

Using spatio-temporal models of population growth and movement to monitor overlap between human impacts and fish populations

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Summary

1. Protected and managed species, including harvested fishes, exhibit spatial and temporal variation in their distribution and productivity. Spatio-temporal variation can arise from differences in habitat quality, human impacts (including harvest), density-dependent changes in per capita productivity, as well as individual movement. Human impacts (e.g. direct harvest) also vary spatially and over time, and monitoring the overlap between impacts and population distribution is necessary to ensure that human impacts are sustainable and to prioritize research and management for populations that are heavily impacted. However, estimating spatio-temporal variation in human impacts and population dynamics while accounting for individual movement has remained computationally challenging for decades.

2. We developed a spatial population growth (also known as ‘surplus production’) model that is inspired by finite element analysis, which estimates spatio-temporal population dynamics given density-dependent population regulation, individual movement and spatially explicit harvest. We demonstrate the method using data for big skate *Raja binoculata* in the California Current from 2003 to 2013 and demonstrate that results can be processed to estimate an upper limit on sustainable harvest (an ‘overfishing limit’). We also conduct a simulation experiment to explore the small-sample properties of parameter estimates.

3. A simulation experiment confirms that real-world sample sizes are sufficient to estimate the sustainable harvest level within 20% of its actual value. However, sample sizes are likely insufficient to reliably estimate movement rates.

4. The spatial population growth model estimates an overfishing limit of 740–890 metric tonnes for big skate from 2010 to 2013, compared with annual harvest < 100 tonnes. This suggests that recent harvest of big skate is likely sustainable, and sensitivity analysis confirms that this conclusion is robust to different potential rates for individual movement.

5. *Synthesis and applications.* We recommend that spatio-temporal population models be used across systems and taxa to monitor the spatial overlap between species distribution and human impacts. For big skate, we recommend management rules triggering additional data collection and assessment effort if harvest rates substantially increase. We also recommend future research regarding spatial management regulations for emerging fisheries.

Key-words: advection–diffusion, Big skate *Raja binoculata*, finite element analysis, Gaussian random field, geostatistics, Gompertz model, overfishing limit, spatial population model, stock assessment, surplus production

Introduction

The distribution and density of natural populations varies tremendously across landscapes and over time due to

variation in habitat quality, environmental conditions and biological interactions (Tingley *et al.* 2009). For example, the spatial distribution of foraging predators frequently changes during population decline and recovery (e.g. Swain, Benoît & Hammill 2015). The intensity of human impacts also varies spatially and over time, so mapping the spatial overlap between impacts and population densi-

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ties is central to assessing conservation and management goals (Smith *et al.* 2010; Rassweiler *et al.* 2014).

Models estimating spatial and temporal variation in population density are increasingly used to track shifts in population distribution subject to environmental and climatic changes (Kotwicki & Lauth 2013; Harsch *et al.* 2014). Spatio-temporal models may improve precision when estimating purely temporal trends in population abundance (Shelton *et al.* 2014). It is feasible to fit spatial models to ecological data while including random or directed movement of individuals (e.g. Hooten & Wikle 2010), and these models are increasingly used to estimate stability and persistence in meta-population models (e.g. Chandler *et al.* 2015). The role of individual movement in species distribution is often studied using data for individual animals (e.g. spatial capture–mark–recapture models, (Royle *et al.* 2012)), but less often using purely count data (although see Chandler & Royle 2013). Demographic models that include movement generally demonstrate important differences in population and community dynamics relative to models that ignore movement (Skelam 1951; Okubo, Hastings & Powell 2001).

Marine ecologists have studied the productivity of fishes and crustaceans using population growth models (which we call ‘surplus production models’, following common terminology in fisheries science) for more than eighty years (Russell 1931; Schaefer 1957). Surplus production models consolidate individual growth, natural mortality and the recruitment of new individuals to the population (‘recruitment’) into a single surplus production function and therefore approximate dynamics using this production function and the rate of human-caused mortality. By combining individual growth, recruitment and natural mortality into a single function, surplus production models represent a very simplified picture of population dynamics and are often used as an introduction to population dynamics for students of ecology and fisheries science. Due to their relative simplicity, surplus production models also represent a natural starting point when developing more complicated models, for example those that approximate dynamics for multiple species simultaneously (Christensen & Walters 2004) or describe patterns emerging from species interactions (Walters & Kitchell 2001).

Despite the central role of surplus production models to fisheries science and the increasing role for statistical estimation of spatial models in applied ecology, there has been little previous research regarding spatial surplus production models for marine species. One counter example is Carruthers, McAllister & Taylor (2011), who estimate density, a production function, and movement among 12 spatial strata for pelagic tuna in the Atlantic Ocean. Carruthers, McAllister & Taylor (2011) used tagging data as well as fishery catches and catch rates to estimate parameters governing production and movement, but assumed that dynamics were ‘deterministic’ (i.e. that the dynamics can be explained by a specified population growth func-

tion without any residual error). Research in marine and terrestrial systems generally demonstrates that estimating stochastic variation in population growth in addition to measurement errors (i.e. using a ‘state-space model’) decreases error when estimating demographic parameters or population abundance (de Valpine & Hastings 2002; Ono, Punt & Rivot 2012). Other studies have estimated population growth and movement among discrete strata (Thomas *et al.* 2005) or have tracked individual movement without explicitly modelling population growth (Chandler & Royle 2013), but we know of no published study that uses state-space estimation of a spatial surplus production model while accounting for advective–diffusive movement of individuals.

In this study, we develop a new spatial surplus production model (which includes advective–diffusive movement, both process and measurement errors, and spatial variation in human harvest rates) to estimate the cumulative overlap between human fishing and population density across a marine landscape. We use a simulation experiment to explore the small-sample properties of the spatial surplus production model when estimating parameters using simulated data. We also demonstrate this model using 11 years of data for big skate *Raja binoculata* in the US waters of the California Current and use results to estimate what level of coastwide harvest is likely to be sustainable for this population. This case study application suggests that big skate harvest in 2003–2013 was likely sustainable, but that large (fivefold) increases in harvest would likely necessitate more detailed assessment of human impacts.

Materials and methods

CONVENTIONAL SURPLUS PRODUCTION MODELS

A surplus production model (often called a population growth model for non-aquatic taxa) typically approximates changes in population abundance b_t from year t to the next year $t + 1$:

$$b_{t+1} = g(b_t) \exp(\varepsilon_t) \quad \text{eqn 1}$$

where $g(\cdot)$ is typically a nonlinear function representing the aggregate effect of natural mortality, production of juveniles, and individual growth rates, and ε_t represents unmodelled variation in population abundance in the transition from year t and $t + 1$. Here and throughout, we specify that errors are multiplicative and positive (i.e. $\exp(\varepsilon_t) > 0$ for all ε_t). As an alternative to eqn 1, we note that population growth models can be constructed to track changes in population numbers following count-valued birth and death functions (e.g. Dail & Madsen 2011). However, we instead treat abundance b_t as a continuous variable because fish populations are generally large such that individual dynamics can be approximated using continuous variables. Reconstructing dynamics also requires specifying the biomass in the first estimated year, b_0 , and this is generally treated as an estimated parameter. Population growth in excess of replacement (termed ‘surplus production’) is often assumed to be zero when biomass is zero or at population carrying capacity (i.e. that $g(b_t) - b_t = 0$ whenever $b_t = 0$ or $b_t = K$, where K is the carrying capacity of

the population). Historically, surplus production has been modelled as reaching a maximum value at some intermediate level of population abundance, although the exact shape of the surplus production function has been debated for several decades (Schaefer 1957; Thorson *et al.* 2012; Mangel *et al.* 2013).

In models for fisheries, surplus production models often explicitly include deaths due to human harvest:

$$b_{t+1} = g(b_t \exp(-u_t f_t)) \exp(\varepsilon_t) \tag{eqn 2}$$

where f_t is fishing effort data and u_t is an estimated parameter defined such that $u_t f_t$ is the instantaneous rate of mortality caused by fishing in year t (termed the ‘fishing mortality rate’). Fishing effort data f_t are only informative if restrictions are imposed upon u_t (e.g. assuming $u_t = u$ for all years). Fishing mortality is here assumed to occur prior to the action of the density-dependent function g . We also follow Meyer & Millar (1999) in assuming that the action of process error ε_t (i.e. change in biomass from year t to $t + 1$ that is not otherwise explained by g or $u_t f_t$) occurs after density dependence and fishing effects. Fishing mortality $u_t f_t$ is estimable given that information regarding total harvest h_t in each year t is available:

$$h_t = b_t(1 - \exp(-u_t f_t)) \exp(\delta_t) \tag{eqn 3}$$

where δ_t is penalized towards zero, for example specified to follow a normal distribution, $\delta_t \sim N(0, \sigma_\delta^2)$, such that the model fits the harvest data as if it were known without error as $\sigma_\delta^2 \rightarrow 0$. Parameters are generally estimated by fitting to an index that is assumed to be proportional to population abundance:

$$c_t = qb_t \exp(\tau_t) \tag{eqn 4}$$

where c_t is an index of population abundance in year t , τ_t is specified to follow a normal distribution, and q is an estimated parameter scaling biomass to the index of abundance (called the ‘catchability coefficient’ in fisheries models). The catchability coefficient is identifiable in surplus production models only if there is sufficient ‘contrast’ in catch and the index data (i.e. an increase in catch is associated with a decrease in the index of abundance). As commonly used, the surplus production model requires that harvest data \mathbf{h} are available in each year, but additional assumptions (i.e. that fishing mortality f_t follows a random-walk process) can avoid this requirement in some cases.

SPATIAL SURPLUS PRODUCTION MODELLING

We next seek to demonstrate how to adapt the conventional surplus production model to approximate spatial population dynamics. We treat population density and surplus production as functions defined at every location s within a specified two-dimensional spatial domain \mathcal{D} , where s is referenced by latitude/longitude or another appropriate 2-dimensional coordinate system, $s \in \mathcal{D} \in \mathbb{R}^2$. Density $\mathcal{B}_t(s)$ at location s and year t is treated as a function (we use script notation to signify function-valued variables), and it arises from a combination of density-dependent, harvest, and movement processes:

$$\mathcal{B}_{t+1} = g(m(\mathcal{B}_t \exp(-u_t \mathcal{F}_t))) \exp(\mathcal{E}_t) \tag{eqn 5}$$

where \mathcal{F}_t is a function representing fishing effort in year t , $\mathcal{B}_t \exp(-u_t \mathcal{F}_t)$ is the product of survival rate $\exp(-u_t \mathcal{F}_t)$ and den-

sity \mathcal{B}_t , $m(\cdot)$ is a movement function representing the net effect of advective and diffusive movement, and g is a pointwise function approximating local density dependence in population dynamics. Given that the action of movement m is prior to density dependence g , density dependence at location s is a function of densities within a local neighbourhood whose size and shape is defined by movement m . Similarly, \mathcal{E}_t is a function representing unexplained variation in dynamics and is specified as being spatially autocorrelated:

$$\mathcal{E}_t \sim \text{GP}(0, C_\varepsilon) \tag{eqn 6}$$

where the mean of the Gaussian process is zero, and C_ε is the spatial covariance function for process errors. Future research could explore alternative restrictions on fishing mortality, for example $\exp(-u_t \mathcal{F}_t^\psi)$ where ψ represents a competitive or cooperative effect of fishing effort on local fishing mortality (Wilberg *et al.* 2010), although we do not do so here.

Movement function m typically includes both random and directed components, termed diffusion and advection, respectively. This function can be calculated from an instantaneous movement rate:

$$\frac{\partial}{\partial t} \mathcal{B} = (\mathbf{u}^T \nabla + \nabla \cdot \Sigma \nabla) \mathcal{B} \tag{eqn 7}$$

where $\mathbf{u}^T \nabla \mathcal{B}$ represents advective movement (where ∇ is the gradient operator, which yields a vector of length two when evaluated at location s because \mathcal{B} is a function defined in two-dimensional space, and \mathbf{u} is a direction vector of length two), and $\nabla \cdot \Sigma \nabla$ represents diffusive movement (where Σ is a 2×2 rotation matrix governing the rate of diffusion in different directions, and if $\Sigma = \mathbf{I}$ then $\nabla \cdot \Sigma \nabla$ reduces to the Laplacian operator).

IMPLEMENTING THE SPATIAL SURPLUS PRODUCTION MODEL

In practical applications, the solution to movement and production defined for all possible locations within a population domain can only be calculated analytically given particular functions for density dependence (Okubo, Hastings & Powell 2001). More generically, however, the model can be approximated using techniques derived from finite element analysis. We first divide the entire spatial domain \mathcal{D} into a set of n_r triangles such that every location $s \in \mathcal{D}$ is within exactly one triangle (see Appendix S1 in Supporting Information). The number of triangles represents a balance between numerical precision and computational speed, and we recommend that future studies confirm that results are unchanged when increasing the number of triangles (as we have done for the results presented in this study). Fish within each triangle are assumed to be homogenous and evenly mixed, such that every location s within triangle r has the same density, harvest rate, surplus production, process error, etc. Therefore, each function in the spatial surplus production model (e.g. density \mathcal{B}_t) is approximated as a piecewise constant function. Triangle r has area a_r (in units km^2) and this area contains abundance $b_{r,t}$ (in units kg.) such that population density at location s in that triangle is $b_{r,t}/a_r$, and we use vector \mathbf{b}_t to refer to the abundance in every triangle. Population abundance changes among years as follows:

$$\mathbf{b}_{t+1} = g(\mathbf{M}(\mathbf{b}_t * \exp(-u_t \mathbf{f}_t))) * \exp(\varepsilon_t) \tag{eqn 8}$$

where \mathbf{M} is a matrix representing annual movement rates among triangles, \mathbf{f}_t is proportional to the amount of fishing activity per

unit area $f_{r,t}$ in triangle r (e.g. the total area swept by bottom trawlers divided by the total triangle area), and u_t is an estimated scaling coefficient such that $u_t f_{r,t}$ is the instantaneous fishing mortality rate. Process error $\boldsymbol{\varepsilon}_t$ again represents spatially correlated, unexplained variation in dynamics:

$$\boldsymbol{\varepsilon}_t \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_\varepsilon) \quad \text{eqn 9}$$

where $\text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_\varepsilon)$ is a multivariate normal distribution with mean zero and covariance $\boldsymbol{\Sigma}_\varepsilon$, where process error covariance $\boldsymbol{\Sigma}_\varepsilon$ between triangles r_1 and r_2 follows a Matérn function of distance:

$$\text{Cov}(\varepsilon_{r_1,t}, \varepsilon_{r_2,t}) = \frac{\tau_\varepsilon^{-2}}{2^{\nu-1}\Gamma(\nu)} (\kappa_\varepsilon |s_1 - s_2|)^\nu K_\nu(\kappa_\varepsilon |s_1 - s_2|) \quad \text{eqn 10}$$

where τ_ε governs the pointwise variance of $\boldsymbol{\varepsilon}$, κ_ε governs the geostatistical range of correlations, ν is the smoothness of the covariance matrix (we assume that $\nu = 1$ in the following), and K_ν is the Bessel function.

To approximate movement rates \mathbf{M} among triangles within the population domain, we define a matrix \mathbf{N} representing instantaneous movement rates among all triangles. \mathbf{N} is negative on the diagonal and positive or zero everywhere else, and the off-diagonal n_{r_1,r_2} is zero if triangles r_1 and r_2 do not share an edge. Instantaneous movement rate \mathbf{N} is further decomposed into movement in each of four cardinal directions, where \mathbf{m} is a vector of parameters representing movement in each cardinal direction. Further details regarding the computation of \mathbf{N} given a set of n_r triangles in a population domain are given in Appendix S2, and code for computing these matrices is provided as an R package *MovementTools* on the first author's GitHub page (https://github.com/james-thorson/movement_tools). Given \mathbf{N} , the matrix \mathbf{M} approximating annual movement rates can be calculated using the matrix exponential operator. During parameter estimation, however, we apply the Euler approximation movement to calculate annual movement rates \mathbf{M} given instantaneous rates \mathbf{N} (see Appendix S3).

In the following, we specify that density dependence follows the Gompertz production function:

$$g(b_{r,t}) = b_{r,t} \exp\left(\alpha + \omega_r - \beta \log\left(\frac{b_{r,t}}{a_r}\right)\right) \quad \text{eqn 11}$$

where α governs the average population density in the absence of fishing, β is the loglinear decline in productivity with increasing density, a_r is the total area of triangle r (this standardizes between triangles of different sizes, so that density dependence $\beta \log\left(\frac{b_{r,t}}{a_r}\right)$ is a function of densities $\frac{b_{r,t}}{a_r}$ rather than abundance $b_{r,t}$), and ω_r represents spatial variation in productivity:

$$\boldsymbol{\omega} \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_\omega) \quad \text{eqn 12}$$

where $\boldsymbol{\Sigma}_\omega$ represents the covariance of spatial variation in productivity, which again follows a Matérn covariance function (Thorson *et al.* 2015c).

Similar to the conventional surplus production model, we must specify abundance $b_{r,0}$ in the first modelled year. We specify initial abundance as:

$$\mathbf{b}_0^* = \mathbf{M} \left(\mathbf{a} * \exp\left(\mu + \frac{\boldsymbol{\omega}}{\beta}\right) * \exp(-u_1 \mathbf{f}_1) \right) \quad \text{eqn 13}$$

where $\mathbf{a} * \exp\left(\mu + \frac{\boldsymbol{\omega}}{\beta}\right)$ approximates abundance as starting in the first year at an estimated offset $\exp(\mu)$ away from the equilibrium

density given a Gompertz production function $\mathbf{a} * \exp\left(\alpha + \frac{\boldsymbol{\omega}}{\beta}\right)$, and \mathbf{b}_0^* therefore represents a first-order approximation to equilibrium abundance given that fishing effort prior to the first year is approximately equal to its value in the first year of data (i.e. that $u_0 \mathbf{f}_0 \approx u_1 \mathbf{f}_1$).

We estimate the spatial surplus production model by specifying that population-wide harvest arises as the sum of harvest in each triangle:

$$h_t = \exp(\delta_t) \sum_{r=1}^{n_r} b_{r,t} (1 - \exp(-u_t f_{r,t})) \quad \text{eqn 14}$$

where δ_t again follows a normal distribution. We specify that available survey data c in triangle r in year t arises from a zero-inflated gamma distribution:

$$\Pr(C = c) = \begin{cases} \exp(-\theta_1 \lambda) & \text{if } c = 0 \\ (1 - \exp(-\theta_1 \lambda)) \text{Gamma}\left(c; \theta_2^{-2}, \frac{\lambda}{(1 - \exp(-\theta_1 \lambda))} \theta_2^2\right) & \text{if } c > 0 \end{cases} \quad \text{eqn 15}$$

where $\text{Gamma}(x; a, b)$ is the probability density function evaluated at x , given shape a and scale b , θ_1 governs how the probability of zero catch scales with predicted density (where $\theta_1 = 0$ implies that increases in density result in larger aggregations but no increase in the probability of encountering an aggregation), θ_2 is the coefficient of variation for catch rates given an encounter, and λ is the expected catch:

$$\lambda = qw \left(\frac{b_{r,t}}{a_r}\right) \quad \text{eqn 16}$$

where q is the catchability coefficient, w is the area swept (or some other measure of relative survey effort) for a given sample, and $b_{r,t}/a_r$ is the population density for triangle r .

The spatial surplus production model requires estimating the magnitude of spatial variation in productivity (τ_ω^2) and unexplained spatio-temporal variation (τ_ω^2), the geostatistical range of spatial and spatio-temporal variability (κ_ω and κ_ε), measurement error parameters $\boldsymbol{\theta}$, the catchability coefficient (q), average productivity (α), the strength of density dependence (β), and instantaneous movement rates (\mathbf{m}), and treats these parameters as fixed effects. However, we assume in the following that spatial variation in productivity and unexplained spatio-temporal variation both have the same geostatistical range (i.e. $\kappa_\omega = \kappa_\varepsilon$) because this assumption appears to slightly improve model convergence. Parameters representing spatial variation in productivity ($\boldsymbol{\omega}$) and spatio-temporal variation in abundance (\mathbf{b}) are treated as random effects and are integrated across when computing the marginal likelihood of fixed effects (Thorson & Minto 2015). Parameters are estimated by fitting to annual harvest (h_t), spatial fishing effort data (\mathbf{f}), catch rates (\mathbf{c}) and area swept for catches (\mathbf{w}). We ease computation by approximating all multivariate normal distributions (i.e. eqns 9 and 12) using a stochastic partial differential equation approximation (Lindgren, Rue & Lindström 2011). The marginal likelihood is approximated using the Laplace approximation, and the gradient of the marginal likelihood with respect to fixed effects is computed via automatic differentiation techniques using the Template Model Builder (TMB) software (Kristensen 2014; Kristensen *et al.* In press). Code implementing the spatial surplus production model in TMB is available as an R package *SpatialProduction* (<https://github.com/James-Thorson/>

spatial_production), and we use three main strategies to reduce computation time during parameter estimation (see Appendix S3). The marginal likelihood is then maximized using conventional nonlinear maximization tools in the R statistical environment (R Core Team 2014), and standard errors for fixed effects are estimated by calculating the inverse of the matrix of second derivatives of the marginal likelihood function with respect to fixed effects, evaluated at their maximum likelihood estimates.

Finally, we demonstrate the use of this spatial surplus production model to estimate a level of coastwide fishery harvest that is likely to be sustainable (termed an ‘overfishing limit’ or OFL). Following previous research, we calculate the OFL_t in each year t as:

$$OFL_t = \left(1 - \exp\left(-\frac{F_{msy}}{M} M_{LH}\right)\right) \sum_{r=1}^{n_r} b_{r,t} \quad \text{eqn 17}$$

where $\frac{F_{msy}}{M}$ is an estimate of the ratio of fishing mortality at maximum sustainable yield to the natural mortality rate (see Zhou *et al.* (2012) for more details), and M_{LH} is the natural mortality rate based on life-history information, such that $\left(1 - \exp\left(-\frac{F_{msy}}{M} M_{LH}\right)\right)$ is an estimate of the fraction of abundance that can be sustainably harvested annually. Variants on this calculation have been used to calculate a limit on annual fishing (termed ‘overfishing limit’) in several fisheries management regions world-wide (Taylor *et al.* 2013; Aydin *et al.* 2014). However, we also recommend future research to estimate sustainable harvest rates from the estimated production function g (i.e. using estimates α , β , and ω).

SIMULATION EXPERIMENT TO DEMONSTRATE MODEL PERFORMANCE

We first conduct a simulation experiment to explore whether the model generates unbiased and precise estimates given the sample sizes available for this case study application. We simulate dynamics in the R statistical environment for each of 100 simulation replicates and define the spatial domain of the population model as the sampling domain of the West Coast groundfish bottom trawl survey (Bradburn, Keller & Horness 2011) along the US waters of Washington, Oregon and California, while approximating the spatial domain using a triangulated mesh with 202 triangles. To simulate input data for the spatial surplus production model, we simulate dynamics over 60 years but simulate data collection over only the final 10 years. Each simulation replicate proceeds as follows:

1. We first simulate a spatial component of fishing intensity (f_t) in eqn 8) as a Gaussian random field using the *RandomFields* package (Schlather 2009) and a temporal component for each year (i.e. u_t in eqn 8) that follows a log-normal distribution with log-mean $\log(0.2)$ and a log-standard deviation of 0.5.
2. We simulate population dynamics, given a moderate level of density dependence ($\beta = 0.5$), and average productivity similar to that seen in the case study application ($\alpha = \log(2.0)$). We specify that spatial variation in productivity (ω) has a marginal standard deviation of 1.0 (in log-space, see eqn 11) and unexplained spatio-temporal variation in dynamics has a log-marginal standard deviation of 0.5. We also simulate a low level of isotropic movement, such that the average probability of residing in a given triangle from 1 year to the next is

96.6%. Given these parameter values, dynamics are simulated as outlined previously (eqns 8 and 11). We note that we use the matrix exponential function to calculate movement rates when simulating data, whereas we use the Euler approximation in the estimation model.

3. Given these simulated dynamics, we calculate total fishery harvest in each year (eqn 14). We also simulate survey catch data for each of 600 samples per year, where each sample in each year occurs at a randomly chosen location within the survey domain. Catch for each survey tow follows a zero-inflated gamma distribution ($\theta_1 = 1.0$, $\theta_2 = 1.0$).

For each simulation replicate, we apply the estimation model for only the final 10 years (i.e. including data and estimating dynamics for only years 51–60). However, we simulate dynamics for the preceding 50 years as a burn-in period to ensure that the simulated dynamics in the first year of the estimation model start from a biologically plausible distribution. This involves providing the estimation model with catch rate data from the 6000 simulated sampling tows in the final 10 years (c), total fishery harvest (h) and data regarding spatial variation in fishing intensity (f_t). We also correctly specify the life-history parameters required to estimate the overfishing limit (eqn 17), that is $\frac{F_{msy}}{M} = 0.87$ and $M_{LH} = 0.2$.

To assess model performance in this simulation experiment, we discard any replicate where the estimation model did not converge (i.e. had a final gradient of the marginal likelihood with respect to a fixed effect >0.01 , or had a Hessian matrix that was not positive definite). For converged replicates, we record all parameter estimates as well as model predictions of the overfishing limit OFL_t and compare these estimated values with the true simulation values. Given that we specify the correct value for life-history parameters (i.e. $\left(1 - \exp\left(-\frac{F_{msy}}{M} M_{LH}\right)\right)$ in eqn 17), evaluating estimation performance for OFL_t is identical to assessing performance in estimating total abundance (i.e. $\sum_{r=1}^{n_r} b_{r,t}$ in eqn 17). As with any new method, we encourage future research testing model performance given other simulation scenarios.

CASE STUDY APPLICATION

As a case study demonstration of the spatial surplus production model, we analyse data for big skate *Raja binoculata* in the US waters of the California Current. This large-bodied elasmobranch reaches a maximum size of 204 cm and a maximum age of 26 years (McFarlane & King 2006). We analyse survey catches in 2003–2013 from the West Coast groundfish bottom trawl survey, which conducts approximately 650 trawl tows every summer at randomly selected locations in the California Current. Each tow of this survey is in contact with the bottom for approximately 15 min (with an area swept of approximately 2 hectares) and involves identifying every fish caught to its species (i.e. it yields a count of big skate caught in every trawl tow along with the location of that tow). Given 11 years of data, this survey provides approximately 7150 sampling tows for use during parameter estimation. For this case study, we approximate the population domain using 202 triangles.

To characterize spatial variation in fishing intensity (i.e. f_t), we use data regarding bottom trawl fishing effort from self-reported fishery logbooks. Logbooks are collected by each state (Washington, Oregon and California) and compiled by PacFIN (a coastwide repository of catch data), and we use a data base that has been preprocessed by the West Coast Groundfish Observer Program (WCGOP). Logbooks include information reporting the

total bottom time for each bottom trawl tow in the groundfish fishery, as well as its location (latitude and longitude) and date. As an alternative data source regarding fishing effort, we also compile bottom trawl fishing data from fishery observers who are contracted by the WCGOP to monitor catches on commercial fishing vessels. Fishery observers have been present on 15–100% of the bottom trawl fishing trips in the California Current since 2002 (the start of our case study analysis), where the exact proportion varies among years (but where limited sampling will not affect our analysis as long as observers are allocated randomly). For either data source, we calculate the total bottom trawl duration in each triangle divided by the area of that triangle as a proxy for fishing intensity for each triangle and year ($f_{r,t}$). A preliminary analysis indicated no substantial or qualitative differences in model results when calculating the spatial allocation of fishing ($f_{r,t}$) from logbook or observer data, so we report results when using logbook data.

Total harvest (h_t) of big skate has previously been estimated for 2002–2013 (Somers *et al.* 2014), but is not available prior to this period due to uncertainty about species composition of elasmobranch catches arising from a lack of observer data prior to 2002. We therefore run the estimation models for 11 years with catch and survey data (2003–2013). Given that data are only available for a small number of years, likely after intensive non-targeted harvest during the 1980s–1990s, we do not have sufficient information to estimate the catchability coefficient for the survey. We therefore follow previous ‘data-poor’ analysis methods (Zhou, Griffiths & Miller 2009; Aydin *et al.* 2014) and assume that the survey catchability coefficient $q = 1$ (i.e. the survey catches all individuals within the area swept by the trawl). Following Taylor *et al.* (2013), for big skate, we assume $\log\left(\frac{F_{my}}{M}\right) \sim N(-1.02, 0.51)$, corresponding to a mean of 0.41 and a 0.55 coefficient of variation, and $\log(M_{LH}) \sim N(-1.90, 0.40)$, corresponding to a mean of 0.16 and a 0.42 coefficient of variation.

Results

SIMULATION EXPERIMENT

Results from the simulation experiment confirm that the spatial surplus production model provides unbiased and reasonably precise estimates of the overfishing limit OFL_t (Fig. 1). In particular, estimates of the sustainable level of harvest have a median relative error near zero for all years, and an 80% simulation interval ranging from -0.15 to 0.20 . A fishery harvest 20% greater than the recommended level is not likely to greatly decrease the capacity of a marine population to produce sustainable catches, so we interpret this level of precision as adequate for sustainable management of most fish stocks. Inspection of the parameter estimates in the simulation experiment (Fig. 2) similarly shows that parameters representing density dependence (β), average densities (α) and the magnitude of spatial variation in density (σ_α) are approximately unbiased (Fig. 2, panels a–c). The correlation between simulated (‘true’) and estimated density at each sampled location across years is generally high (>0.9), signifying that spatial count data and accurate information regarding the spatial distribution of fishing effort is sufficient to

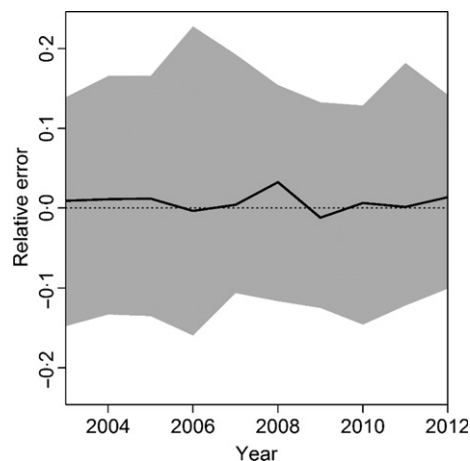


Fig. 1. Summary of the relative error when estimating the annual overfishing limit in a simulation experiment, calculated as $RE_t = (\widehat{OFL}_t - OFL_t)/OFL_t$, where \widehat{OFL}_t is the estimate from the estimation model and OFL_t is the true value for that simulation replicate. The shaded area shows the 80% simulation interval, and the solid black is the median estimate for each year (the dotted line indicates zero, i.e. an ideal estimate).

reconstruct spatio-temporal patterns in population density (Fig. 2f). However, we detect substantial positive bias in estimates of spatio-temporal error and movement probabilities (Fig. 2d–e). We also note that 15 of 100 replicates did not converge (i.e. had a gradient of the marginal likelihood >0.01 for at least one fixed effect), although results are similar using either a more or less strict criterion for convergence.

CASE STUDY APPLICATION

Based on results in the simulation experiment, we conclude that the spatial surplus production model is not able to accurately estimate movement rates given the quantity of data and time-series length that is available in the case study example. We therefore proceed by exploring three alternative assumptions regarding movement rates for big skate, that is assuming that movement is absent ($m_{east} = m_{north} = m_{west} = m_{south} = 0$), low ($m_{east} = m_{west} = 0.056$, $m_{north} = m_{south} = 0.113$, where these values are chosen such that movement north–south occurs at twice the rate of movement east–west, and that the probability of residing in a given triangle between years is 0.95 on average), or moderate ($m_{east} = m_{west} = 0.116$, $m_{north} = m_{south} = 0.232$, such that residence probability is 0.9 on average). These three models (and higher rates of movement) give almost identical estimates of the overfishing limit (Fig. 3), so we proceed by summarizing results from the ‘low movement’ scenario.

Densities of big skate are estimated to vary greatly over space, with highest densities ($>50 \text{ kg km}^{-2}$) nearshore off the Oregon and Washington coasts (Fig. 4; see Table 1 for parameter estimates). Densities decrease off the California Coast south of Cape Mendocino, with the exception of a nearshore area with elevated densities near the Sacramento

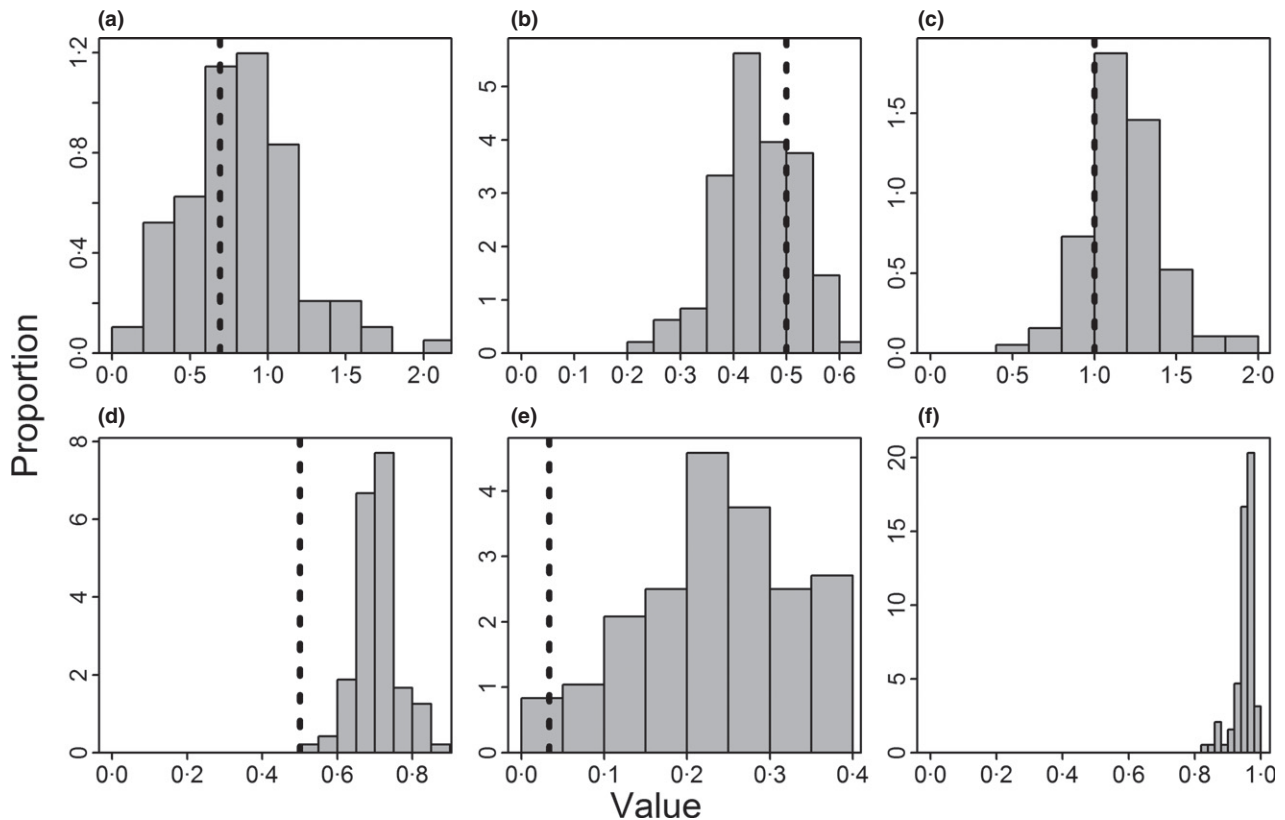


Fig. 2. Distribution of parameter estimates for (a) average density, α , (b) density dependence β , (c) marginal standard deviation of spatial variation in productivity σ_{ω} , (d) marginal standard deviation of residual error in spatio-temporal dynamics σ_{ϵ} , (e) average probability of an individual fish remaining in triangle r between year t and $t + 1$, (f) correlation between true density $u_{r,t}$ and estimated density $\hat{u}_{r,t}$. Panels (a–e) show a dashed vertical line giving the true value in the simulation experiment, whereas the correlation in panel (f) would ideally have a value of 1.0 for each replicate.

Delta, and densities are significant ($>5 \text{ kg km}^{-2}$) all the way to the southern border with Mexico. Densities are generally lower offshore than nearshore across the entire coast, although offshore densities are greatest near northern California. Similarly, some years show a noticeable change in coastwide density, for example from 2010 to 2011, when the high-density areas off northern Oregon and southern Washington show an appreciable decrease in density. A comparison of the observed harvest with an estimate of the annual overfishing limit in each year (Fig. 3) shows that harvest rates have been considerably below target levels for all years from 2003 to 2013 and have been declining over time. This conclusion holds despite substantial fluctuations in the estimate of total abundance during this period, with depressed abundance during 2006–2008 and elevated abundance in 2010–2013.

Discussion

We have demonstrated how to approximate spatially explicit population dynamics using individual movement, density-dependent production and unexplained dynamical variation that is spatially correlated. This approximation is inspired by finite element analysis, a technique that is widely used in engineering applications to approximate

partial differential equations (e.g. thermodynamical systems). Specifically, we define a set of triangles that encompasses the population domain and assume that all variables are homogenous and instantaneously mixed within a given triangle. The function representing spatial variation in density is approximated as being piecewise constant within each triangle, and advection–diffusion operators are approximated using matrices of instantaneous movement rates. This approximation builds upon recent computational improvements for spatio-temporal models, for example the use of the Laplace approximation for maximum likelihood estimation and the use of the stochastic partial differential equation approximation to Gaussian random fields (which is highly efficient relative to other spatial rank-reduction techniques according to Wikle & Hooten (2010)). Our use of the Euler approximation in particular allows for a highly efficient implementation, where the probability distribution for random effects representing population density at spatially distant triangles or non-consecutive years is conditionally independent. This finite element framework also allows for easy changes in spatial resolution, where the analyst can choose to use more or fewer triangles to approximate spatial variation, depending on the spatial scale that is biologically relevant. As a final benefit, the finite element

approach allows for easy implementation of irregularly shaped population boundaries (such as the coastline of the US West Coast). We used boundaries that fish are

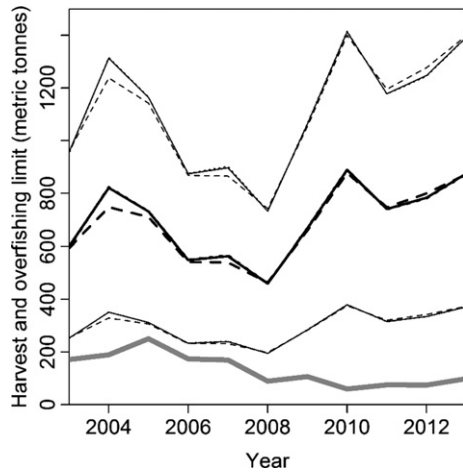


Fig. 3. Estimate of overfishing limit, \widehat{OFL}_t , for three movement rates (thick dashed line: no movement; thick solid line: 95% residence probability; thick dotted line: 90% residence probability) and its estimation interval, $\widehat{OFL}_t \exp(\pm SE[\log(\widehat{OFL}_t)])$, where $SE[\log(\widehat{OFL}_t)]$ is the estimated standard error of the log-OFL (intervals plotted with thinner lines above and below overfishing limit estimate), plotted against observed fishery harvest (thick grey line).

unable to cross in this study ('reflective boundaries'), but note that future research could explore boundaries that cause fish to 'disappear' from the modelled portion of the population after crossing ('absorptive boundaries').

The spatial surplus production model generalizes several previous spatial and spatio-temporal models in ecology. If movement rates are negligible (i.e. $\mathbf{N} = \mathbf{0}$ such that $\mathbf{M} = \mathbf{I}$) and there is no human harvest (i.e. $\mathbf{h} = \mathbf{0}$), then the model reduces to the spatial Gompertz model (Thorson *et al.* 2015c). A non-spatial Gompertz model has been generalized for analysis of community dynamics (Ives *et al.* 2003; Hampton *et al.* 2013), and we envision that our spatial production model could similarly be useful for analysis of community dynamics given movement and human harvest. If density dependence is strong (i.e. $\beta = 0$, such that abundance tends to return to equilibrium in each year), then movement rates have no impact on model results and the model reduces to a spatial regression such as those used when standardizing abundance data in marine stock assessment models (Thorson *et al.* 2015b). Finally, if spatial variation is absent (i.e. the correlation matrix for spatial variation and spatio-temporal error is a matrix of ones and fishing effort is constant spatially), then the model reduces to the conventional non-spatial Gompertz model, which has previously been used

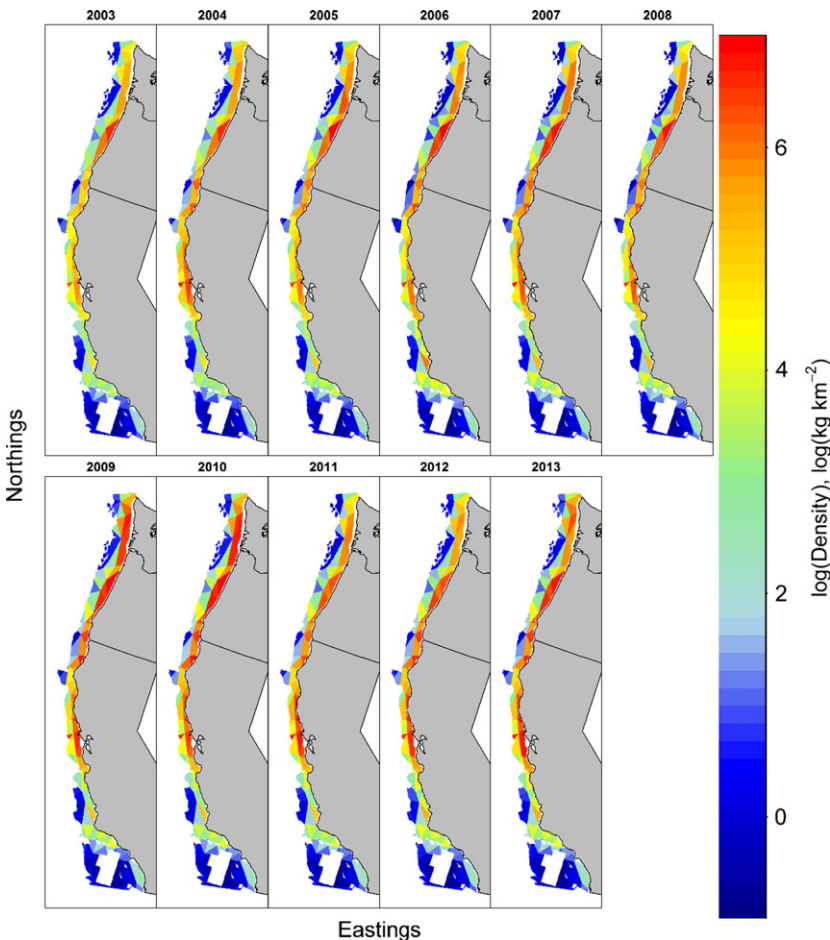


Fig. 4. Estimated density of big skate in the US waters of the California Current (colour scale is shown on the right-hand side of the plot).

Table 1. Parameter estimates and standard errors for spatial surplus production model applied to big skate in the US waters of the California Current

Name	Symbol	Estimate	Standard error
Median productivity	α	1.993	0.895
Density dependence	β	0.756	0.178
Parameter governing offset between initial and equilibrium abundance	μ	2.417	1.010
Parameter governing the range of spatial correlations	$\log(\kappa)$	0.069	0.181
Parameter governing the magnitude of spatial variation in productivity	τ_{ω}	0.102	0.026
Parameter governing the magnitude of otherwise unexplained spatio-temporal variation	τ_{ϵ}	0.448	0.131
Log-rate of decay in probability of zero catches with increasing local density	$\log(\theta_1)$	-2.292	0.035
Log-coefficient of variation in positive catches	$\log(\theta_2)$	0.038	0.020
Derived quantities			
Log-standard deviation of spatial variation	$\log(\sigma_{\omega})$	0.950	0.263
Log-standard deviation of spatio-temporal variation	$\log(\sigma_{\epsilon})$	-0.531	0.168

to guide design of adaptive management regimes in fisheries (Walters & Ludwig 1987).

Our case study application involving big skate in the US portion of the California Current indicates that recent harvest rates are considerably lower than is likely to be sustainable based on life-history analyses (Zhou *et al.* 2012; Taylor *et al.* 2013). Research increasingly supports the use of tiered monitoring programs for all species that are impacted by any human activity within marine systems (Smith *et al.* 2008). Assessing the potential impact of every human activity on every marine species would be infeasible and extremely costly, but is potentially feasible using a tiered monitoring system in which species with low levels of catch are assessed using qualitative methods (Level 1), potentially followed by rapid and high-throughput quantitative techniques (Level 2), and only then followed by intensive stock assessments (Level 3, following definitions in Hobday *et al.* (2011)). The spatial surplus production method is conceptually similar to other Level 2 techniques that compare survey estimates of population abundance with a measure of fishing effort (e.g. Zhou, Griffiths & Miller (2009)), and we therefore recommend its use as a monitoring tool for species that are impacted but do not otherwise have a high likelihood of strong human impacts. If the spatial surplus production model for big skate had indicated a greater ratio of observed to sustainable harvest, we would then recommend that more data-intensive methods be used for its assessment (Maunder & Punt 2013; Methot & Wetzel 2013).

The spatial surplus production model builds upon a growing toolbox of spatial modelling techniques in population and community ecology. Multispecies (a.k.a. 'joint') distribution models are increasingly used to identify spatial areas that can efficiently protect high-density or species-rich habitats (Clark *et al.* 2013; Pollock *et al.* 2014; Thorson *et al.* 2015a), and spatial models for invasive species are increasingly feasible when interpreting monitoring data (Hooten & Wikle 2010). The adoption of spatial population models for marine species has previously been hindered by a lack of information regarding the

spatial distribution of fishing impacts. In this study, we have used data from fishery logbooks to estimate the spatial distribution of fishing effort and have combined this with coastwide estimates of total fishery catch. Extending the model prior to 2002 (e.g. using survey catch rate data starting in 1977) is infeasible for big skate because earlier coastwide harvest has not previously been estimated. However, logbook data otherwise could be used for other species to discriminate coastwide spatial patterns in fishing effort as early as 1987, so the spatial surplus production model developed here could be used to reconstruct historical dynamics for other species.

Our simulation experiment illustrated that movement rates cannot be reliably estimated given the quantity of data available in our case study. However, this imprecision does not appear to degrade estimation performance for other model parameters or derived quantities given the data available for well-sampled fish stocks off the US West Coast. We suspect that precise estimation of movement parameters will require tagging data (e.g. Caruthers, McAllister & Taylor (2011)). Movement of tagged fish from the release location to the recapture location can be analysed as a Poisson-distributed generalized linear model, where the probability of transition from one triangle to another in t years (conditional on survival of the tagged individual) is equal to the movement matrix \mathbf{M} raised to the t -th power. Evaluating estimation performance in this case, and identifying a suitable case study application, is an active area of research for the authors.

The spatial surplus production model is also intended as a starting point for developing population models that include age, length and sex structure. Incorporating samples of length, age or sex composition can be accomplished in multiple ways. Given that only a subsample of caught individuals is measured for sex, length or age, and given that the intensity of age/length/sex subsampling is statistically independent of catch rates, these length, age and sex composition samples can be approximated using a Poisson distribution. However, many sampling programs subsample a fixed number of fishes for each tow

(e.g. measure age for at most five individuals per sampling tow), and this induces a correlation between subsampling intensity and catch rates. This circumstance is termed ‘preferential sampling’ in the geostatistical literature (Diggle, Menezes & Su 2010) and results in well-known biases in estimates of age, length and sex structure. We therefore recommend research regarding preferential sampling for spatially structured population models.

Similarly, future research could seek to estimate the catchability coefficient. In this study, we assume that $q = 1$, that is that all individuals within the area swept by the survey are subsequently caught. We note, however, that catchability would need to be considerably higher (i.e. $q > 2.5$) for harvest to exceed the annual overfishing limit in any year from 2003 to 2013. The assumption that $q = 1$ is commonly made in data-poor assessment methods in the USA (Taylor *et al.* 2013; Aydin *et al.* 2014) and Australia (Zhou, Griffiths & Miller 2009), and it will be wrong whenever a substantial portion of fishes either avoid capture ($q < 1$), or the effective area swept is greater than the nominal area swept due to herding behaviours ($q > 1$). The catchability coefficient is estimable in at least three circumstances. First, it can be estimated whenever increases in fishery catch are associated with decreases in catch rates (e.g. by treating a fishery as a depletion experiment). This technique would require extending the time series of information regarding the spatial distribution of fishing effort to periods of high fishing rates (typically prior to 2000 for bottom-associated fishes in the California Current). Secondly, the catchability coefficient can be estimated whenever information regarding growth and mortality rates, compared with age or length structure, gives direct information regarding fishing mortality rates (Hordyk *et al.* 2014; Thorson & Cope *In press*). Thirdly, it can be estimated when tag–recapture data give auxiliary information regarding fishing mortality rates. We speculate that technique #1 (extending fishing effort data) will be most applicable for future assessments of big skate, because routine collection of tagging or age information is lacking for this species, and the catches of elasmobranchs were not sampled early enough to capture the periods of historically high catch rates.

Finally, we encourage future simulation modelling research to determine the average management performance of the spatial surplus production model when combined with different possible pre-determined rules for managing fishery harvest (termed ‘harvest control rules’, e.g. see Ichinokawa *et al.* (2015)). In particular, this evaluation will likely require exploration of the assumption that sustainable harvest rates can be derived from the population’s natural mortality rate. Harvest control rules could also be specified as being area-specific, which would presumably be important for maintaining biomass targets in each area given spatial variation in fishing rates. Area-specific harvest control rules could be particularly useful for monitoring human impacts in developing fisheries, where individual ports or processing facilities might begin to develop a particular fishery faster than others.

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Data accessibility

Survey catch rate data: available from <http://www.nwfsc.noaa.gov/data> (available starting March 2016).

Fishery logbook data: Fishery logbook data have not been archived because these data are sensitive according to the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act. The data are stored by PacFIN but the version used here has been processed by the West Coast Groundfish Observer Program. Please contact Kayleigh Somers (kayleigh.somers@noaa.gov) for access.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Plot of big skate densities for each year.

Appendix S1. Generating the set of triangles used to approximate spatio-temporal dynamics.

Appendix S2. Movement matrix computation on a triangulated mesh.

Appendix S3. Strategies to reduce computation time.