation in population dynamics (e.g., expected recruitment) and status (e.g., realized recruitment, average weight, and expected catch rates). This approach is illustrated by modifying the Deriso-Schnute

delay-difference model and applying to data typically available for marine fishes. This is a simple but generic population-dynamics model that explicitly includes individual growth, natural and fishing mortality, and recruitment, and hence represents a starting-point for developing spatially explicit dynamical models. The spatial delay-difference model estimates spatial variation in expected recruitment, as well as annual variation in recruitment. When applied to simulated data, the spatial delay-difference model accurately reconstructed spatial patterns in recruitment, both regarding overall production (**A**) and annual deviations away from this expectation (**E**). When applied to data for rex sole in the Gulf of Alaska, this approach demonstrated considerable spatial variation in recruitment among years, with some years having higher recruitment in Southeast Alaska than the Western Gulf of Alaska (or vice-versa), and other years having high (or low) recruitment coastwide. The spatial delay-difference model thus represents a starting point for future modelling efforts to identify environmental conditions associated with high (or low) local recruitment.

The spatial delay-difference model also projects population dynamics forward given estimated spatial variation in recruitment, and hence provides a simple way of estimating spatial variation in population densities over time. If the model presented here were used for assessing stock status (rather than focusing on its estimates of spatial variation in recruitment), it could perhaps best be viewed as a spatial extension to a data-poor or “data-moderate” stock assessment model. In essence, the spatial delay-difference model integrates spatially-referenced data on population density (from resource surveys) to infer spatial variation in recruitment, which is then forward-projected while assuming that adult dynamics (i.e., mortality, selectivity) are constant across space and time. In practice, spatial variation in survey data could reflect spatial variation in either fishing or natural mortality, spatial patterns in selectivity and/or availability to the

survey gear, or sampling variability. Temporal variation in selectivity is an ongoing research topic in spatially aggregated models for marine populations (Martell and Stewart 2014), and estimating natural mortality rates (let alone spatial or temporal variation) is difficult even in fully age-structured stock assessment models (Garrison et al. 2011). One benefit of the spatial delay-difference model (relative to existing age-structured models) is that it integrates the analysis of raw survey data (typically done using an index standardization model; Maunder and Punt 2004) within the task of building a population dynamics model (also see Maunder and Langley 2004).

We note that the spatial delay-difference model lacks several common features of population dynamics models for marine species. Specifically the spatial delay-difference model lacks both (1) density-dependent variation in expected recruitment, and (2) movement of individuals after recruitment. We briefly address these and other potential concerns below.

Density-dependent variation in recruitment is the primary type of density dependence included in most dynamical models for marine populations. Density-dependent recruitment, in addition to individual growth and natural mortality, contributes to the shape of the surplus production curves seen in marine populations (Thorson et al. 2012, Mangel et al. 2013). Specifying that expected recruitment is independent of spawning biomass represents the limit of extreme compensation for the Beverton-Holt stock-recruit relationship, and will result in overestimates of optimal fishing mortality rates as well as underestimating the ratio of spawning biomass at maximum sustainable yield to its average unfished value for some species (Mangel et al. 2013). However, many marine populations have extreme variability in recruitment that is unexplained by stock-recruit models (Thorson et al. 2014), and we have used a state-space modelling approach to allow available data to estimate annual recruitment, thus decreasing the influence of the expected value. Furthermore, stock assessments for marine species used to set

annual fishing targets typically use biological reference point (BRP) proxies because estimating the stock-recruit relationship is extremely difficult for most individual populations (Dorn 2002). Therefore, assuming a constant value for expected recruitment still allows the use of BRP proxies for estimating overfishing and overfished status. Movement of individuals prior to the age of recruitment is not modeled explicitly, as the estimate of expected recruitment includes both spatial variation in productivity and subsequent immigration and emigration of pre-recruits. In the case that a species migrates substantially prior to their age at recruitment, Λ (representing spatial variation in average recruitment) will then be interpreted as spatial variation in settlement of juveniles (i.e., it includes spatial variation in productivity, plus the net effect of immigration and emigration prior to recruitment). Auxiliary information on the spatial movements and distributions of pre-recruit life-stages, perhaps from egg and larval surveys, may help to disentangle movement from spatial variation in productivity.

We also have not modeled movement of adults after the age at recruitment, which amounts to the assumption that adults move over a smaller scale than the distance between spatial “knots” that are used to approximate variation in population density. Future studies could explore including movement using auxiliary tagging data (Sibert et al. 1999) or directly via information in catch rates (Carruthers et al. 2011). Adult movement could be approximated generically using a combination of advection and diffusion equations (Sigrist et al. In press). However, we have not done so because including adult movement may eliminate the sparseness of the estimated random fields representing recruitment. We recommend that future research explore sparse methods for modelling adult recruitment, so that we can continue to build upon the fast computational approach afforded by the stochastic partial difference equation approach to random fields (Lindgren et al. 2011). Finally, we assumed in this study that fishing mortality

was constant across space. While there is a large literature on fleet dynamics and fishing behavior that supports the idea of selective fishing (Branch et al. 2006, van Putten et al. 2012), we cannot estimate spatial variation in fishing intensity with the data types used here. Future research should therefore standardize spatially referenced catch data, for use when estimating spatial variation in fishing mortality.

Despite the future research topic identified above, we note that the spatial delay-difference as presented here is already useful as a time-series smoother for spatial-explicit fisheries data, for use in simple management procedures. Previous research has noted that delay-difference and surplus production models provide a simple alternative to other simple time-series smoothers (McAllister et al. 1999), and hence can filter measurement error from biologically meaningful variation in population dynamics. For example, a state-space surplus production model has been applied to the two-species complex of Bering Sea/Aleutian Islands rougheye and shortraker rockfish (Spencer and Ianelli 2005). Similarly, the spatial delay-difference model could be used to develop spatially explicit management procedures (e.g., involving the allocation of allowable catch among multiple fishing fleets and/or ports), and provide a data-poor or data-moderate alternative to more detailed spatial models that consider movement patterns (Fu and Fanning 2004, Spies et al. in preparation). However, spatial models must be used to characterize the degree of spatial variation in recruitment that is plausible before appropriate simulation tests can be designed (Punt 2008), so the proposed model should be applied to several real-world populations before we can start to test its performance using biologically plausible simulation scenarios.

We also note that future research could develop fully age-structured models using the random field approach introduced here. These models would continue to be highly separable

(and hence computationally efficient) given that the survival function is stochastic (Gudmundsson and Gunnlaugsson 2012). For almost 100 years, age-composition samples have remained the gold-standard for inferring variation in recruitment in marine fishes (Hjort 1926), and spatially explicit age-structured models would allow spatial variation in recruitment to be inferred with a high degree of confidence. However, the appropriate likelihood for age-composition data remains hotly-debated (Maunder 2011, Hulson et al. 2012), and the average-weight approach used in the spatial delay-difference model ensures that compositional and catch rate information are given similar weighting when estimating stock status and recruitment variation (in accordance with suggestions from Francis 2011).

Regardless of these potential extensions for the spatial delay-difference model, we propose that spatial models could be informative regarding the influence of global (e.g., climate trends and oscillations) and local (e.g., upwelling and ocean eddies) processes of fish recruitment. Spatial models may increase the effective sample size for meta-analytic tests of environmental links to recruitment, e.g., by swapping space for time when exploring an environmental link for recruitment (Ward et al. 2010). Spatially explicit population dynamics models will also propagate estimation uncertainty when analyzing spatially referenced data, and hence may be more useful for testing environmental links than approaches that rely upon model-estimated recruitment time series (Thorson et al. In press-a). Finally, spatial models for recruitment will likely be necessary to distinguish the impact of environmental drivers or density dependence that occurs at small spatial scales, because testing environmental links using spatially aggregated recruitment may obscure any ecological process occurring at small scales (Hastings 1993, Ray and Hastings 1996). For these reasons, we propose that spatial population models may provide a solution to the well-recognized failure of environmental models to predict future recruitment in

many cases (Myers 1998), and could complement a growing literature regarding the impact of climate change on fish populations (Cheung et al. 2009).

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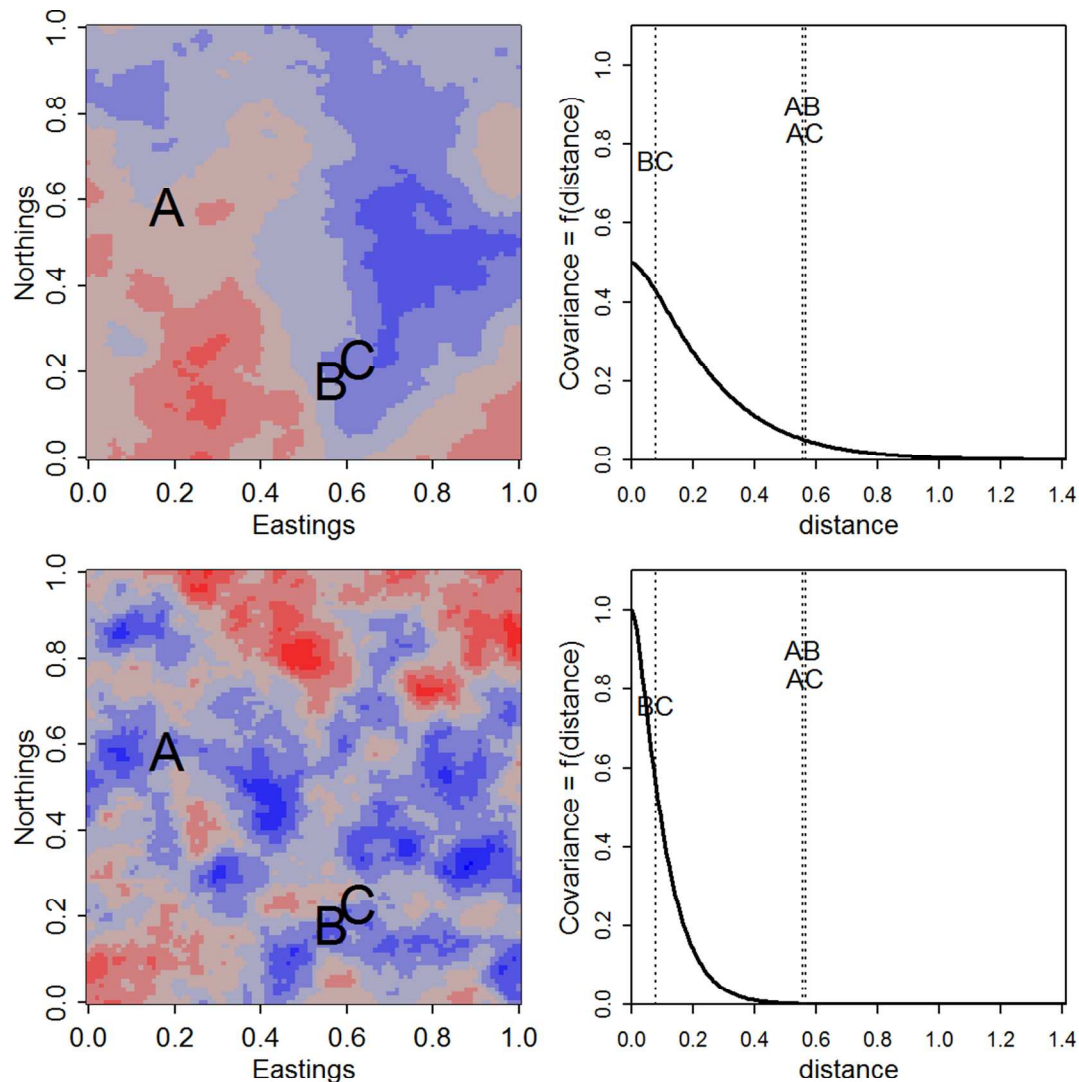
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749 California, Mexico. *J. Appl. Ecol.* **47**: 47–56. doi: 10.1111/j.1365-2664.2009.01745.x.
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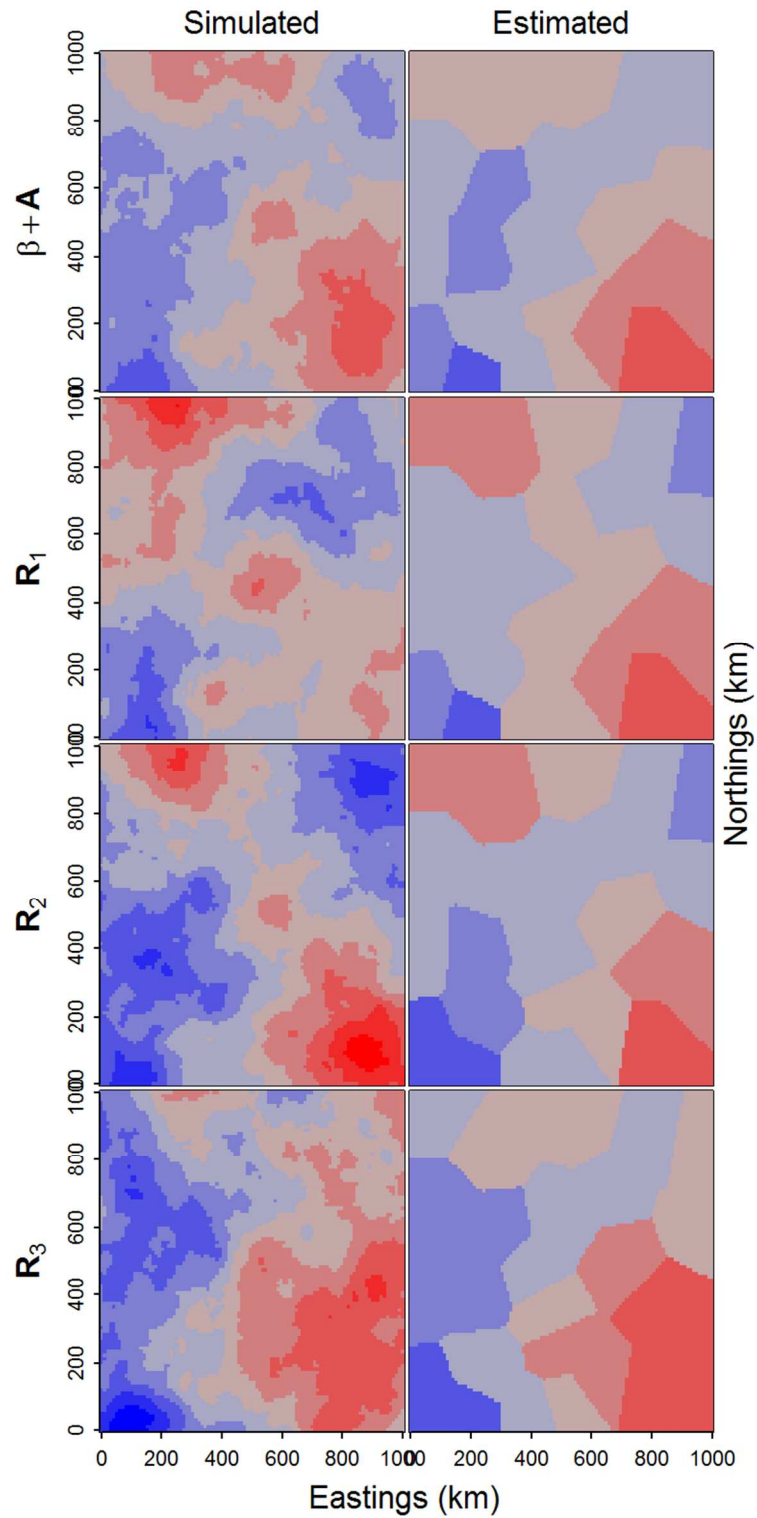
751 Fig. 1 – Examples of random fields (left column: blue=low value; grey=near zero value;
 752 red=high value) as well as how covariance changes as a Matérn function of distance between
 753 points (right column), where both random field shows three randomly selected locations (A, B,
 754 and C) as well as the distance and covariance among them (e.g., where AB is the distance
 755 between points A and B).



756

757 Fig. 2 – Comparison of simulated (“true”; left column) and estimated (right column) distribution
758 for median recruitment (top row; red: high value; grey: middle values; blue: low values), as well
759 as the first three years of realized recruitment (2nd, 3rd, and 4th rows).

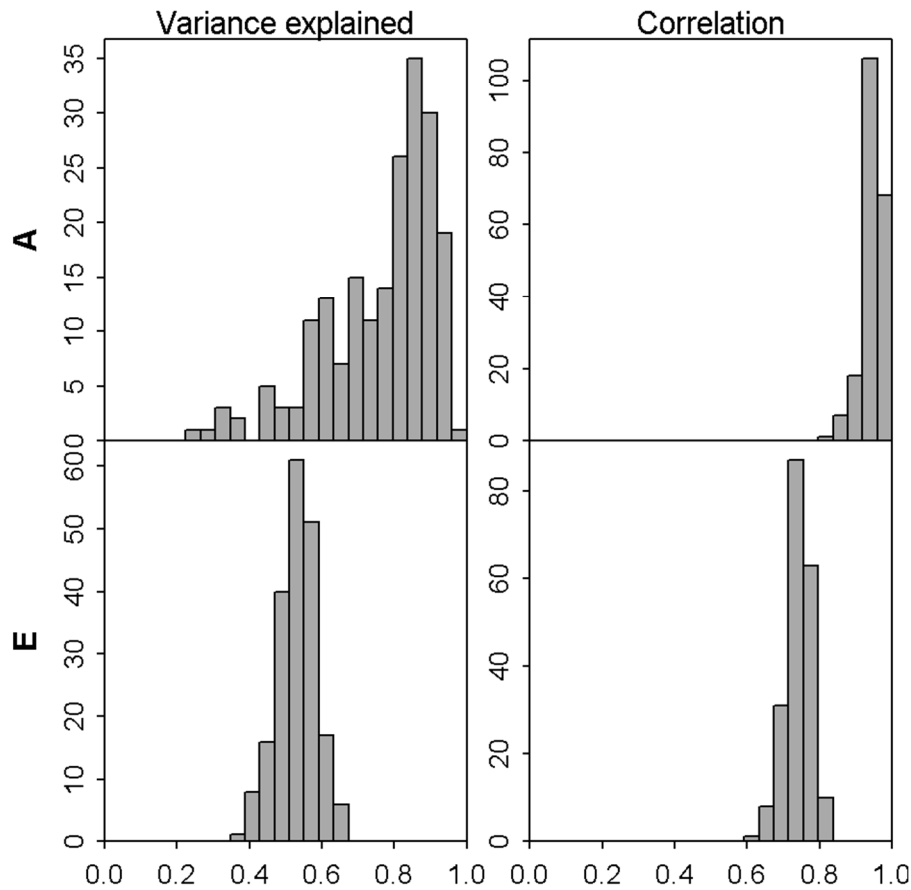
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Fig. 3 – Histograms showing the proportion of variance explained ($\sum_{i=1}^n (\mathbf{X} - \hat{\mathbf{X}})^2 / \sum_{i=1}^n \mathbf{X}^2$, where \mathbf{X} is a simulated random field and $\hat{\mathbf{X}}$ is its estimate) and the correlation between true and estimated spatial variation in recruitment **A** or annual variation **E**.



767 Fig. 4 – Map of location for every survey observation for rex sole (grey dots) as well as the 100
768 knots (red dots) used to approximate spatial variation in recruitment.

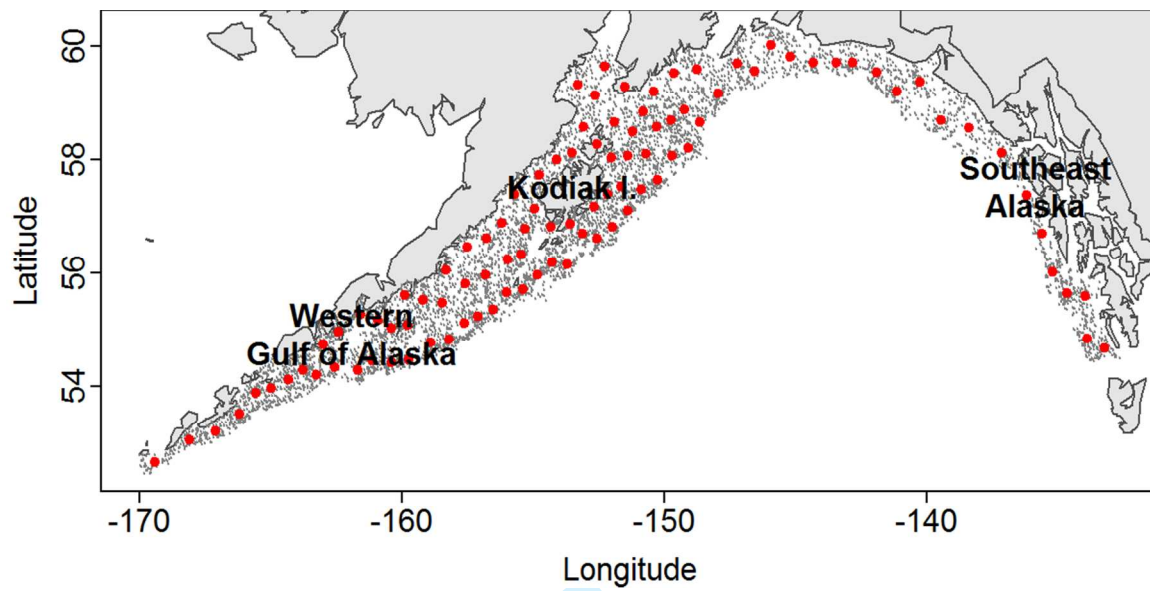


Fig. 5a – Estimates of spatial variation in median recruitment (indiv./km.²) for rex sole (red: high recruitment; blue: low recruitment; see key for exact scale)

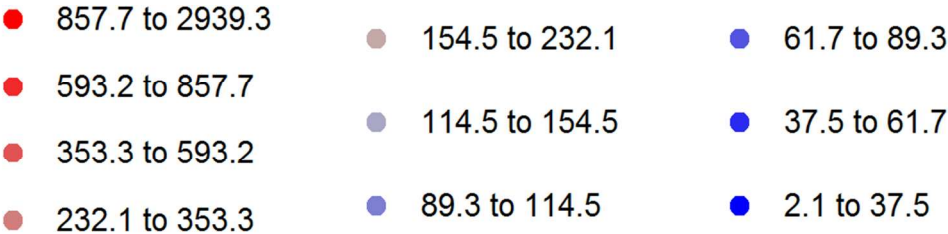
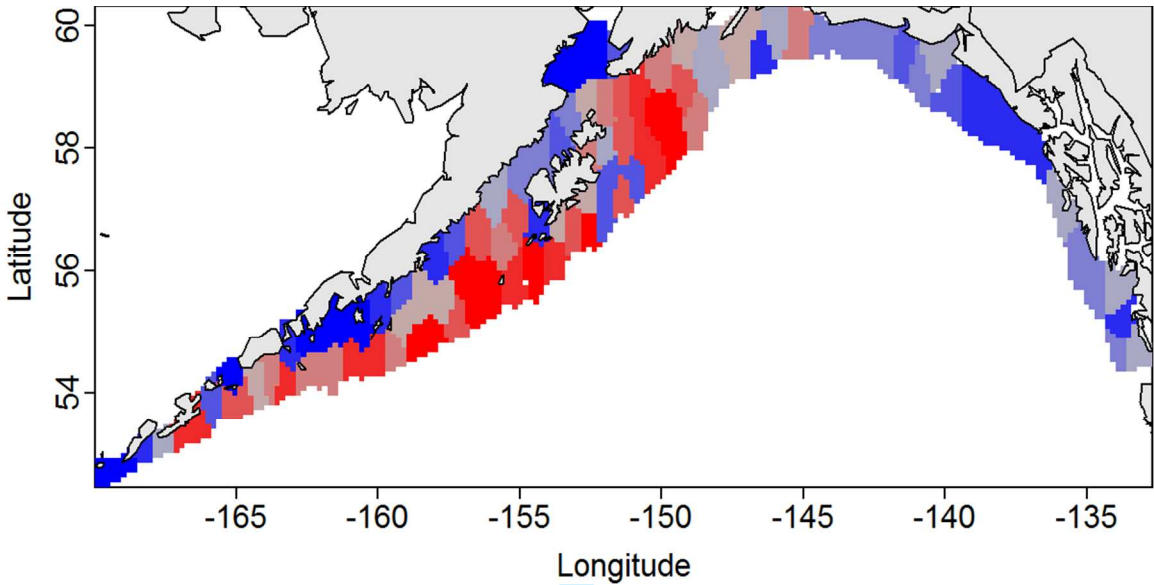
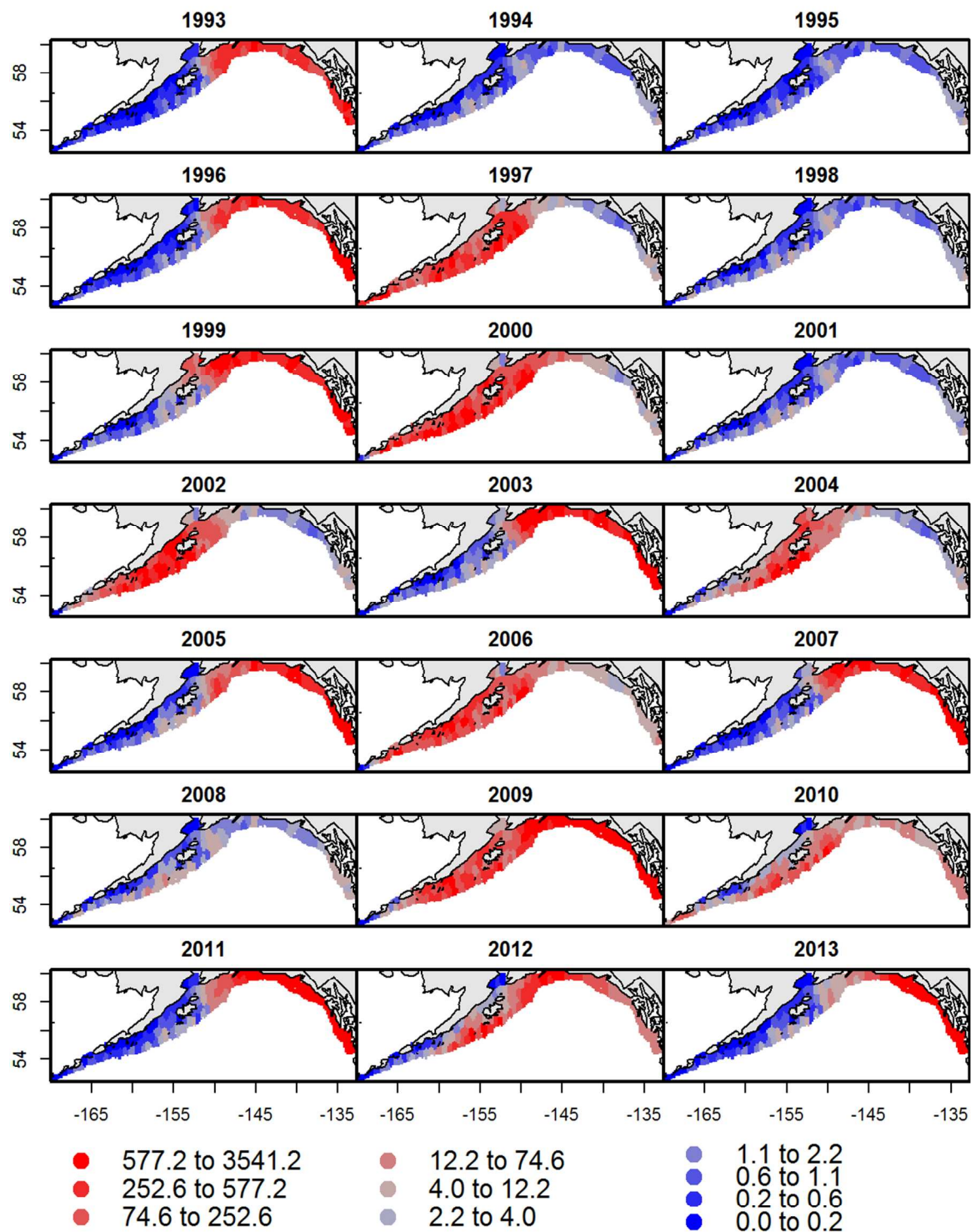


Fig. 5b – Estimates of recruitment (indiv./km.²) of rex sole in every year 1993-2013 (red: high recruitment; blue: low recruitment; see key for exact scale)



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Fig. 6 – Estimated (black line) and 95% confidence interval (red region; $\pm 1.96 \cdot SE$, where SE is the estimated standard error) for abundance (numbers), spawning biomass (kg.), average weight (kg./indiv.), recruitment (numbers), instantaneous fishing mortality rate (yr^{-1}), and depletion (unitless) for rex sole from 1993-2013 from the spatial delay-difference model.

