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Spatio-temporal variation in size-structured populations using fishery data: an application to shortfin mako (*Isurus oxyrinchus*) in the Pacific Ocean

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Abstract

We develop a length-disaggregated spatio-temporal delta-generalized linear mixed model (GLMM) and apply the method to fishery-dependent catch rates of shortfin mako sharks in the North Pacific. The spatio-temporal model may provide an improvement over conventional time-series and spatially stratified models by yielding more precise and biologically interpretable estimates of abundance. Including length data may provide additional information to better understand life history and habitat partitioning for marine species. Nominal catch rates were standardized using a GLMM framework with spatio-temporal and length composition data. The best fitting model showed that most hotspots for "Immature" shortfin mako occurred in the coastal waters of Japan, while hotspots for "Subadult and adult" occurred in the offshore or coastal waters of Japan. We also found that size specific catch rates provide an indication that there has been a recent increasing trend in stock abundance since 2008.

Keywords: spatio-temporal model, catch per unit effort, length data, shortfin mako, template model builder

1. Introduction

Reliable indices of population abundance are an important type of data for stock assessment (Francis 2011). For stocks lacking designed fishery independent surveys, fishery catch-per-unit effort (CPUE) data provide information on trends in stock abundance that is otherwise missing. Abundance indices provide not only trends, but can be used to estimate population scale when combined with catch in population dynamic models (Lee et al. 2014). Key to the use of these data is the assumption that the change in the index is proportional to changes in population abundance (Wilberg et al. 2010). Much attention has been devoted to estimation of CPUE from fishery dependent catches and effort (Maunder and Punt 2004). Methods for standardizing CPUE data rely on introduction of auxiliary information to separate changes due to changing population abundance from those due to changes due to fishing practices and other factors. For widely dispersed stocks, the effects of spatial heterogeneity of both fish and fisheries need to be considered with respect to the assumption of proportionality between estimates of CPUE and population abundance. This becomes even more important when large areas of the stock distribution receive little or no effort and assumptions about these areas becomes influential on estimates of stock trend (Walters 2003; Carruthers et al. 2010; Carruthers et al. 2011).

Spatio-temporal modeling methods have been introduced to deal with spatial variation in population distribution and density. Spatio-temporal methods can be used to estimate population abundance indices using formal statistical tools such as likelihood functions and sampling designs (Bez 2002; Kristensen et al. 2014; Nishida and Chen 2004; Petitgas et al. 2014; Petitgas 1998; Roa-Ureta and Niklitschek 2007; Thorson et al. 2015b, 2015c). Recent studies show that the approach may yield more precise, biologically reasonable, and interpretable estimates of abundance than common methods such as GLM (generalized linear model) and GLMM (generalized linear mixed model) (Shelton et al. 2014; Thorson et al. 2015b) by reducing sample selection bias and filling in the spatial gaps common in fishery-dependent data (Walter et al. 2014; Carruthers et al. 2011; Thorson et al. 2016).

Spatial and temporal changes in the size (or age) structure of the population is an important aspect of the population abundance because marine fishes such as billfishes and oceanic pelagic sharks show evidence of spatial size (or age/stage) segregation (Nakano and Nagasawa 1996; Piner et al. 2013).

Inclusion of auxiliary information about length into spatio-temporal methods allows prediction of the annual trends of the standardized CPUE by length which may better accounts for changes in spatial patterns of size structure of the stock. Kristensen et al. (2014) developed a spatio-temporal dynamics model for Skagerrak cod (*Gadus morhua*) and Thorson et al. (2015a) developed a stage-structured model for rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska using information from different types of survey gear. These models incorporated size-structured information and described abundances of different size classes and spatial bycatch risk. It would be therefore useful to illustrate the temporal changes in the size specific CPUE using the fishery dependent data for pelagic sharks, which could be used to distinguish juvenile and nursery habitats for these species, similar to recent length-structured spatio-temporal analysis of survey trawls for shallow-water hake in the Benguela current (Jansen et al. 2016).

Shortfin mako (*Isurus oxyrinchus*) is a large and highly migratory shark species, and is widely distributed in the Pacific Ocean between 50°N to 50°S (Compagno 2001). Shortfin mako is susceptible to overexploitation due to slow growth rates, maturity at a late age, and low fecundity (Compagno 2001). Female shortfin mako attain maturity at a much larger size and older age (256 cm PCL: pre-caudal length / approximately 17 years old) than males (156 cm PCL / approximately 5 years old) (Semba et al. 2011). In the western and central North Pacific, mainly 60-240 cm PCL (0-20 years old) individuals are caught as bycatch by Japanese commercial pelagic longline fisheries targeting tuna and billfish (Kai et al. 2015). Standardized CPUE of shortfin mako in the North Pacific were estimated using the onboard observer data from 1995 to 2010, however, the historical trends of population abundance were poorly estimated due to the misspecification of the model (See Table 1. Clarke et al. 2013). Therefore, improvement of the estimates is needed to assess the status of shortfin mako stocks with greater accuracy and precision.

The objectives of this paper are to develop a length-disaggregated spacio-temporal delta-GLMM using fishery-dependent catch-rate data and to apply the method to shortfin mako in the western and central North Pacific. This method is used to predict not only the temporal (yearly) changes in the CPUE but also the spatio-temporal distribution of CPUE for the different growth stages (size classes) of shortfin mako. Improvements in both standardized CPUE and understanding of spatial patterns of shortfin mako should result in better assessment and management of the stock.

2. Materials and Methods

2.1. Data sources

Catch and effort data of Japanese shallow-set longliners operating in the western and central North Pacific from 2006 to 2014 were used to estimate the spatio-temporal variation in population density for shortfin mako in the last nine years. We have a long time series of the catch and effort data from 1994 to 2014 but we used the data from 2006 to 2014 due to the limitation of the reliable length data. The set-by-set data used in this study included information on species of sharks, catch number, amount of effort (number of hooks), number of branch lines between floats (hooks between floats: HBF) as a proxy for gear configuration, and location (longitude and latitude) of set, with a resolution of 2 × 2 degree square. Only the shallow-set data were used in the analysis. The shallow-set data could be determined because fishermen changed the depth of the gear to change the target species, and the number of HBF varied depending on the depth (Nakano et al. 1997). We defined the shallow-set fishery by the use of a small number of HBF (3 - 5). The hooks of the regular longline gear using these HBFs are estimated to hang at the depth around 50 to 120 m (Suzuki et al. 1977).

The National Research Institute of Far Seas Fisheries in Japan commenced a project to collect the length data of shortfin mako caught by Japanese coastal and offshore longline fishery in 2003. The fishermen in the Kesennuma fishing port measure the precaudal length (PCL) of shortfin mako on the boat. The Kesennuma fishing port is located in the northeast part of the Japanese mainland and it is well known for its large landings of tuna, billfish and sharks (Ishimura and Bailey 2013). The longliner recorded the size and other auxiliary information such as sex and exact location of the starting position of each sets in addition to the information of the logbook data. We used the length data during 2006 and 2014 because many inaccurate records were included in the earlier periods during 2003 and 2005. The size data of each individual caught by shallow set longliner was collated with the catch record of shortfin mako in the logbook of the longline boat with a resolution of 2 x 2 degree square and year and quarter. We then multiplied the catch rates from length-aggregated catch records by the proportion-at-size in the longliner logbook data and analysed these length-disaggregated catch rates. When a given 2x2 square did not have both longliner catch records and logbook data in a given quarter or year, we did not include that location in that time period in the model. Available data include the average location and time of all sets with a resolution of 2 x 2 degree square and year and quarter. The detailed information about the data aggregation was summarized in Appendix A (Table A1).

The available data covered core areas of shortfin mako catch in the western and central North Pacific (24 -44°N and 138°E -160°W) (Fig. 1) and four seasons. Four seasons (quarters 1 to 4) were defined as follows: Q1 was spring from January to March; Q2 was summer from April to June; Q3 was fall from July to September; and Q4 was winter from October to December. The fishery data provide enough quantitative data to estimate the year-specific changes in the species distribution function and relative trends of CPUE for growth stages of shortfin mako in the western and central North Pacific.

Three growth stages were defined as follows: "Juvenile" denotes the body size smaller than 90 cm PCL (age-0), "Immature" denotes the body size between 90 cm and 160 cm PCL, and "Subadult and adult" denotes the body size larger than 160 cm PCL.

2.2. Spatio-temporal model with length composition data

Size and CPUE data originate from two different sampling processes, such that length measurement and catch per shot are not always directly matched. Then, the density estimate per station (i.e. grid cell) is informed by the CPUE data and then decomposed by the estimated contribution of each size class. The decomposition of the CPUE trend into individual size classes is the novel feature in this study. Previous studies that incorporated auxiliary length information into spatial and temporal models (Kristensen et al. 2014; Nielsen et al. 2014; Thorson et al. 2015a; Jansen et al. 2016) have focused on research trawl survey data based on underlying randomly stratified sampling designs, whereas we attempt to fit both length and CPUE to shallow-set longline fishery data. The fisheries-dependent data is collected from a highly unbalanced sampling design due to systematic changes in the spatial effort allocation and targeting behavior of the fleet (Carruthers et al. 2010, 2011; Thorson et al. 2016). A spatio-temporal modeling approach can in some cases account for fishery targeting occurring at large spatial scales, and is therefore appropriate to account for some common forms of bias that arise when analyzing in fishery-dependent catch rates (Thorson et al. 2016).

We develop a model that accounts for both size-specific spatio-temporal variabilities in the distribution and the relative trends of catch rate of shortfin mako in the last nine years in the western and central North Pacific. We use a length-structured spatio-temporal model for this task, so that we can explicitly decompose variance into additive components representing variation among years and size classes (Krisensen et al. 2014). We then use the model to predict density at unsampled locations, times and length classes, to provide a best-estimate of the distribution of species, relative trends of total abundance, and length compositions. Spatio-temporal and length modelling of CPUE data assumes that nearby locations and nearby size classes should have similar density estimates during each time interval. The correlation between statistical stations (latitude and longitude) and length classes (length bins) in a given interval is then used to estimate density in each year for all stations and length classes, including stations and length bins that do not have data in a given period. We then visualize the predictions of spatio-temporal variation in density and the temporal (yearly) changes in the total abundance for the different growth stages (size classes).

2.3. Model description

The spatio-temporal model incorporating length data estimated the density d (s, t, q, l) in each station s (latitude and longitude with a resolution of 2 × 2 degree square), year t (where t=1 in signifies 2006 and t=9 signifies 2014), quarter q (signifying a three-month quarter, where q=1 in signifies Q1(Jan-March) and q=4 in signifies Q4(Oct-Dec)) and body length l (bin #1: 50-80 cm; #2: 80.1-90cm; #3: 90.1-100, …, #12: 180.1-190 cm; #13: 190.1-340 cm., e.g., where the first bin is all individuals less than or equal to 80cm, and the last bin is all individuals greater than 190 cm). After estimating parameters, we then calculate juvenile density as the sum of density for 50-80 cm and 80.1-90 cm (i.e., the 1^{st} and 2^{nd} length bins), immature as the sum of density for 90.1-100 cm to 150.1-160 cm (i.e., the 3^{rd} to 9^{th} length bins), and subadult and adult as density for larger than 160.1 cm (i.e., the sum of the 10^{th} to 13^{th} length bins).

We modeled variation in density among both years and quarters, to capture both annual trends in abundance and quarterly changes in catch rates. Each station, year, quarter and length-bin had the density:

$$d(s,t,q,l) = \exp\left(d_0(t) + \gamma(s) + \tau(l) + \theta(s,t,l) + \delta(q) + \sum_{j=1}^{n_j} \beta_j x_j(s,t,q,l)\right) \qquad (1)$$

where $d_0(t)$ represents intercept for year *t*, $\gamma(s)$ represents spatial variation (the average density in station *s* relative to the average station) , $\tau(l)$ represents the non-parametric impact of length on expected catch rates (the average density in length *l* relative to the average length), $\theta(s,t,l)$ represents an interaction term and spatio-temporal and length variation (variation in density for station *s*, year *t* and length *l* after accounting for spatial, temporal and length variation), $\delta(q)$ is an offset that represents the impact of quarter (*q*) on average density, β_j is the effect of the j^{th} covariate on predicted density, and $x_j(s,t,q,l)$ is the value of the j^{th} covariate for a given location, year, quarter, and length-category. In the following, we use as covariate the length of the individual (i.e., $n_j = 1$ and $x(s,t,q,l) = l$), which generates a log-linear increase or decrease in expected density with length, but future research could incorporate additional habitat variables. The marginal (common to all spatial stations and times) length variation,$\tau(l)$, is modeled using a first-order autoregressive process (AR1) to explain the correlations among length bins.:

$$\boldsymbol{\tau} \sim MVN(0, \sigma_\varepsilon^2 \mathbf{R}_\tau) \qquad (2)$$

where MVN is a multivariate normal distribution with mean 0 correlation matrix $\mathbf{R}_\tau$, and pointwise variance σ_ε^2:

$$\mathbf{R}_\tau(l,l') = \rho_\tau^{|l-l'|} \qquad (3)$$

where ρ_τ is a parameter governing autocorrelation, while |*l*-*l'*| is the difference in length among samples in length-bin *l* and *l'*. ρ_τ is the magnitude of autoregression (where $\rho_\tau = 0$ implies that all lengths are statistically independent, while $\rho_\tau = 1$ implies that total density approaches a random-walk process among lengths). The model (Eq. (1)) includes both a parametric effect of length (by including a log-linear impact of length on expected catch using parameter β_j) and a non-parametric effect of length (by including a first-order autoregressive component using $\tau(l)$). We therefore interpret this as a "semi-parametric" model with respect to the impact of length on catch rates (e.g., Kristensen 2014; Thorson and Taylor 2014).

Spatial variation $\gamma(s)$ is modeled as a Gaussian random field (GRF), which reduces to a multivariate normal distribution when evaluated at a finite set of stations (Thorson et al. 2015c):

$$\boldsymbol{\gamma} \sim MVN(\mathbf{0}, \boldsymbol{\Sigma}_{spatial}) \tag{4}$$

where $\boldsymbol{\Sigma}_{spatial}$ is spatial covariance for the random field and approximated using a Matérn correlation function with smoothness $\nu = 1$:

$$\boldsymbol{\Sigma}_{spatial}(s, s') = \frac{{\sigma_\gamma}^2}{\Gamma(\lambda)2^{\nu-1}} \cdot (\kappa|\mathbf{H}(s - s')|)^{\nu} K_\nu(\kappa|\mathbf{H}(s - s')|) \tag{5}$$

where $|s\text{-}s'|$ is the Euclidian distance between two generic locations s and s', σ_γ is the marginal variances of the spatial random field, Γ is the gamma function, and K_ν is the modified Bessel function of second kind (Lindgren et al. 2011). This covariance function calculates the correlation between $\boldsymbol{\gamma}$ at stations s and s' given their distance $|s\text{-}s'|$ after linear transformation $\mathbf{H}$ which accounts for geometric anisotropy (see supplementary in Thorson et al. 2015a). If the spatial covariance structure is equivalent in all directions, it can be described as a function of distance only and is said to be isotropic (i.e. $\mathbf{H}$ is a two-dimensional identity matrix). If the spatial covariance structure varies in different directions, then it is a function of the distance and direction and is said to be anisotropic (where the directions of slow and fast decorrelation are given by $\mathbf{H}$). Isotropic processes form an inadequate basis in modelling many spatially distributed data, while $\mathbf{H}$ is essentially a linear transformation of coordinates as is common for estimating stationary anisotropy (Budrikaite and Ducinskas 2005). $\kappa > 0$ is a scaling parameter related to the range that means the distance at which the spatial correlation becomes almost null. We use a stochastic partial differential equation (SPDE) approximation to this function, and can calculate the geostatistical range ($\frac{\sqrt{8\nu}}{\kappa}$) as the distance at which correlation is close to 10 %, for each smoothness parameter $\nu > 1/2$ (Lindgren et al. 2011). We used the Matérn correlation function because previous research demonstrated how the probability of GRFs could be calculated efficiently given this assumption (Diggle and Ribeiro 2007; Lindgren et al. 2011; Roa-Ureta and Niklitschek 2007). GRF is a convenient statistical approach for implementing a 2-dimentional smoother for a response variable (in this case, catch) over spatial dimensions (Thorson et al. 2015b). The spatio-temporal and length variation, $\theta(s,t,l)$, is modeled by combining the GRF for spatial variation with first-order autoregressive process (AR1) for temporal and length variation:

$$\mathrm{vec}(\boldsymbol{\theta}_t) \sim MVN(\mathbf{0}, \boldsymbol{\Sigma}_{spatial} \otimes \mathbf{R}_\theta) \tag{6}$$

where $\mathrm{vec}(\boldsymbol{\theta}_t)$ is the vectorized value of $\theta(s,t,l)$ for all stations and length-bins in year t, $\otimes$ is the Kronecker product where if $\mathbf{A}$ is an m x n matrix and $\mathbf{B}$ is a p x q matrix, then the Kronecker product $\mathbf{A} \otimes \mathbf{B}$ is the mp x nq block matrix:

$$\mathbf{A} \otimes \mathbf{B} = \begin{bmatrix} \boldsymbol{a}_{11}\mathbf{B} & \cdots & \boldsymbol{a}_{1n}\mathbf{B} \\ \vdots & \ddots & \vdots \\ \boldsymbol{a}_{m1}\mathbf{B} & \cdots & \boldsymbol{a}_{mn}\mathbf{B} \end{bmatrix}, \tag{7}$$

$\mathbf{R}_\theta$ is the correlation in $\boldsymbol{\theta}_t$ among length-bins

$$\mathbf{R}_\theta(l, l') = \rho_\theta^{|l-l'|} \tag{8}$$

where ρ_θ is a parameter governing autocorrelation among length bins for the spatio-temporal variance component. In the following, $\delta(q)$ represents a increase or decrease in expected catch rates for each quarter relative to the 1st quarter ($\delta(1) = 0$ to ensure identifiability). We included both the covariate length as well as the AR1 for length variation, and we interpret this as a semi-parametric specification of the effect of length on expected catch rates. We estimated a separate standard deviation for spatial (σ_γ)

and spatio-temporal and length (σ_θ) components, but estimated the same decorrelation distance (κ) for the processes, using the implicit assumption that dynamics were defined by a "characteristic scale" that defined decorrelation distance for each of them. Following the parameterization from Lindgren et al. (2011), we estimated a magnitude parameter η for each spatial (η_γ) and spatio-temporal and length (η_θ) process and the corresponding standard deviation was then calculated as:

$$\sigma_\gamma = 1/\sqrt{4\pi\eta_\gamma^2)} \quad (9)$$

where the other standard deviation (i.e., σ_θ) was calculated similarly (from η_θ). Aside from this, we also estimated a magnitude parameter η for length (η_τ) process.

Expected catch λ_i is a function of density and fishing effort f_i (number of hooks), $\lambda_i = d(s_i, t_i, q_i, l_i) f_i$, and is compared with the observed catch (in numbers) c_i for the i-th observation, in station s_i, year t_i, quarter q_i and length l_i. Count data of the sharks typically included many observations with zero catch and a few observations with large values when the sharks were aggregated (Bigelow et al. 1999; Ward and Myers 2005). Population trends of by-catch species such as sharks are commonly estimated using the delta lognormal model to account for the occurrence of excess zeros (Lo et al. 1992; Zuur et al. 2009) and the negative binomial model or gamma model to account for overdispersion (Brodziak and Walsh 2013). The delta lognormal model is a combination of the probability of non-zero catches ("encounter") assuming a logistic model and the probability of positive catch rates ("catch rates for each encounter") assuming a log-normal model.

Because the compiled spatio-temporal data of shortfin mako showed evidence of excess zeros (51.3%) and the dispersion ratio (variance/mean = 34.9), we assume that available catch data c arises from the following delta (a.k.a. two stages) model, where the probability that a given sample is non-zero:

$$\Pr(C > 0) \equiv p = \left(\frac{1}{1+\exp(-z_0)}\right) \times (1 - \exp(-z_1\lambda)) \quad (10)$$

where z_0 governs the encounter probability given very high local densities (i.e., $p \rightarrow \frac{1}{1+\exp(-z_0)}$ as $\lambda \rightarrow \infty$), and z_1 governs how the probability of encounter increases with local expected catch λ. Catches then follow a lognormal distribution or a gamma distribution:

$$\Pr(C = c|c > 0) = \text{Lognormal}\left(C; \log\left(\frac{\lambda}{p}\right), \sigma^2\right) \tag{11}$$

$$\Pr(C = c|c > 0) = \text{Gamma}\left(C; \frac{1}{CV^2}, \frac{\lambda CV^2}{p}\right) \tag{12}$$

where Lognormal ($x; m, \sigma^2$) is the lognormal probability density function evaluated at x, given log-mean m and log-standard deviation σ, σ is the time-varying (i.e. yearly changes in) log-standard deviation for catch rates given an encounter, Gamma ($x; \alpha, \beta$) is the probability density function of a gamma distribution with shape α and scale β, evaluated at x, CV is the coefficient of variations for catch rates given an encounter, and these equations are defined such that $median(C) = \lambda$.

Parameters representing temporal (year) variance (d_0), spatial covariance (κ and η_γ), length variance (ρ_τ and η_τ), spatial-temporal and length covariance (κ, ρ_θ and η_θ), covariates of respective length (β) and quarter (δ), and residual variation (σ) were estimated as fixed effects while integrating across random effects representing spatial (station), length, and spatio-temporal and length variations (see Appendix Table A2). This integral was approximated using the Laplace approximation, and the fixed effects were estimated using gradient information as provided by Template Model Builder (TMB), which is an R package (R Core Team 2013) for fitting statistical latent variable models to data. It was inspired by ADMB (Fournier et al. 2012). The details of TMB are described by Kristensen et al. (2016). Further details regarding GRF estimation can be found in Thorson et al. (2015b, 2015c).

After estimating the fixed effects by maximizing the marginal likelihood of the data, the distribution of catch rates of shortfin mako were predicted from the random effects using Empirical Bayes (i.e., by fixing them to the value that maximizes the joint likelihood with respect to random effects, while fixed effects are set to their maximum likelihood estimates; Appendix B). We used a recent bias-correction algorithm to account for retransformation bias when predicting and visualizing total abundance and size composition (Thorson and Kristensen 2016). Model convergence was confirmed by ensuring that the hessian matrix was positive definite and that the absolute-value of the final gradient of parameters was less than 0.1.

2.4. Model selection and diagnostics

We selected the most parsimonious model using Akaike Information Criterion (AIC; Akaike 1974) and percent deviation (Maunder and Punt 2004). AIC identifies which model greater support had given available data: this model-selection is appropriate given that TMB implements maximum marginal likelihood estimation (Hoeting et al. 2006, Thorson et al. 2015c). Latter methodology examined a common ad hoc response that is to require each addition of model complexity to explain more than some agreed minimum (0.5 % was arbitrarily given) of additional percent deviation (%) explained (Maunder and Punt, 2004). First, we chose the best model with regards to the error distribution of positive catch part in the zero-inflated model and the necessity of the anisotropy from the following four models:

Model-A: delta-lognormal distribution model without anisotropy,

Model-B: delta-lognormal distribution model with anisotropy,

Model-C: delta-gamma distribution model without anisotropy,

Model-D: delta-gamma distribution model with anisotropy,

where the full model in Eq. (1) was used for these models. Second, we chose the best model with regards to the combinations of the explanatory variables for the selected model in the first model selection. We also compared the yearly changes in predicted catch rates among multiple models for first and second model selection. Coefficient of variations (CV) and confidence intervals of annual changes in the CPUE were calculated for the best-fitting model using the information matrix and delta-method (Fournier et al. 2012). We also examined the standard regression diagnostic statistics for the best-fitting model to identify model misspecification and heteroscedascity (Maunder and Punt 2004).

3. Results

The delta-lognormal distribution model with anisotropy and most complex model including temporal (quarter), spatial (station), length (precaudal length) and spatio-temporal and length variances as random effects was identified as the most parsimonious model by AIC (Table 1). Overall, the trend in predicted CPUE was almost similar among four models, however, the difference of the error distribution had a large impact on the trends in predicted CPUE in spite of the random field (Fig. 2a). The predicted CPUE was slightly changed if we added sequentially random effect components to the null model (Fig. 2b). These results and the marginal standard deviation (SD) in Table 1B indicated that the interaction terms and station had more impact on the changes in the trends than single length effect. Percent deviation also supported the result of the model selection by AIC (Table 1). We also examined the goodness-of-fits for the best fitting model using residual diagnostics plots (Appendix C). We then used the best fitting model to predict both the temporal (yearly) changes in the CPUE and also the spatio-temporal distribution of CPUE for the different growth stages of shortfin mako.

Average overall spatial distribution of the predicted CPUE showed that most of the hotspots for shortfin mako were in the coastal (32–42 °N and 136–146 °E) and offshore (34–44 °N and 150–170 °E) waters off Japan (Fig. 3a). The predicted CPUE in offshore water tended to be lower than those in the coastal waters with the highest CPUE was found between 36–38 °N and 142–144 °E. The results were similar to the spatial distribution of the nominal CPUE except that the CPUE is generally higher at the northern boundary (Fig. 3b).

Predicted annual CPUE exhibited a slight decline to the lowest level in 2008, and then sharply increased until 2009 and increased again in 2014 (Fig. 4). Uncertainty in CPUE estimates is larger in the most recent years (2012-2014) than in the early years (2006-2008).

Predicted CPUE by pre-caudal length intervals (cm) was dome shaped with the highest CPUE peaking at a length bin from 140 to 150 cm PCL (Fig. 5). This was a sharp contrast from the nominal peak in CPUE which occurred at length bin from 110 to 120 cm PCL. The overall mean length of predicted CPUE (146 cm PCL) was shifted to larger sizes compared to that of nominal CPUE (138 cm PCL) because the nominal CPUE by size class represented the pooled length weighted by the data (nominal catch divided by effort) and predicted CPUE by size class is weighted by area (predicted catch based on the spatial effect divided by effort). Uncertainty in CPUE estimates is larger in the middle ranges of the length classes (length from 110-170 cm PCL) than both sides (smaller than 100 cm PCL and larger than 170 cm PCL).

The average spatial distribution of the predicted CPUE for the three growth stages (Fig.6) shows that most of the hotspots for “Juvenile” shortfin mako smaller than 90 cm PCL were in the offshore waters off Japan (Fig.6a), while most of the hotspots for “Immature” shortfin mako between 90 and 160 cm PCL were in the coastal waters off Japan (Fig.6b). Most of the hotspots for “Subadult and adult” shortfin mako larger than 160 cm PCL (Fig. 6c) were in the offshore waters off Japan with some higher CPUE located in coastal waters (34–36 °N and 138–142 °E). The predicted CPUE hotspots were similar to those of nominal CPUE observations except that the nominal CPUE for juveniles was patchy (Fig. 6d-f).

Yearly changes in the predicted CPUE for different growth stages are shown in Fig.7 and Table A3. The values in Table A3 was calculated using the equations in Appendix D. Predicted CPUE of "Juvenile" shortfin mako had a decreasing trend except in 2009 and 2014 and high CPUE were observed in 2006, 2009 and 2014 (Fig. 7a). The sharp increase in CPUE for juveniles from 2013 to 2014 was unlikely to occur for a low fecundity species like shortfin mako. Predicted CPUE of "Immature" shortfin mako illustrated a slight decline to the lowest level in 2008, and then gradually increased and approached to approximately 1.5 in 2014 (Fig. 7b). The trends in the CPUE time series is strongly similar to those for all size classes in Fig. 4 because Japanese shallow set longline fishery dominantly catch the immature size classes between 90-160cm in PCL (see Fig. 5). The CVs of the predicted CPUE for "Immature" shortfin mako were smaller than those for "Juvenile" and "Subadult and adult" shortfin mako (Table A3). Predicted CPUE of "Subadult and adult" shortfin mako exhibited an increasing trend with larger CVs in accordance with the length of the elapsed time (Table A3). The fishing effort (number of hooks) showed a gradual decreasing trends since 2007, declining to approximately 0.5 million hooks in 2011 due to the Great East Japan Earthquake. Fishing effort increased in 2012 and maintained at approximately 0.75 million hooks until 2014.

The spatial distributions of the predicted CPUE for different growth stages showed that the locations of hotspots were not fixed through time (Fig. 8). "Juvenile" shortfin mako hotspots varied primarily latitudinally with one instance of a coastal hotspot. For the others (i.e. "Immature", "Subadult and adult", "All stages"), annual variability in hotspots of CPUE were high and the numbers of hotspots were increased in more recent years than early years especially for "Subadult and adult" stage. During 2014 there was a particularly large hot spot for juveniles at the northern border, which probably caused the dramatic increase in the CPUE index for juveniles in that year.

Predicted CPUE by pre-caudal length (cm) showed similar dome shapes across years (Fig. 9). The years 2010 and 2013 were the most strongly peaked (at length bins from 140 to 150 cm PCL) with the other years estimated to have broader peaked CPUE (130-160 cm PCL).

4. Discussion

We developed a length-disaggregated spatio-temporal delta-generalized linear mixed model and applied the method to shortfin mako sharks in the North Pacific. Inclusion of auxiliary length data into the spatio-temporal model provided a tool to better understand life history and habitat partitioning for marine species such as shortfin mako shark.

Oceanic pelagic sharks such as a shortfin mako typically have relatively little reliable data because of the low economic values of these sharks compared with the more valuable species such as tuna and billfish (Bonfil 1994; Walker 1988). Because stocks of pelagic sharks are often data poor (e.g., shortfin mako, which only has reliable length data starting in 2006), fishery indicators such as CPUE trends often provide the only information on stock status (ISC 2015). However, spatial shifts in fishing operations and the large spatial boundaries of stocks has made standardization of fishery catch rates problematic.

The spatio-temporal model used in this study predicted both density and length composition in areas where there is no data or inadequate data by explicitly considering the correlation of the data regarding the body length in addition to the space and time (Shelton et al. 2014; Thorson et al. 2015b). Thorson et al. (2015b) raised a concern about the spatio-temporal model which may result in biased estimates when fishing effort is correlated with population abundance (Diggle et al. 2010). However, Japanese longline fishery does not target shortfin mako, so that this may not be a problem. It is true that the spatio-temporal method will be subject to bias and increased variance if the hotspots of the shortfin mako overlaps with those of other target species, but this should also be true with more classical standardization methods.

In this study, we used a time varying standard deviation for the statistical model. The fitting to the data could be better given a separate log-standard deviation for catch rates for each year because the observation errors fluctuate with changes in the operational patterns of the fishery for each year, although the number of the parameter is increased. In addition, it was shown that the inclusion of a stochastically time-varying common variance component can lead to substantial improvements in the fit of the time series (Bos and koopman 2010).

Generalized linear mixed model commonly bases the AIC on the marginal model with the random effects integrated out which may lead model selection to favor including more covariates than is optimal (Greven and Kneib 2010). Hoeting et al. (2006) demonstrated that the corrected AIC for a spatio-temporal model was superior to the standard approach of ignoring spatial correlation in the selection of explanatory variables. However, we used a standard AIC because the corrected AIC is similar to the standard AIC for large sample size.

In this modeling, we did not explicitly account for the differences in distribution or density between males and females because many records of length were associated with individuals for which the sex was not measured. Oceanic pelagic sharks such as a shortfin mako show evidence of remarkable sexual segregation in the estimated distribution (Mucientes et al. 2009) and sexual dimorphism occurs (Bishop et al. 2006; Semba et al. 2009). Separately modelling spatio-temporal density for males and females would allow future analyses to identify differences in spatial distribution (and potentially different exploitation rates) for males and females as well as annual trends of the standardized catch rate by sex, and we recommend this line of future research. The spatio-temporal maps might provide the geographical segregation of species by sex from year to year and might be useful to identify the essential habitat such as pupping grounds and mating grounds. Ohshimo et al. (2016) reported that there was no strong evidence for sexual differences in the distribution patterns or environmental preferences for juvenile shortfin mako. However, their survey periods and areas are limited, so it is valuable to repeat those studies using more complete data in future work. Future spatio-temporal models could account for missing data about individual sex by treating sex as a random effect (where observed catch rates follow a mixture distribution with two components). However, this requires prior information regarding the proportion by sex for each length category, and would therefore require further model development.

The analysis we present is generally applicable and should be considered as a standard tool in fisheries stock assessment. CPUE data is typically standardized for factors such as area, season, and gear characteristics to develop indices of relative abundance, but the most common procedures (e.g. GLMs) give equal weight to each data point (Maunder and Punt 2004). However, since the index is supposed to represent the whole stock, the data may not be evenly spread over all areas biasing the index and some form of area weighting should be used. The spatio-temporal approach automatically provides area weighting in addition to augmenting areas with no or little data (Thorson et al. 2015b). However, our approach takes this one step further to include length structure in the analysis. Despite CPUE data being standardized to produce an index of abundance, the accompanying composition data that is used to estimate the selectivity representing the index (i.e. the age or size of fish represented by the index) is not standardized or area weighted. Use of our approach would harmonize the use of CPUE and composition data for creating indices of abundance for use in contemporary stock assessment models.

Hiraoka et al. (2016) reported that annual target shifts by Japanese shallow-set longliner occurred seasonally and geographically; the greatest change in target species, from swordfish to blue shark, occurred in spring (April–June). They used 10th percentile of the swordfish CPUE values to incorporate this variable target behavior into the abundance index. We applied the same target indicator (rank of swordfish CPUE) to reduce the influences of the target behavior on the CPUE prediction of shortfin mako (Appendix E). The results indicated that the target changes between two target species had a small impact on the annual trends in the CPUE of shortfin mako (Fig. A3). Since shortfin mako shark is bycatch species unlike the swordfish and blue shark, the target shifts may not largely influence on the trends in the CPUE.

We used state-of-the-art methods to standardize the catch and effort data, including extending the geostastical method to include length data. Three conclusions were derived from the application study: (1) most of the hotspots for “Immature” shortfin mako between 90 and 160 cm PCL occurred in the coastal waters of Japan, while most of the hotspots for “Subadult and adult” larger than 160 cm PCL occurred predominately in the offshore waters of Japan: (2) the predicted CPUE for the different growth stages provided an indication that the recent stock trends of shortfin mako in the western and central North Pacific was better than that in mid-2000s: (3) part of the juvenile population is probably outside the range of the fishery during some years and therefore the CPUE based index of abundance for juveniles is unreliable. Further research and testing of this promising approach is recommended towards making it a widely applicable standard tool for fisheries assessments.

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Tables

Table 1. Summary of the model selection information from A) four analyses, including error distribution of positive catch model (lognormal or gamma), random field (anisotropic or isotropic), the number of parameters, the negative log-likelihood (NLL), the reduction in AIC (ΔAIC) from the best-fitting model, absolute value of the maximum gradient, marginal standard deviation for spatial variation and apatio-temporal and length variation; and B) eight analyses. , including the catch rate predictor of random effect. "Null" denotes no random effects, "Station" denotes random effects of statistical station (latitude and longitude), "Length" denotes random effects of body length, and "Station:Length:Year" denotes random effects of station, length and year.

A)

Model	Error distribution of positive catch model	Random field	Number of parameters	Deviance	ΔAIC	Maximum gradient	Marginal SD of spatial variation	Marginal SD of spatio-temporal and length variation
Model A	Lognormal	Isotropic	30	88261	53	0.065	0.243	1.217
Model B	Lognormal	Anisotropic	32	88205	0	0.017	0.198	1.218
Model C	Gamma	Isotropic	30	89434	1226	0.005	0.240	1.221
Model D	Gamma	Anisotropic	32	89383	1179	0.038	0.207	1.225

B)

Model	Catch rate predictors of random effect (RE)	Number of parameters	Deviance	Percent deviance (%)	ΔAIC	Maximum gradient	Marginal SD of spatial variation	Marginal SD of spatio-temporal and length variation
Model 1	Null	23	99919		11697	0.018		
Model 2	Station	27	98741	1.179	10527	0.019	0.59	
Model 3	Length	26	95099	3.689	6883	0.016		
Model 4	Station + Length	30	93718	1.453	5510	0.032	0.61	
Model 5	Station: Length: Year	29	88504	5.564	293	0.067		1.84
Model 6	Station + Station: Length: Year	30	88502	0.001	294	0.007	0.29	1.81
Model 7	Length + Station: Length: Year					0.145		
Model 8	Station + Length + Station: Length: Year	32	88205	0.337	0	0.017	0.20	1.22

Figure Legends

Fig. 1 Map of the operational areas of Japanese commercial fisheries (mean number of hooks) and sampling areas of length data (length composition) in the western and central North Pacific. The map is drawn using the shallow-set fleet subset used for the analysis.

Fig. 2 Yearly changes in predicted CPUE relative its average for shortfin mako for (a) four models with two different error distributions with and without anisotropy, and (b) seven models with the explanatory variables sequentially added to the null model. Please see an appendix D for the calculation method of the quantity.

Fig. 3 Overall spatial distribution of predicted CPUE relative its average for shortfin mako (upper figure) We also plot the nominal CPUE relative to its average (lower figure). Please see an appendix D for the calculation method of the quantity.

Fig. 4 Yearly changes in predicted CPUE relative its average for shortfin mako (black solid line with filled circle). Grey solid line denotes the nominal CPUE relative to its average, shadow denotes the 95 % confidence intervals, and the horizontal dotted line denotes mean value of relative values (1.0). Please see an appendix D for the calculation method of the quantity.

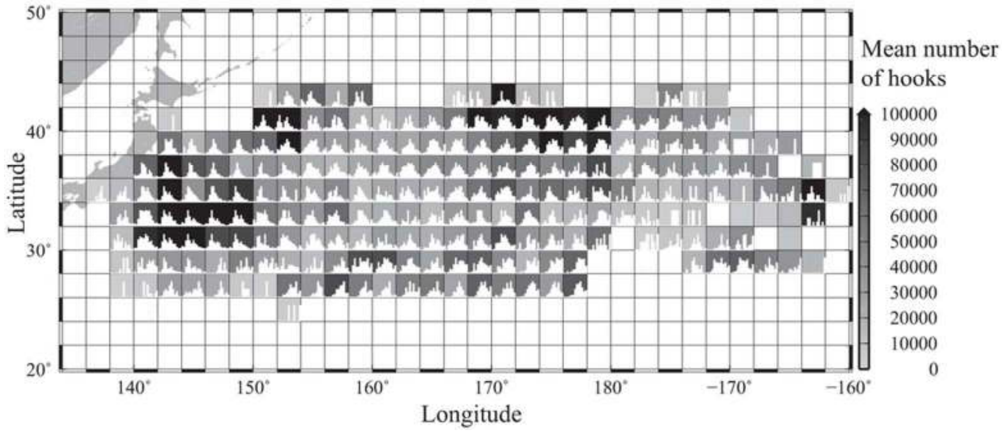
Fig. 5 Length (Pre-caudal length) specific changes in predicted CPUE relative to its average for shortfin mako (black solid line with filled circle). Grey solid line denotes the nominal CPUE relative to its average, shadow denotes the 95 % confidence intervals, and the horizontal dotted line denotes mean value of relative values (1.0). Please see an appendix D for the calculation method of the quantity.

Fig. 6 Overall spatial distribution of predicted CPUE relative its average for three growth stages of shortfin mako:(a) Juvenile :(b) Immature :(c) Subadult and adult. We also plot the nominal CPUE relative to its average for the three growth stages of shortfin mako (right figures). Please see an appendix D for the calculation method of the quantity.

Fig. 7 Yearly changes in predicted CPUE relative its average (black solid line with filled circle) for three growth stages of shortfin mako :(a) Juvenile :(b) Immature :(c) Subadult and adult. Grey solid line denotes the nominal CPUE relative to its average for the three growth stages of shortfin mako, shadow denotes the 95 % confidence intervals, and the horizontal dotted line denotes mean value of relative values (1.0). We also plot the number of hooks (x 1000), representing the yearly changes of available data for shortfin mako (figure d). Please see an appendix D for the calculation method of the quantity.

Fig. 8. Time (year) specific changes of the spatial distributions of log-scaled predicted CPUE for three growth stages and all combined stages of shortfin mako :(a) Juvenile :(b) Immature :(c) Subadult and adult :(d) All stages. Please see an appendix D for the calculation method of the quantity.

Fig. 9 Length (Pre-caudal length) and time (year) specific changes in predicted CPUE relative its average for shortfin mako. Black solid line denotes the average length specific distribution across all years, shadow denotes the 95 % confidence intervals, and the horizontal dotted line denotes mean value of relative values (1.0). Please see an appendix D for the calculation method of the quantity.



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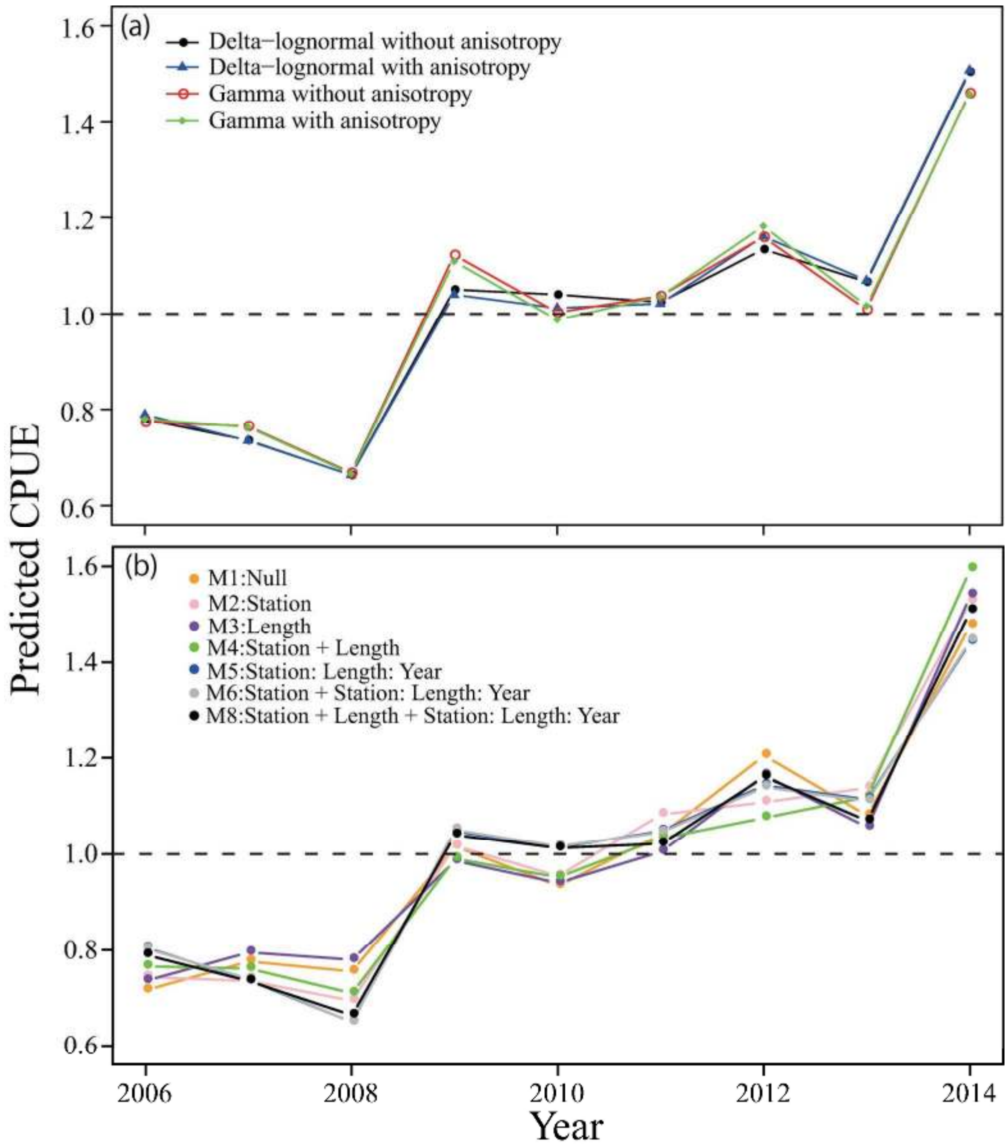

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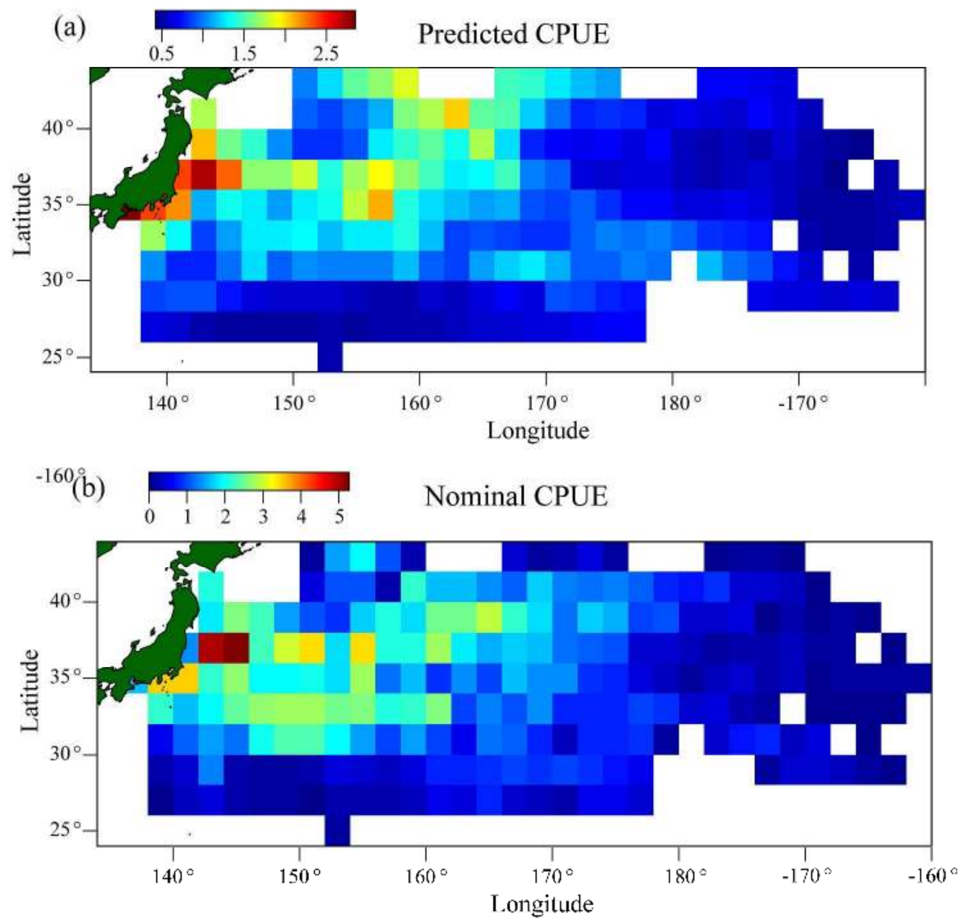

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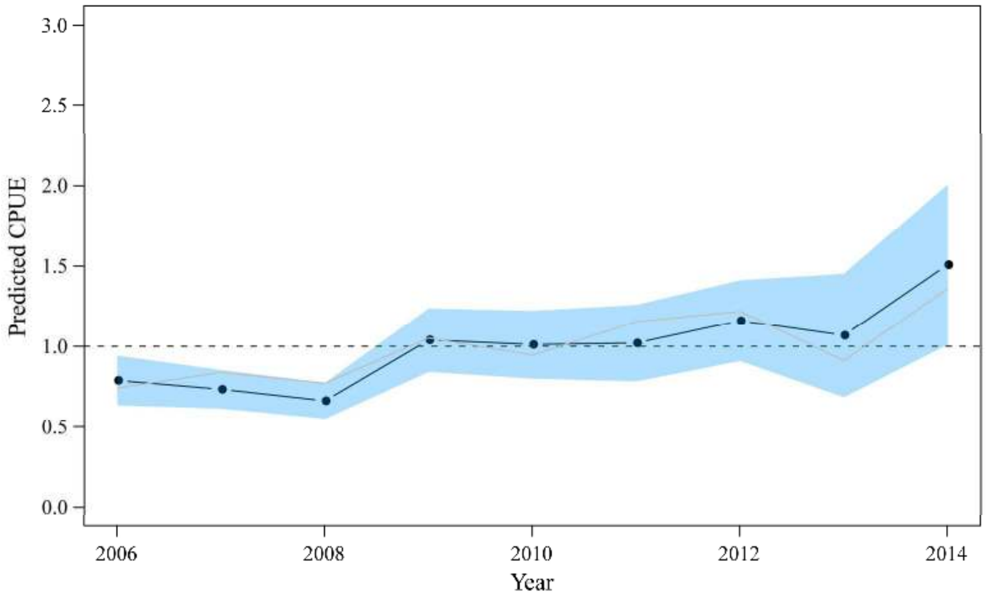

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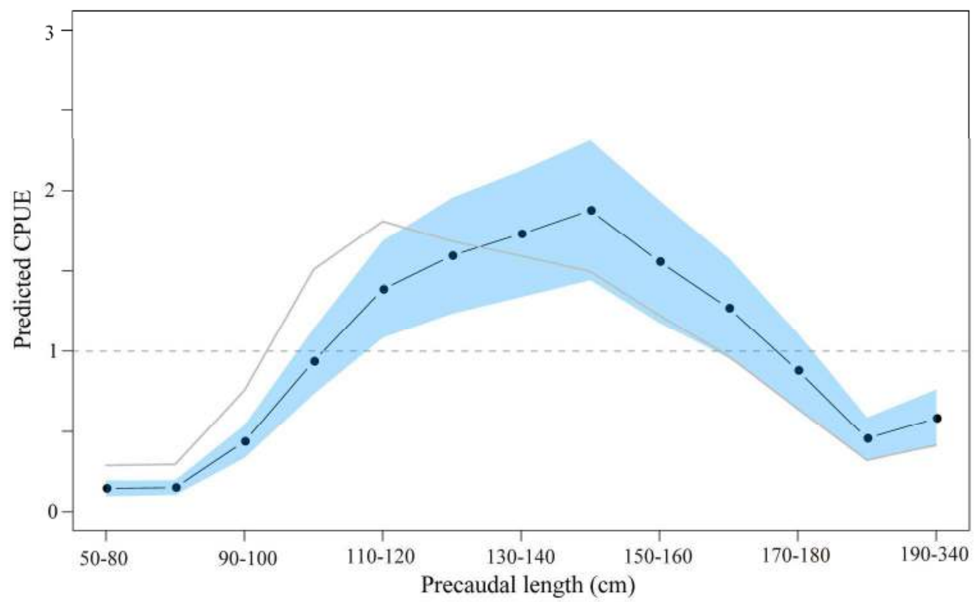

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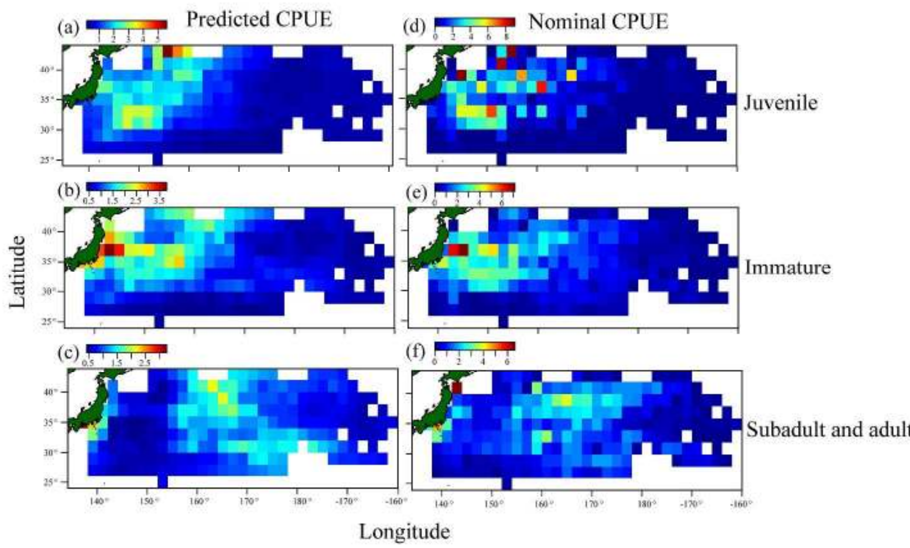

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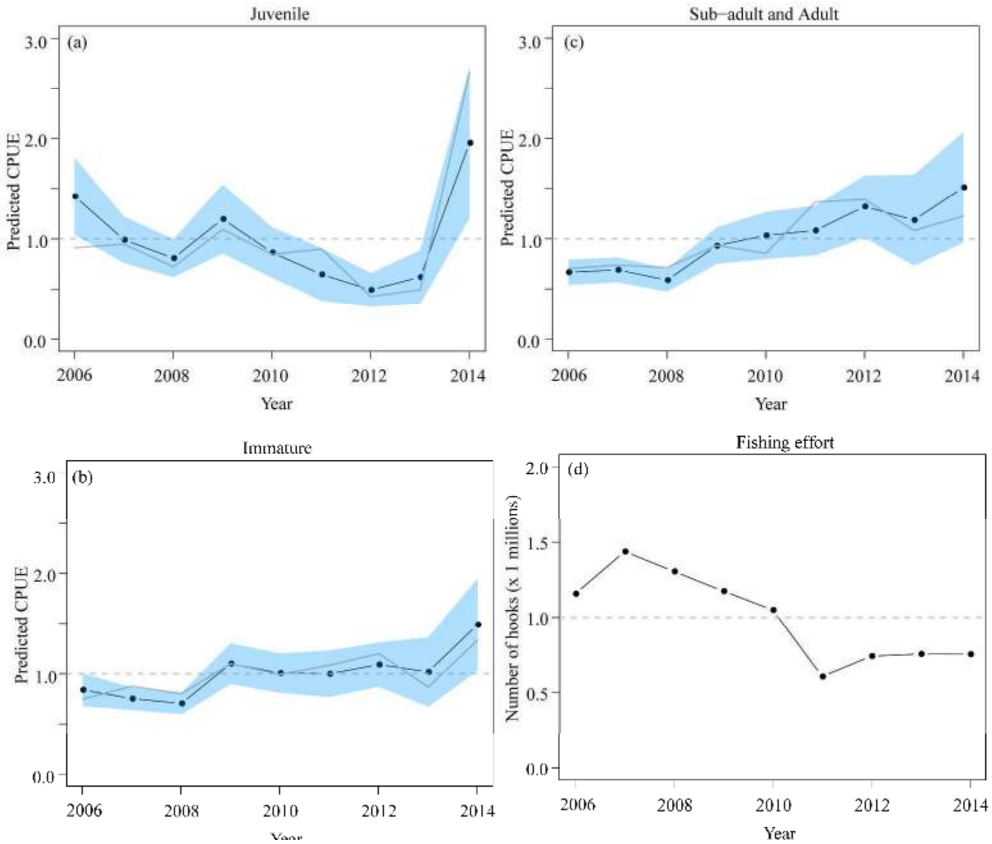

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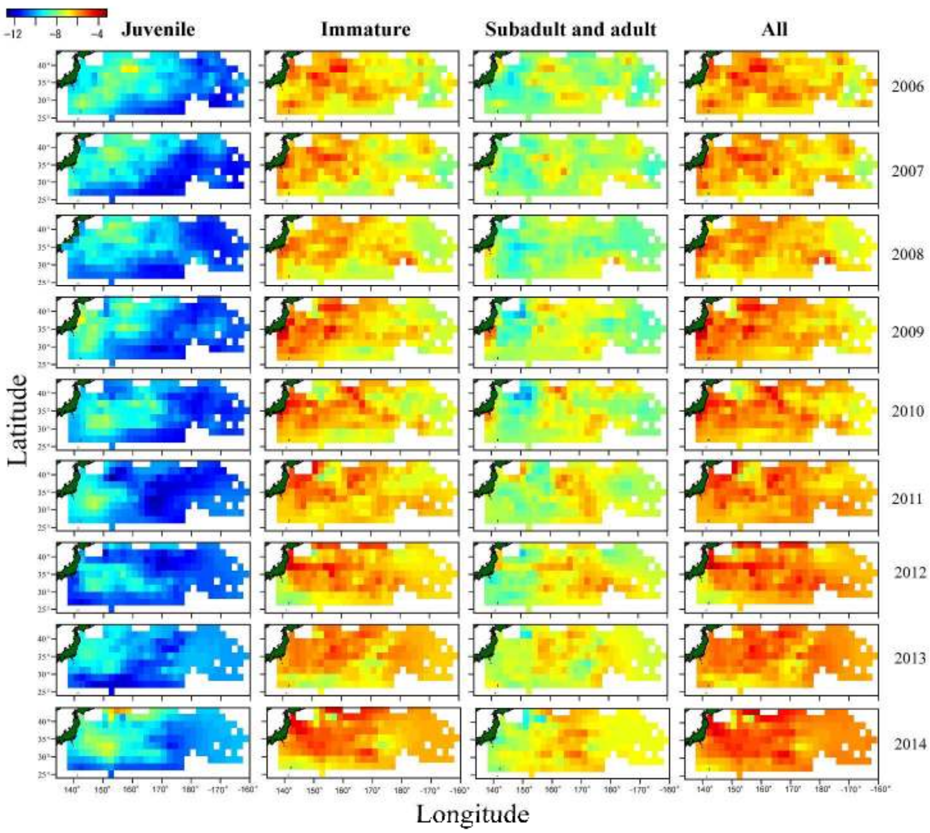

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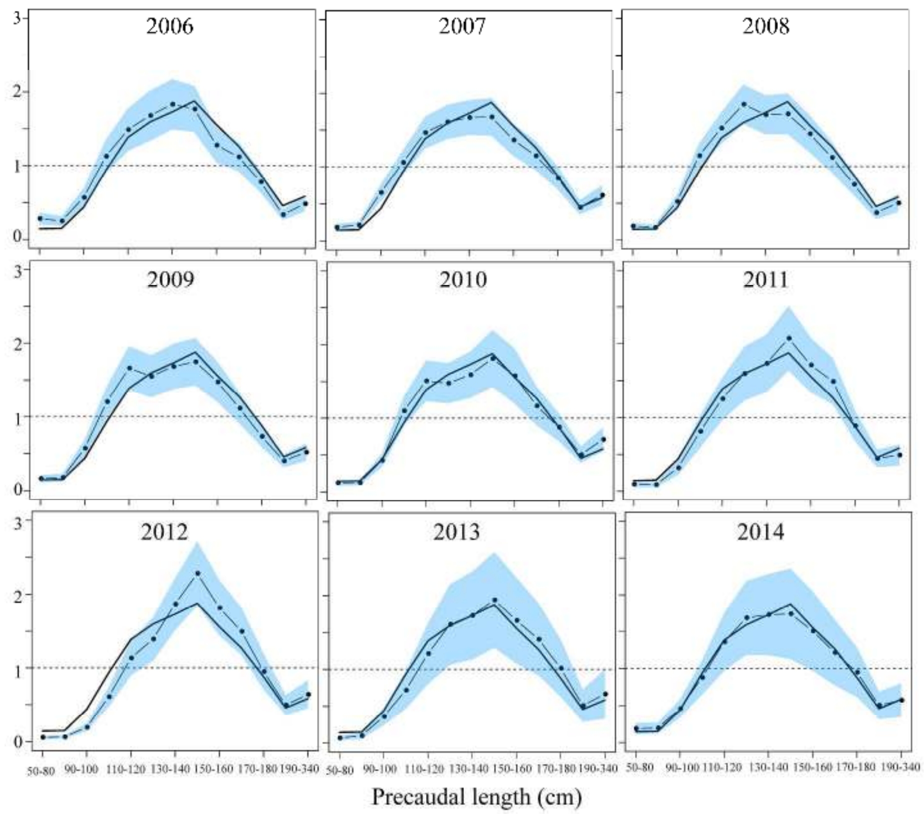

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Appendices

Appendix A

A1. Basic statistical information about shortfin mako catch

The proportion of the catch number of mako shark caught by Japanese offshore and distant water shallow-set longliner accounts for approximately 93% (111,318 in number /119,645) to total catch by Japanese offshore and distant water longliner during 2006 and 2014 (if we defined the shallow-set fishery has a gear 3-5 hooks per floats in an operation). Of there, the proportion of the catch number of mako shark caught by Kessennuma boat accounts for approximately 94% (104,864/111,318) to total shallow-set catch during 2006 and 2014. Total number of size sample collected by Kesennuma boat was 72,355 during 2006 and 2014.

A2. Summary of data aggregation

(1) For logbook catch data, we aggregated the set-by-set data (i.e. one operation data including year, quarter, latitude and longitude, number of hooks, catch number of shortfin mako and other species) by station (i.e. latitude and longitude) and year-quarter. Set by set data was summed up with regards to the catch number and number of hooks. There is no reduction in the total number of catch as well as hooks in this aggregation.

(2) For size data, we aggregated the set-by-set data (i.e. one operation data including year, quarter, latitude and longitude, body length of shortfin mako) by station, year-quarter and length bins. Set by set data was summed up with regards to the total number of catch at each length-interval. There is no reduction in the total number of size data.

(3) We combined the catch data with size data based on the same station and same year-quarter. If there is either (1) no size data at the specific station and in a specific year-quarter, or (2) no catch data at the specific station and in a specific year-quarter, then we do not include any data for that station and year-quarter. We summarized the information about the data aggregation in Table A1 and the maps of nominal CPUE before and after the data aggregation (Fig. A1). Note that the number of set by set data after aggregation denotes the number of data aggregated by station and year-quarter.

Appendix B

B1. Estimation methods of the random effects (Kristensen et.al. 2016)

Let $f(u, \omega)$ denote the negative joint log-likelihood of the data and the random effects. This depends on the unknown random effects $u \in R^n$ and parameters $\omega \in R^m$, where *R* is a real *n*- and *m*-space. The TMB package implements maximum likelihood estimation and uncertainty calculations for *u* and *ω*. The maximum likelihood estimate for *ω* maximizes

$$L(\omega) = \int_{R^n} \exp(-f(u,\omega))\, du \tag{A1}$$

w.r.t. *ω*. Note that the random effects *u* have been integrated out and the marginal likelihood $L(\omega)$ is the likelihood of the data as a function of just the parameters. We use $\hat{u}(\omega)$ to denote the minimizer of $f(u, \omega)$ with respect to *u*; i.e.,

$$\hat{u}(\omega) = \arg\min_u f(u,\omega) \tag{A2}$$

We use $H(\omega)$ to denote the Hessian of $f(u, \omega)$ with respect to *u* and evaluated at $\hat{u}(\omega)$; i.e.,

$$H_{i,j}(\omega) = \frac{\partial^2}{\partial \hat{u}_i(\omega) \partial \hat{u}_j(\omega)} f(\hat{u}(\omega), \omega) \tag{A3}$$

The Laplace approximation for the marginal likelihood $L(\omega)$ is

$$L^*(\omega) = \sqrt{2\pi^n} \det(H(\omega))^{-0.5} \exp(-f(u,\omega)) \tag{A4}$$

We then use a gradient-based nonlinear minimizer to identify the values $\widehat{\omega}$ of parameters ω that maximizes this approximation to the marginal likelihood:

$$\widehat{\omega} = \arg\max_{\omega} L^{*}(\omega) \tag{A5}$$

This approximation is widely applicable including models ranging from non-linear mixed effects models to complex space-time models.

Appendix C

C1. Diagnostics plots of goodness-of-fits

The goodness of fits were examined using four types of residual plots obtained from positive catch data: (1) standardized residuals versus the fitted values can assess whether model misspecification is occurring: (2) square root of the absolute values of the standardized residuals versus the fitted values can assess whether the variance changes as a function of the predicted value: (3) the observed versus the predicted values can assess qualitatively whether the explanatory variables are indeed able to reduce the variance in the data: (4) quantile and quantile plots can assess the normality. Overall, the model fit to the data was not bad (Fig. A2). The residuals were slightly biased toward the negative directions. Sqrt(Abs(Residuals)) had a tendency to increase as the predicted value was increased. The predicted CPUEs were smaller than observed CPUEs. Q-Q plots indicated that the left ends of the plots were largely deviated from the straight line.

We used only the positive catch data to plot the diagnostics because the binomial data with a logistic regression is very complicated to treat the residual patterns. If the true value is 0, we always overestimate the fitted value and residual should be negative. If the true value is 1, we always underestimate the fitted value and residual should be positive. Then, we have two lines of the residual plots across positive and negative lines.

Appendix D

Calculation method of each quantity

Annual abundance (i.e. CPUE which is defined as catch number over number of hooks) is calculated as the sum of abundance for each station and length interval, averaged across quarter:

$$d(t) = \sum_{s=1}^{226} \sum_{l=1}^{13} d(s, t, q, l), \tag{A6}$$

where $d(s, t, q, l)$ is defined in Eq. (1), $d(t)$ is total abundance at year t. The overall year relative to its average is

$$d^{*}(t) = d(t) / \left(\frac{1}{n_t} \sum d(t)\right). \tag{A7}$$

Nominal CPUE for combined stations, length interval and quarter is calculated as follows:

$$u(t) = \sum_{s=1}^{226} \sum_{q=1}^{4} \sum_{l=1}^{13} c(s, t, q, l) / \sum_{s=1}^{226} \sum_{q=1}^{4} \sum_{l=1}^{13} f(s, t, q, l) \tag{A8}$$

where $u(t)$ is nominal cpue at year t defined by a division of catch number c averaged over s, q, and l divided by number of hooks f averaged over s, q, and l. The overall year relative to its average is

$$u^{*}(t) = u(t) / \left(\frac{1}{n_t} \sum u(t)\right)). \tag{A9}$$

The coefficient of variation (CV) for estimated CPUE for combined three growth stages in year t is calculated as:

$$CV\big(d(t)\big) = \frac{SE\big(d(t)\big)}{d(t)} \tag{A10}$$

where $CV(d(t))$ is the coefficient of variation of total abundance in year t and $SE(d(t))$ is the standard error for annual abundance (as estimated using Template Model Builder).

Length specific changes in abundance are calculated as the sum of abundance for each station and year, averaged across quarter:

$$d(l) = \sum_{s=1}^{226} \sum_{t=1}^{9} d(s,t,q,l), \tag{A11}$$

where $d\,(s, t, q, l)$ is defined in Eq. (1), $d\,(l)$ is total abundance at length-bin l. The overall length intervals relative to its average is

$$d^{*}(l) = d(l) / \left(\frac{1}{n_l} \sum d(l)\right). \tag{A12}$$

Nominal CPUE for combined stations, overall year and quarter is calculated as follows:

$$u(l) = \sum_{s=1}^{226} \sum_{q=1}^{4} \sum_{t=1}^{9} c(s,t,q,l) / \sum_{s=1}^{226} \sum_{q=1}^{4} \sum_{t=1}^{9} f(s,t,q,l) \tag{A13}$$

where $u\,(l)$ is nominal cpue at length interval l defined by a division of catch number c averaged over s, q, and t divided by number of hooks f averaged over s, q, and t. The overall length interval relative to its average is

$$u^{*}(l) = u(l) / \left(\frac{1}{n_l} \sum u(l)\right)). \tag{A14}$$

The coefficient of variation (CV) for estimated CPUE at length interval l is calculated as:

$$CV\big(d(l)\big) = \frac{SE\big(d(l)\big)}{d(l)} \tag{A15}$$

where $CV\big(d(l)\big)$ is the coefficient of variation of total abundance at length-interval l and $SE\big(d(l)\big)$ is the standard error for annual abundance (as estimated using Template Model Builder).

In the following, we presented and interpreted maps of density that include the effect of fixed effects and random effects. Here, the average spatial distribution of predicted catch rate for each year was calculated as:

$$\bar{d}(s,t) = \sum_{l=1}^{13} d(s,t,q,l) \tag{A16}$$

where $d(s,t,q,l)$ is defined in Eq. (1), $\bar{d}(s,t)$ is the density at location *s* and time *t* summed over length intervals *l* is 13, the sum of quarter q is omitted because q is a fixed effect with no interactions , and where plot the density:

$$d_t^*(s) = \frac{d(s,t)}{\left(\frac{1}{n_s}\sum d(s,t)\right)} \qquad \text{(A17)}$$

Appendix E

The influence of the target changes

Swordfish catch ratios (i.e., CPUE) were ranked based on ten equal percentile categories (e.g., 0 to <10 %, 10 to <20 %, etc.) for each year, and the ranks were used as target indicators (Hiraoka et al. 2016). We used the catch number records for swordfish and blue shark from the same set-by-set logbook data as used for the prediction of the CPUE for shortfin mako. We evaluated the influence of the target changes through a comparison with the annual trends in the CPUE using the best-fitting model with and without target indicator. For example, a set with the highest swordfish CPUE within certain years would be categorized as rank 10, indicating that blue shark was relatively under-targeted in that set.

Appendix references

Hiraoka, Y., Kanaiwa, M., Ohshimo, S., Takahashi, N., Kai, M., and Yokawa, K. 2016. Trend in the relative abundance of the blue shark Prionace glauca based on the activities of Japanese distant water and offshore longliners in the North Pacific. Fish. Sci. **82**: 687-699.

Kristensen, K. 2014. TMB: General random effect model builder tool inspired by ADMB [online]. R package version 1.6.2. Available from https://cran.r-project.org/web/packages/TMB/index.html [accessed 18 January 2017]

Appendix tables

Table A1 Summary of data aggregation by A) year and B) quarter.

A)

Year	Catch number of mako shark (before)	Catch number of mako shark (after)	Number of size data (before)	Number of size data (after)	Number of set by set data (before)	Number of set by set data (after)	Positive catch ratio of set by set data (before)	Positive catch ratio of set by set data (after)	Number of hooks (before)	Number of hooks (after)
2006	13,180	10,299	7,800	7648	5123	3200	0.57	0.53	18,583,512	15,319,327
2007	15,139	14,460	13,130	12702	5823	4022	0.58	0.50	21,148,480	18,876,303
2008	12,532	12,080	10,571	10113	5312	3610	0.61	0.52	19,185,566	17,139,978
2009	15,751	14,802	8,008	7936	4582	3290	0.65	0.49	16,220,017	15,345,066
2010	13,202	11,907	6,282	6238	4181	2702	0.64	0.48	15,388,103	13,785,927
2011	9,208	8,398	4,777	4705	2356	2145	0.73	0.44	8,766,168	7,958,559
2012	11,202	10,833	6,918	6841	2900	2473	0.66	0.51	10,506,429	9,710,781
2013	8,547	8,257	5,420	5310	3192	2363	0.65	0.48	10,866,447	9,909,735
2014	12,557	12,292	9,449	9389	3072	2231	0.75	0.57	10,216,910	9,838,298

B)

Quarter	Catch number of mako shark (before)	Catch number of mako shark (after)	Number of size data (before)	Number of size data (after)	Number of set by set data (before)	Number of set by set data (after)	Positive catch ratio of set by set data (before)	Positive catch ratio of set by set data (after)	Number of hooks (before)	Number of hooks (after)
1	33,729	32,561	21,908	21,605	10,785	5,633	0.69	0.54	37,990,354	36,575,575
2	30,343	26,183	16,598	16,084	9,191	8,753	0.64	0.44	33049087	29,311,644
3	20,075	19,053	14,399	14,158	6,222	5,442	0.69	0.49	22511714	20,889,069
4	27,171	25,531	19,450	19,035	10,343	6,208	0.53	0.56	37330477	31,107,685

Table A2. List of all parameters and the estimates for the best-fitting model.

No	Parameter name	Symbol	Type	Estimates
1	Distance of correlation (Spatial random effect)	κ	Fixed	0.27
2	Northings anisotropy	h_1	Fixed	1.46
3	Anisotropic correlation	h_2	Fixed	0.98
4	Parameter governing pointwise variance (Spatial random effect)	η_γ	Fixed	1.43
5	Parameter governing pointwise variance (Length random effect)	η_τ	Fixed	0.30
6	Parameter governing pointwise variance (Spatio-temporal and length random effect)	η_θ	Fixed	0.23
7	Correlation parameter of length bins	ψ	Fixed	0.17
8	Parameter governing autocorrelation (Length random effect)	ρ_τ	Fixed	0.16
9	Parameter governing autocorrelation (spatio-temporal and length random effect)	ρ_θ	Fixed	0.85
10-18	Intercept for year	d_0	Fixed	Not shown
19-21	Temporal variance (quarter effect)[a]	δ	Fixed	Not shown
22	Scale parameter of zero catch ratio	z_1	Fixed	0.74
23	Scale parameter of zero catch ratio	z_0	Fixed	2.73
24-32	Log-standard deviation for catch rates for year	σ	Fixed	Not shown
33	Spatial residuals	γ	Random	Not shown
34	Length residuals	τ	Random	Not shown
35	Spatio-temporal and length residuals	θ	Random	Not shown

a: Offset of density in quarter 2-4 from density in quarter 1

Table A3. Summary of yearly changes in CPUE predicted by spatio-temporal model for three ("Juvenile", "Immature", and "Subadult and adult") and a combined ("All") growth stages along with the corresponding estimates of the coefficient of variation (CVs), and yearly changes in the nominal CPUE and fishing effort (number of hooks x 1millions). The values are predicted using the best fitting model and scaled by average CPUE.

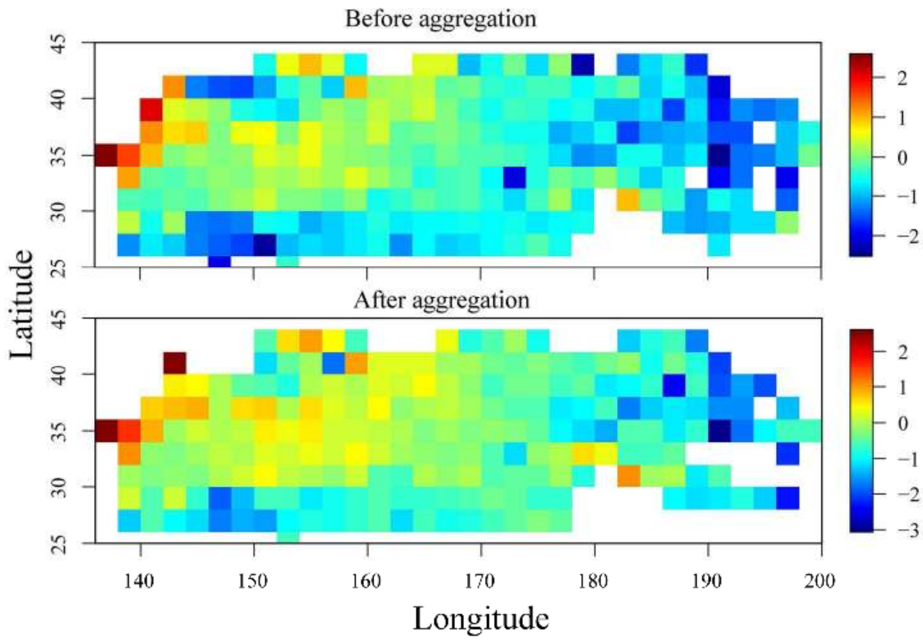
Year	Predicted				Nominal				CV				Effort
	All	Juvenile	Immature	Adult	All	Juvenile	Immature	Adult	All	Juvenile	Immature	Adult	All
2006	0.79	1.42	0.84	0.67	0.74	0.91	0.75	0.70	0.10	0.14	0.10	0.10	0.10
2007	0.73	0.99	0.75	0.69	0.84	0.95	0.88	0.74	0.08	0.12	0.08	0.09	0.08
2008	0.66	0.81	0.70	0.59	0.77	0.72	0.80	0.71	0.08	0.12	0.08	0.10	0.08
2009	1.04	1.20	1.10	0.93	1.05	1.09	1.10	0.93	0.09	0.15	0.09	0.10	0.10
2010	1.01	0.86	1.01	1.03	0.95	0.85	0.99	0.85	0.10	0.15	0.10	0.12	0.11
2011	1.02	0.65	1.00	1.08	1.16	0.90	1.08	1.36	0.12	0.21	0.12	0.12	0.12
2012	1.16	0.49	1.09	1.32	1.22	0.43	1.20	1.39	0.11	0.17	0.10	0.12	0.11
2013	1.07	0.62	1.02	1.18	0.91	0.49	0.87	1.08	0.18	0.22	0.17	0.19	0.18
2014	1.51	1.96	1.49	1.51	1.36	2.66	1.33	1.22	0.17	0.20	0.16	0.19	0.17

Appendix Figure Legends

Fig. A1 Maps of log-scaled nominal CPUE (catch/number of hooks x1000) by station before and after the data aggregation.

Fig. A2 Diagnostic plots of goodness-of-fit for the most parsimonious model selected by AIC.

Fig. A3 Yearly changes in predicted CPUE relative its average for shortfin mako (black solid line with filled circle) with target effect (solid line with filled circle) and without target effect (solid line with filled triangle). Target effect (Hiraoka et al., 2016) is defined as a ranking of swordfish catch ratio (i.e., CPUE for each set) based on ten equal percentile categories (e.g., 0 to <10 %, 10 to <20 %, etc.) for each year. Grey solid line denotes the nominal CPUE relative to its average, and the horizontal dotted line denotes mean value of relative values (1.0).



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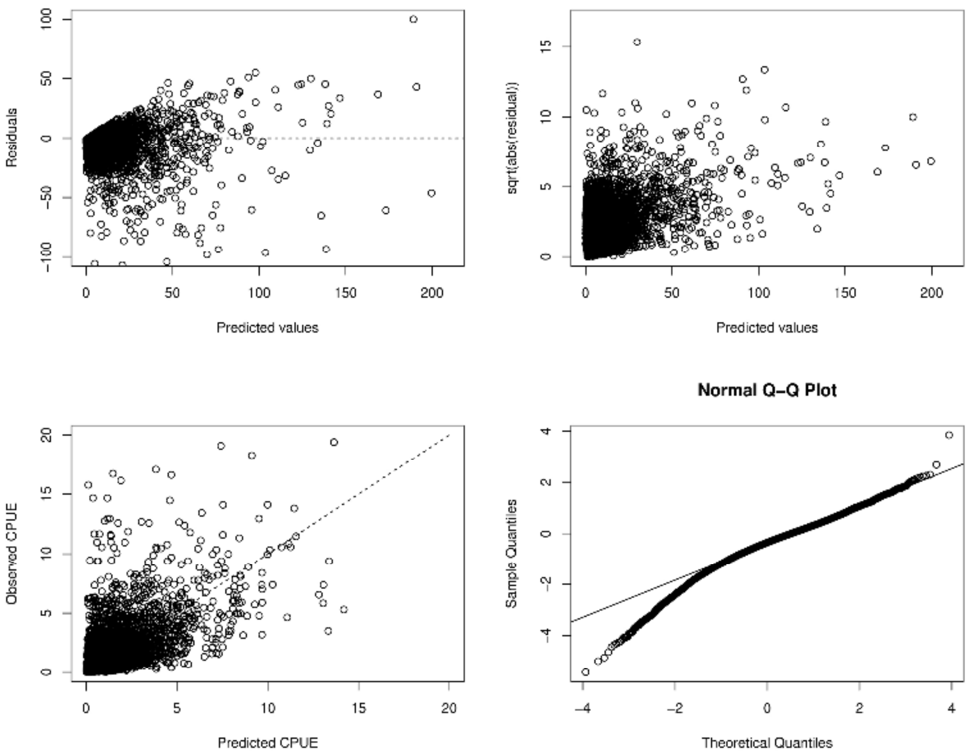

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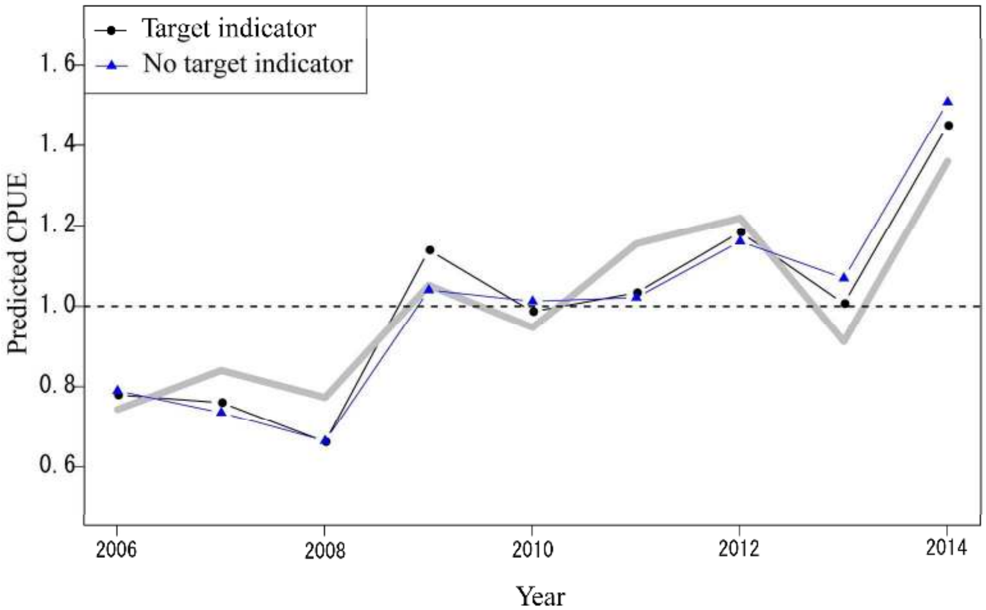

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