

# **Species distribution and temperature range of select Pacific groundfish species occurring in Queen Charlotte Sound and Hecate Strait, British Columbia**

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by

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## ABSTRACT

McMillan, A.K.L., Lecomte, J-B. and Hunter, K.L. 2021. Species distribution and temperature range of select Pacific groundfish species occurring in Queen Charlotte Sound and Hecate Strait, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 3426: iv + 66p.

Species distribution models are developed through a framework of ecological knowledge, data collection methods, and statistical analyses to estimate the distribution or potential habitat of a given species. Developing each component involves consideration of the limitations of each framework component, such as sampling logistics or poorly understood physiology. Here, we apply a Bayesian hierarchical model that accounts for the structure of trawl catch biomass data to estimate the spatial distribution of 18 species sampled by DFO synoptic trawl surveys off the northern coast of British Columbia. This model uses a compound Poisson-Gamma distribution to represent the spatial structure of the trawl biomass and a log-linear link function to account for influences of depth, temperature, and survey year. Model performance was species dependent and favoured species with greater spatial representation in the data.

## RÉSUMÉ

McMillan, A.K.L., Lecomte, J-B. and Hunter, K.L. 2021. Species distribution and temperature range of select Pacific groundfish species occurring in Queen Charlotte Sound and Hecate Strait, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 3426: iv + 66p.

Les modèles de répartition des espèces sont élaborés à partir d'un cadre de connaissances écologiques, de méthodes d'acquisition de données et d'analyses statistiques pour estimer la répartition ou l'habitat potentiel d'une espèce donnée. L'élaboration de chaque composante implique la prise en compte des limites de chaque composante du cadre, comme la logistique d'échantillonnage ou une physiologie mal comprise. Ici, nous appliquons un modèle hiérarchique bayésien qui tient compte de la structure des données sur la biomasse des prises des chaluts pour estimer la distribution spatiale de 18 espèces échantillonnées par des relevés synoptiques au chalut du MPO au large de la côte nord de la Colombie-Britannique. Ce modèle utilise une distribution composée Poisson-Gamma pour représenter la structure spatiale de la biomasse du chalut et une fonction de lien log-linéaire pour rendre compte des influences de la profondeur, de la température et de l'année du relevé. Le rendement du modèle dépendait des espèces et favorisait les espèces ayant une plus grande représentation spatiale dans les données.

## Introduction

Understanding species habitat distributions is key to decision making for climate change adaptation and spatial prioritization programs in the marine environment. A species' habitat is delineated by multiple factors such as the abiotic environment, species interactions, and dispersal capabilities (Soberón & Peterson, 2005). It is often exceedingly difficult to directly observe and categorize species habitats, especially in the marine environment due to logistical limitations of sampling methods as well as the cryptic nature of many species. Species distribution models provide estimates of distributions of species in geographic space (Soberón et al., 2017). Though new model approaches, such as joint species distribution models, are active areas of research, accepted SDM approaches generally exclude species interactions and dispersal to limit the complexity of the model, relying on the target species response to environmental gradients as an estimate of the species habitat.

Conceptually, species distribution models can be broken into three components (Austin, 2002): 1) the ecological model consisting of the ecological theory used and tested for the target species as well as the context for interpretation of model results; 2) the data model accounting for the methods of collection, measurement, and estimation of data; and 3) the statistical model comprising of the statistical methods used to fit the model and derive inference. Nephin et al. (2020) have distilled much of this conceptual framework for species distribution modelling and applied it to 12 species on Canada's Pacific coast. The ecological model depends largely on the goals of the study, and the scale of the model as well as the managerial context will greatly influence how the subsequent data and statistical models are structured. The statistical component of Nephin et al.'s (2020) framework focusses on the methods such as Generalized Linear Models and Boosted Regression Trees while also recommending ensemble methods for more robust predictions.

Distributions and habitat preferences have often been inferred through the development of correlative models that rely on environmental data (Guisan & Thuiller, 2005); however, if there is a mismatch between the statistical model and the processes underlying the data then model inference and extrapolation from training data will suffer (Martin et al., 2005; Santika & Hutchinson, 2009). Correlative models can predict well even without ecological and data model considerations but can fall victim to data issues such as spatial autocorrelation, sampling bias, and zero inflation. In some cases, these issues can be dealt with through careful data processing before fitting a statistical model. In other cases, issues of zero inflation can be accommodated using an appropriate positive distribution model such as a Tweedie distribution. Importantly, this approach accounts for the stochastic properties of true zeros, but not the observer limitations resulting in false zeros. Here, we focus on the use of a compound Poisson-Gamma (CPG) distribution, a member of the Tweedie family to model species presence and biomass in groundfish trawl surveys. The flexibility of this model also allows environmental variables to be included as model coefficients using standard generalized linear modelling methods (Lecomte et al., 2013a; Lecomte et al., 2013b).

Lecomte et al., (2013b) developed and tested a hierarchical Bayesian application of the CPG model similar to the model developed by Ancelet et al. (2010), which uses exponential rather than gamma variables. The model was then applied to biomass data from scientific bottom trawl surveys. Using the CPG approach, the density of catch occurrences is modelled by the Poisson distribution while the catch biomass is gamma distributed. Variables such as depth and temperature were included in a linear model linked to the intensity of catch occurrences. Another distinction of the CPG model is the direct inclusion of effort by scaling the Poisson intensity parameter by the sampling volume at a given location. Lecomte et al., (2013a) found the direct inclusion of effort to give more robust estimates than relying on a generalized linear model to estimate effort as a covariate or using effort as an offset. This method can

describe the habitat associations while taking into account the spatial variability of sampling volume. Probability of association with habitat features (e.g., temperature, depth, and sediment type from Lecomte et al., 2013b) generated from this model provide potential for ecological inference.

Our objectives were to: 1) apply the Lecomte, et al. (2013b) hierarchical Bayesian model to predict the spatial structure of survey biomass density as a function of temperature, depth and survey year for 18 groundfish species in Hecate Strait and Queen Charlotte Sound, British Columbia; and 2) use the modelled distribution to estimate the probability of presence relative to bottom temperature. Results are presented in-text for two species, Arrowtooth Flounder (*Atheresthes stomias*) and Shortspine Thornyhead (*Sebastolobus alascanus*), while results for the remaining species are included in appendices.

## **Methods**

### **1.1 Biological data**

The data used in this study were collected during stratified random bottom trawl surveys conducted by Fisheries and Oceans Canada (DFO) in 2005, 2007, 2009 and 2011 (Nottingham et al., 2017; Olsen et al., 2007, 2009c, 2009a, 2009b; Williams et al., 2018; Workman et al., 2008). Bottom trawl surveys were conducted between May and June in Hecate Strait and between July and August in Queen Charlotte Sound for each of the four years. Stations were chosen at random in strata defined by depth. The number of tows per survey ranged from 156 to 257 usable tows and the duration of tows was approximately 20 minutes. Biomass (catch weight in kg) was recorded for all species (Figure 1, Appendix 1). Surveys were conducted aboard chartered commercial trawling vessels using Atlantic Western IIA trawl nets. Effort is represented by sampling volume, defined here as the number of tows within a given grid cell. Grid cell dimensions were generated from environmental data, detailed in the next section.



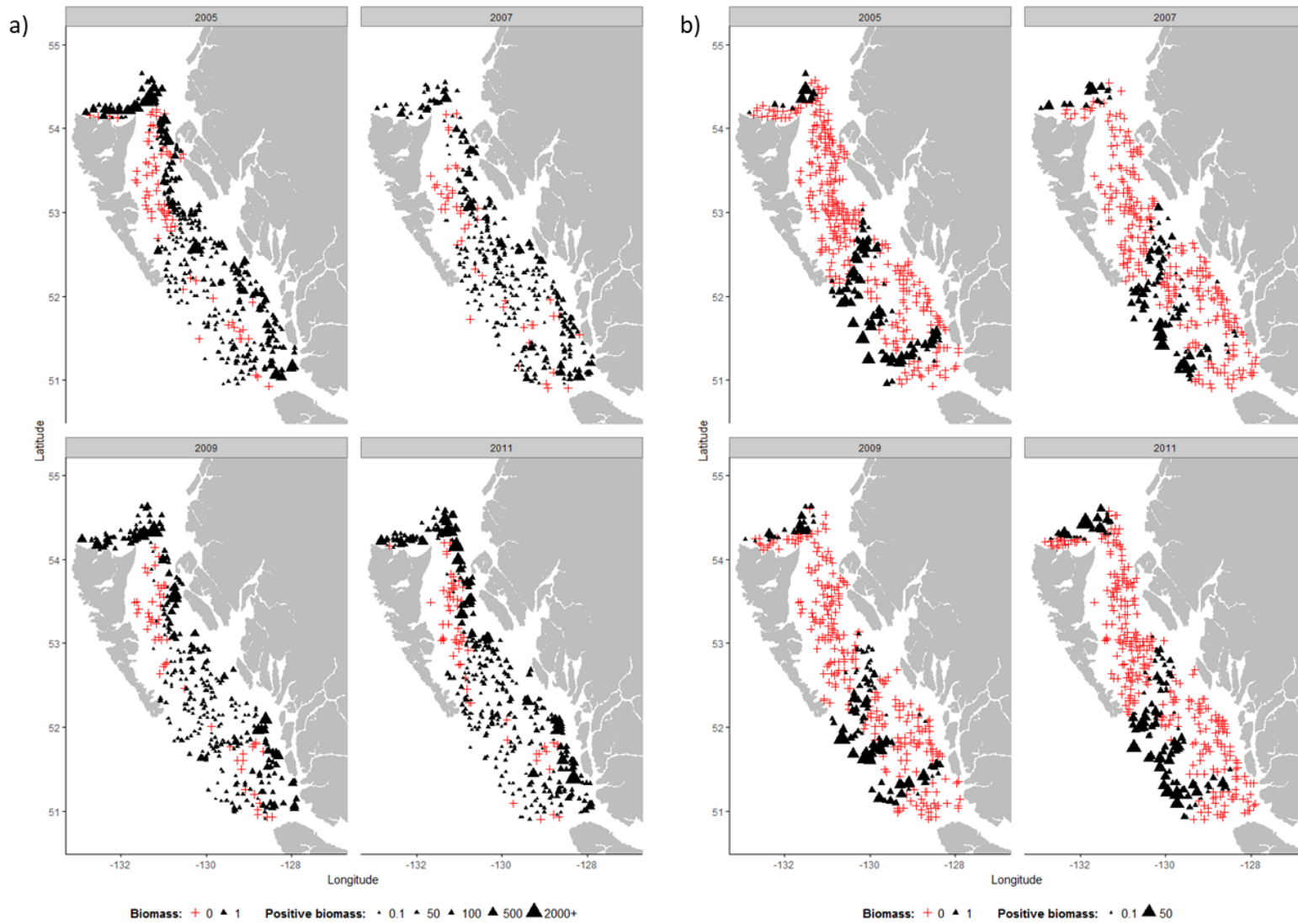


Figure 1. Locations of observed biomass for a) Arrowtooth Flounder (*Atheresthes stomias*) and b) Shortspine Thornyhead (*Sebastolobus alascanus*) for each survey year. Red crosses represent observed absences while black triangles represent positive biomass. Triangle size is scaled to each species' catch biomass in kilograms.

## 1.2 Environmental data

The environmental data was included as a continuous, regular grid across the study area hereafter referred to as the environmental grid. Temperature in degrees Celsius, and depth in meters were included in the grid. Bottom temperature values were generated by a Regional Ocean Model System (ROMS) at a 3km by 3km resolution. Depth values were retrieved from the British Columbia Marine Conservation Analysis (BCMCA) database and interpolated over a grid matching the resolution of the temperature data. The environmental grid created a common data source for model training and prediction.

ROMS is a terrain following, primitive equation model which has been used extensively to model various regions of the world's oceans (Haidvogel et al. 2008). The BC coast implementation is forced by NARR (North American Regional Reanalysis 2004) atmospheric data, and lateral boundary conditions are extracted from the Simple Ocean Data Assimilation project, or SODA (Carton and Giese 2008). Tidal forcing is applied at the open boundaries using the output from a North-East Pacific tidal model (Foreman et al. 2000). In addition, the ocean model is forced by freshwater monthly discharge from BC major rivers, derived as in Morrison et al. (2012). The model domain extends from the Columbia River to the Alaska Panhandle and is used to hindcast the 33-year period 1979–2011. Details of the model setup as well as an extensive model validation can be found in Masson and Fine (2012).

To construct the model, the catch data was aggregated to match the resolution of the environmental grid. We note that this aggregation was at the expense of modelling the data on a finer spatial scale. However, this aggregation was necessary to fit the CPG model and matches an appropriate spatial scale for the environmental data. We applied a compound model around the number of species occurrences within a grid cell, the number of tows within a grid cell, and mean biomass of a grid cell. Including these characteristics of the catch data allowed the model to account for variance within a grid cell as well as scale the data by effort. Environmental data were standardized to allow for easier estimation of environmental coefficients.

## 1.3 Species distribution model

We applied the Lecomte et al., (2013b) model to predict a distribution of biomass as a function of temperature, depth, and survey year for 18 groundfish species (Table 1). As defined by Lecomte et al. (2013a), this model applies a Bayesian hierarchical approach by representing the data in two substructures. In the first substructure, the number of positive catches and their biomass are represented by the CPG model. The second substructure represents the relationship of depth, bottom temperature, and survey year as covariates in a generalized linear model (GLM). The GLM is incorporated with the CPG substructure as a log-link function to the Poissonian intensity parameter, the average number of positive catches at a site. The parameters of the model substructures were estimated using Bayesian inference. The aim of this approach is to accurately represent the process of sampling living organisms in a stratified random design, where an observation variable, such as biomass, can have zeros and is strictly positive and continuous (Foster and Bravington 2012; Lecomte et al., 2013b).

Table 1 Selected Pacific groundfish species

Species common name	Scientific name
Arrowtooth Flounder	<i>Atheresthes stomias</i>
Bocaccio	<i>Sebastes paucispinis</i>
Canary Rockfish	<i>Sebastes pinniger</i>
Spiny Dogfish	<i>Squalus acanthias</i>
Dover Sole	<i>Microstomus pacificus</i>
English Sole	<i>Parophrys vetulus</i>
Greenstripe Rockfish	<i>Sebastes elongates</i>
Pacific Cod	<i>Gadus macrocephalus</i>
Petrale Sole	<i>Eopsetta jordani</i>
Pacific Ocean Perch	<i>Sebastes alutus</i>
Spotted Ratfish	<i>Hydrolagus colliei</i>
Rock Sole	<i>Lepidopsetta bilineata</i>
Redstripe Rockfish	<i>Sebastes proriger</i>
Rex Sole	<i>Glyptocephalus zachirus</i>
Sablefish	<i>Anoplopoma fimbria</i>
Silvergray Rockfish	<i>Sebastes brevispinis</i>
Shortspine Thornyhead	<i>Sebastolobus alascanus</i>
Widow Rockfish	<i>Sebastes entomelas</i>

### Model structure

Applying the hierarchical approach, for each survey year,  $t$ , and every site,  $s$ , corresponding to the 3km x 3km grid cells, there is an unknown number of aggregations, or patches of organisms,  $N_{t,s}$ . The patches are Poisson distributed with an intensity parameter  $\lambda_{t,s}$ , representing the expected mean number of patches, and a scaling parameter,  $V_{t,s}$ , representing fishing effort:

$$N_{t,s} \sim \text{Poisson}(V_{t,s}\lambda_{t,s}). \quad (1)$$

For each patch,  $i$ , within a site, biomass is estimated through a Gamma distribution,  $M_{t,s,i}$ . We assume that the patch biomass values are independent and identically distributed with shape and rate parameters,  $a$  and  $b$ :

$$M_{s,t,i} \sim \text{Gamma}(a, b). \quad (2)$$

Aggregating to the grid resolution, the estimated biomass for site  $s$ ,  $Y_{t,s}$ , can be calculated by the sum of the biomass at each patch. If, however, the number of patches falls to zero, the estimated biomass must also equal zero:

$$Y_{t,s} = \begin{cases} \sum_{i=1}^{N_{t,s}} M_{t,s,i}, & N_{t,s} > 0 \\ 0, & N_{t,s} = 0 \end{cases}. \quad (3)$$

The three equations above constitute the CPG substructure of the model. The linear model linking the observations to the environmental data is connected to the CPG model through the intensity parameter of equation 1. We assume effects of bottom temperature, depth, and year drive the density of species occurrences within a grid cell. The environmental variables are introduced in the model as covariates in a log-linear relationship with the intensity parameter,  $\lambda_{t,s}$ :

$$\log(\lambda_{t,s}) = \mu + \beta_0 X_{\text{Temp}_{t,s}} + \beta_1 X_{\text{Depth}_{t,s}} + \beta_2 X_{\text{Year}2_{t,s}} + \beta_3 X_{\text{Year}3_{t,s}} + \beta_4 X_{\text{Year}4_{t,s}}, \quad (4)$$

where  $\mu$  is the intercept,  $X_{t,s}$  is a variable recorded at year  $t$  and site  $s$  and  $\beta$  is the coefficient associated with this variable. The effect an environmental covariate,  $X_{t,s}$ , has on  $\lambda_{t,s}$  is proportional to its coefficient,  $\beta$ . The year effect is incorporated into the model with the first year omitted as a baseline (i.e., the 2005 year effect is scaled to 0) and subsequent years producing effects relative to the baseline.

Equations 1 through 4 make up the structure of the model, but in order to solve the equations the parameter values need to be estimated. The rate and shape parameters describing the gamma distribution of biomass, as well as the environmental coefficients and intercept of the log-linear ecological model were estimated through Bayesian inference. Any assumptions about how these parameters vary within the modelled environment can be represented as a probability distribution, known as a prior distribution or simply as a prior, that is then assigned to the corresponding parameter (Table 2).

Table 2: Model parameters, their role and priors used in the model

Parameter	Role	Prior
$a$	positive biomass	Gamma(0.1,0.1)
$b$	positive biomass	Gamma(0.1,0.1)
$\mu$	Intercept	Normal(0,10)
$\beta_0$	Log-linear temperature effect on patch intensity	Normal(0,10)
$\beta_1$	Log-linear depth effect on patch intensity	Normal(0,10)

$\beta_2, \beta_3, \beta_4$ 

Log-linear year effects on patch intensity

Normal(0,10)

## Bayesian inference

For Bayesian inference, prior distributions are defined for each parameter. To simplify prior definition, temperature and depth values were standardized to a mean of zero and standard deviation of one. Since the latent relationships between catch density and the linear coefficients ( $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4$  and  $\mu$ ) are unknown, we attributed very weakly informative priors to these parameter estimations (Table 2). The parameters for positive biomass,  $a$  and  $b$ , were given priors that will constrict biomass to reasonable values while still being sufficiently vague for the purpose of regularization. The model equations described above were coded in the BUGS coding language (see Appendix 2) and run using the NIMBLE package in R statistical software (de Valpine et al., 2017; de Valpine et al., 2020). Using a Markov Chain Monte Carlo (MCMC) simulation, the model ran for 80,000 iterations with a burn-in period of 50,000. The remaining 30,000 iterations were thinned by 100 iterations to account for within-chain autocorrelation, producing 300 samples from the MCMC simulation.

## Model prediction

Model predictions,  $Y^{new}$ , are made conditional on the observed values,  $Y^{obs}$ . In this application, the posterior predictive distribution of the biomass quantity is given by:

$$[Y^{new}|Y^{obs}] = \int [Y^{new}, \theta|Y^{obs}]d\theta, \quad (5)$$

where  $\theta$  represents a vector of estimated parameters (Table 2). For predictions in unsampled sites within the study area, temperature and depth values are taken from the corresponding grid cell of the ROMS layer and the interpolated bathymetry layer, respectively. The expected catch density,  $\lambda^{new}$ , is calculated with the new covariate values and the predicted biomass,  $Y^{new}$ , is sampled from the CPG substructure.

### 1.4 Model convergence

Simulating the target distribution of species response with MCMC requires an assumption that the resulting posterior distribution is stationary over the target distribution. To assess this assumption, independent MCMC simulations were run until parameter values converged on the same distribution. Model convergence for each estimated parameter was assessed graphically through trace plots of the posterior distributions, and numerically by calculating the potential Scale Reduction Factor ( $\hat{R}$ , Gelman et al. 2004).  $\hat{R}$  compares the between-chain variation with the within-chain variation of the MCMC simulations, and as the number of iterations approaches infinity,  $\hat{R}$  declines to 1. For this study, we used 1.1 as a threshold of precision, as suggested in Gelman et al. (2004), with values below this threshold as evidence consistent with convergence.

The posterior distributions of the parameters were produced for each species (Appendix 4). In addition to the  $\hat{R}$  statistic, evidence of convergence is produced when the posterior distribution of each MCMC chain and parameter are centered on the same value. Pair plots show the posterior distributions of all estimated parameters and the correlation between them (Appendix 4). It should be noted that strong correlations between parameters do not necessarily affect model predictions, but the interpretation of these predictions must be made with caution as the parameter effects cannot be reliably separated.

## 1.5 Posterior Predictive Checking

Model performance is commonly assessed by calculating how well the model can recreate, or fit, observed values given the same environmental data. Following the methods of Lecomte et al., (2013b), we assessed the fit of posterior predictions with observed data through posterior predictive checking. Observed and replicated data from the posterior distribution were standardized to a  $T$  statistic, calculated as a Bayesian residual sum of squares. P-values were calculated as the probability that the  $T$  value of the replicated data is less than the  $T$  value of the observed data. In this comparison, a p-value close to 0.5 suggests the posterior is consistent with the observed data.

## 1.6 Temperature range and probability of presence

The second objective of this study is to provide estimates for the probability of presence relative to bottom temperature for each of the modeled species. We derived probability of presence from the proportion of positive biomass in the posterior distribution, averaged over all survey years. We then mapped these probabilities to the bottom temperature values of their respective grid cell. The subsequent temperature range was truncated to match the temperature range recorded during the synoptic trawl surveys (4.46 – 12.9 C). Ninety-five percent credible intervals were included for each predicted probability.

## Results

### 2.1 Model performance

We calculated two metrics of model performance. The first metric is the potential scale reduction factor testing for convergence of MCMC simulations ( $\hat{R}$ ).  $\hat{R}$  values for all parameters were well below the threshold of 1.1 in all species. Consistent with the  $\hat{R}$  results, the individual parameter posterior distributions did not show any notable divergence between chains when plotted (Appendix 3). Across species, parameters displayed slight skewness or multi-modal shape but this did not affect the convergence of the means. The estimated parameter values for each species are shown in Appendix 5. The second metric, posterior predictive checking, compared the Bayesian residual sum of squares of data replicated from the posterior distribution with those of the observed data, producing a probability that the replicated values fall below the observed values (Table 3). A p-value close to 0.5 suggests a well fitted model. The best fit species models were Arrowtooth Flounder, Rex Sole, and Spotted Ratfish, with p-values between 0.4 and 0.5. Moderately performing species (p-value 0.3-0.4) included Dover Sole, Pacific Cod, and Spiny Dogfish. Relatively poor fitting (p-value 0.1 – 0.3) species included Canary Rockfish, English Sole, Greenstriped Rockfish, Pacific Ocean Perch, Petrale Sole, Redstriped Rockfish, Rock Sole, Sablefish, Shortspine Thornyhead, and Silvergrey Rockfish. Species with the poorest result for this performance metric were Bocaccio and Widow Rockfish. Species models that displayed a better fit according to posterior predictive checking were built from observation data consisting of larger catch biomass that is more evenly spread out across the study area (See Figure 1 and Appendix 1).

Table 3. P-values of each species model representing the probability that a replicated posterior value is less than the associated observed value. A p-value close to 0.5 denotes a well fitted model.

Species	p-value
Arrowtooth flounder	0.459
Bocaccio	0.054
Canary Rockfish	0.112
Dover Sole	0.372
English Sole	0.283
Greenstriped Rockfish	0.145
Pacific Cod	0.319
Petrale Sole	0.249
Pacific Ocean Perch	0.272
Rock Sole	0.169
Redstriped Rockfish	0.142
Rex Sole	0.417
Sablefish	0.233
Silvergrey Rockfish	0.296
Shortspine Thornyhead	0.171
Spiny Dogfish	0.328
Spotted Ratfish	0.433
Widow Rockfish	0.050

## 2.2 General results of temperature and depth on model species

The hierarchical model incorporates different data structures to account for different underlying processes affecting observations, such as the difference between sampling efficiencies and environmental conditions producing an absence in species observations. Despite these structures, if there are too few species occurrences, the observation data will be too insensitive to the model parameters to inform the predictions. Species data with such a low prevalence may still produce relatively well-fitting models, but these models are likely overfitting the data and predictions will be heavily biased. Insufficient prevalence was seen in Bocaccio, Canary Rockfish, Widow Rockfish, Petrale

Sole, Greenstripe Rockfish, and Redstripe Rockfish and as such, predictions for these species are not presented in this report. For the twelve species that did have sufficient catch data, model results are provided in Appendices 3 through 8.

Predicted mean biomass was slightly higher in 2005 compared to subsequent years, consistent with observed data (figure 2, Appendix 6). Credible intervals were shown to be increasing across 2007 to 2011 for many species, suggesting an increasing uncertainty in subsequent years.

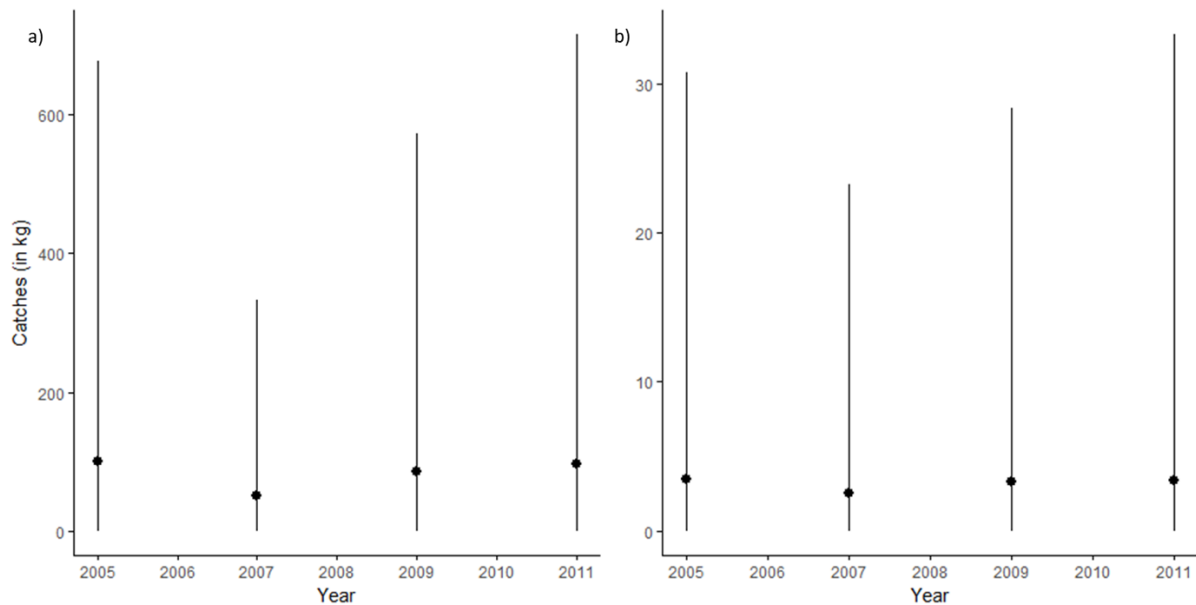


Figure 2. Catch biomass in Kg of a) Arrowtooth Flounder and b) Shortspine Thornyhead for each survey year estimated from the posterior predictive distribution. Points represent mean biomass and lines represent the 95% credible interval for the respective year.

Estimated parameter values (Appendix 5) and the correlations between parameters (Appendix 4) show the relative strength and direction of the effect of depth and temperature on species distributions (i.e. positive or negative effect for temperature or depth). In the case of Arrowtooth Flounder, there was a negative effect of both depth and temperature. Shortspine Thornyhead showed a slight positive effect of depth and a strong negative effect from temperature. The correlation between the temperature and depth coefficients were very high for all species and above 0.8 for the two species described here.

Including spatially co-occurring environmental predictors in a model necessitates an expectation of covariation between those predictors. Correlations between model parameters for the 12 modeled species can be viewed in pair plots (Appendix 4). Temperature and depth parameters, as expected, were highly correlated. Predicted biomass followed depth and temperature contours, highlighting bathymetric features of the study area (Figure 3, Appendix 7). Each year was included as a categorical variable in the linear environmental model. For most species the year parameters were highly correlated with each other as well as with the model intercept. These correlations make it difficult to isolate the effect of any particular year.



Probability of presence for each species model was plotted over observed temperatures (Figure 4, Appendix 8). Strong relationships between presence and temperature were seen in a few species (e.g., Shortspine Thornyhead, Dover Sole, and Pacific Ocean Perch) where probabilities from zero to one were observed across the temperature range and credible intervals of median presence were small. Arrowtooth Flounder showed a moderate relationship between probability of presence and temperature, with credible intervals becoming more variable in colder temperatures (Figure 4). In other species, probabilities were lower across the temperature range and credible intervals varied drastically, such as in the case of Spiny Dogfish and Pacific Cod (see Appendix 8).

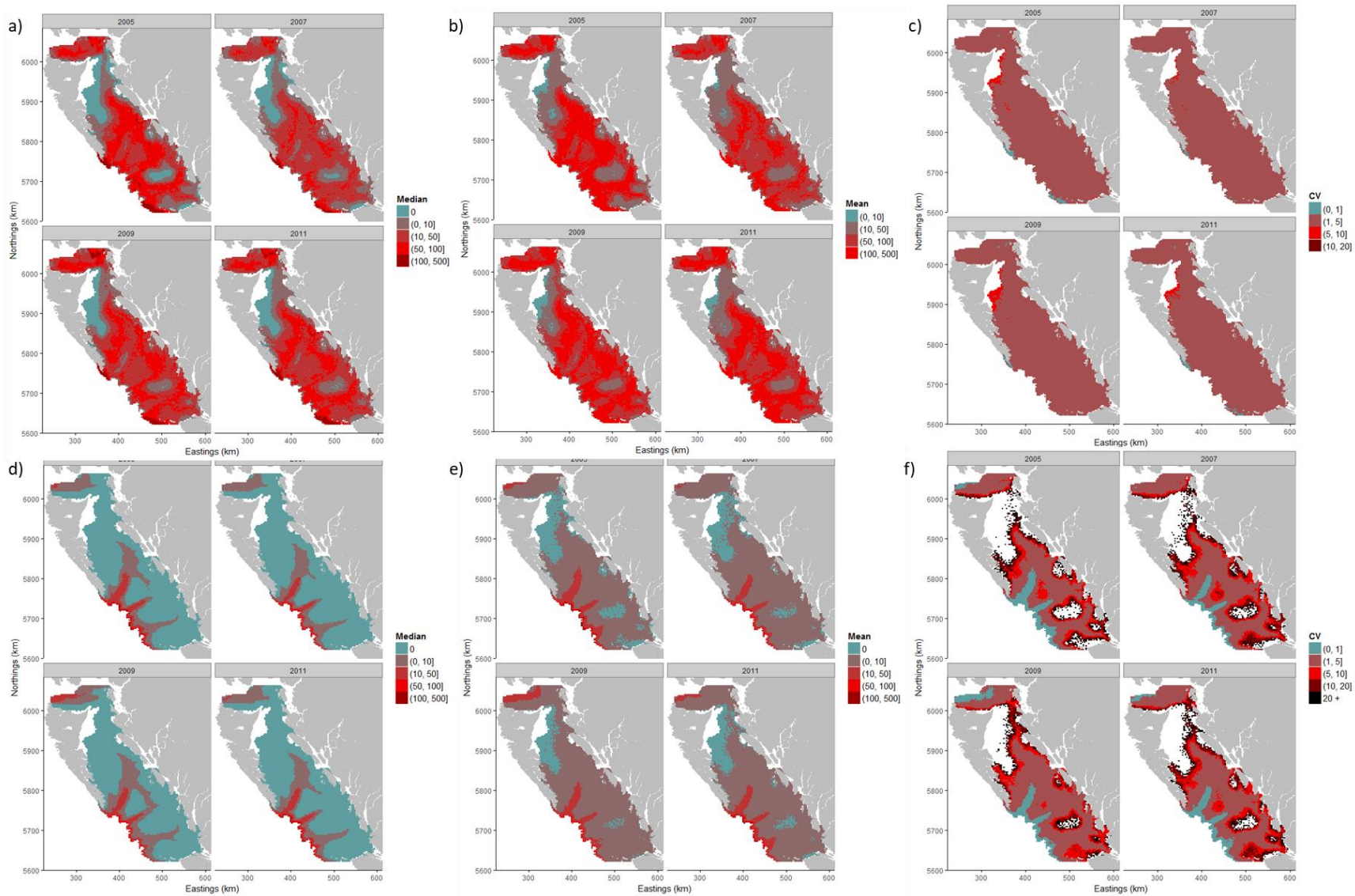


Figure 3. Predicted median biomass in kg, mean biomass in kg, and coefficient of variation for Arrowtooth Flounder (a, b, c) and Shortspine Thornyhead (d, e, f) for each survey year.

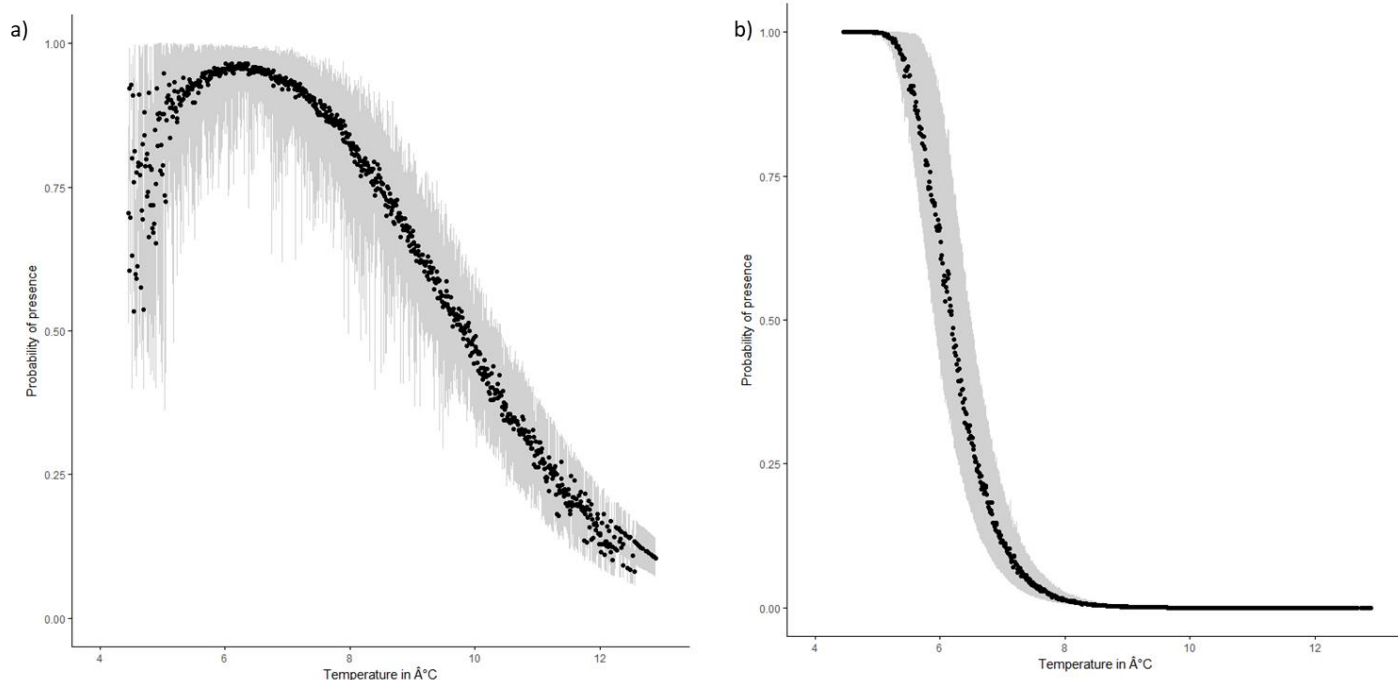


Figure 4. Probability of presence across bottom temperature for a) Arrowtooth Flounder and b) Shortspine Thornyhead. Each dot and line represent a 3 x 3 km cell. Dots represent means and lines represent 95% credible intervals.

## Conclusion

Modelling survey biomass has often produced mixed results when using popular SDM methods as it is difficult to represent the localized variability of biomass at the coarse scale often used for model predictor variables. The CPG approach used in this study incorporated a data model to represent the stochastic structure of trawl biomass in conjunction with the ecological model representing species occurrence. With the same model applied to multiple species, results were dependent on species representation in the data such as prevalence and magnitude of catches. Bayesian ecological models typically use non-informative priors as ecological processes are unknown *a priori* (Lemoine, 2019), therefore the model outputs rely mostly on observed data. The authors acknowledge the difference in life histories across modelled species as other sources of variance that may not be accounted for in the model structure.

While the compound model structure has gained support for representing continuous data such as trawl catch biomass (Ancelet et al., 2010; Anderson et al., 2019; Lecomte et al., 2013b; Stefánsson, 1996), the representation of the species-environmental relationship as a linear function is a matter of debate. The increased use of models such as Generalized Additive Models, MaxEnt, and various decision tree methods that can easily represent a variety of non-linear features gives evidence to a more complicated relationship between a species' response and its environment. Rockfishes are known for their wide variety of habitat use across species with a high degree of fidelity to those habitats (Rooper et al., 2010). Previous habitat modelling has highlighted Shortspine Thornyhead habitat association with sponges and corals (Du Preez & Tunnicliffe, 2011; Rooper & Martin, 2009). Fidelity to a specific habitat may help explain the poor model fit for Shortspine Thornyhead and Pacific Ocean Perch while still showing a tightly fit relationship between presence and temperature. In flatfishes, Dover Sole habitat has been

strongly associated with depth, with sediment type and temperature as important classifying variables (Eastwood et al., 2003). The model presented in this report performed moderately well for Dover Sole, likely due to the strong relationship with temperature but discrepancies between predicted and observed biomass may be due to the omission of sediment type from this model. These habitats are likely defined by more than temperature and depth.

In the second objective, interpreting the relationship of a species' presence with temperature using predicted probability of presence must be taken in context of the species model itself. There did not appear to be a direct link between a model's fit and the strength of the relationship of temperature with species presence. In the most dramatic example, Shortspine Thornyhead displayed a tight relationship between temperature and probability of presence; however, posterior predictive checking suggested a consistent over-estimation from the model. In this example, the strong relationship between temperature and presence may have more to do with a strong spatial autocorrelation of the data, as the catch data for this species is mainly restricted to the deeper troughs of Queen Charlotte Sound. Arrowtooth Flounder and Dover Sole were species that displayed relatively clear trends between presence and temperature while performing well in posterior predictive checking. These species were also caught more evenly across the survey area, further suggesting a spatial limitation to the model. Accounting for spatial autocorrelation is possible using the model approach presented here by including a random field as done by Lecomte, et al. (2013b). A random field would likely improve model performance, and produce more generalized predictions, but these improvements are still limited by data quality.

The model applied in this paper addresses underlying structures in trawl catch data often not taken into account within species distribution modeling methods, though by no means assumes to fully represent the habitat or ecosystem. As mentioned above, the environmental variables that adequately represent a species' habitat are largely dependent on the species being modelled. Possibly the largest assumption in this and many species distribution models is the independence of species occurrence from other species. A species may respond differently to the same environmental conditions based on the presence of other species interacting as competitors, predators, or prey. Research in subjects such as meta-community theory addresses species interactions (Thompson et al., 2020).

The assumption of a static distribution is common in species distribution modelling. This simplification is useful for producing a snapshot of a distribution or habitat given available information, but it is unclear how stable that snapshot is. Of the species for which the model achieved viable outputs, all but two species were negatively associated with both temperature and depth. These outputs suggest that the majority of the species we investigated prefer cooler temperature and relatively shallower water. If these species are occurring near their environmental thresholds for temperature and depth, any increase in temperature would force species to shift to cooler latitudes rather than deeper depths. However, Dover sole and Sablefish were negatively associated with temperature and positively associated with depth and are thus associated with cooler temperature and deeper habitat. These two species may be able to escape warmer temperature by moving deeper. Further investigation outside of the temporal and spatial window of this model is necessary to test this interpretation. Species responses to environmental change may be more accurately understood through climate velocity approaches that capture finer-scale and faster changes within important fisheries areas such as the British Columbian continental shelf (English et al., 2021).

In conclusion, a thoughtful incorporation of a data model into the structure of the statistical method of a species distribution model produced a viable, though species-dependent result. This result highlights the importance of developing all three component models in a distribution or habitat model to allow the

subsequent understanding of these components to recursively shape the structure of species distribution models.

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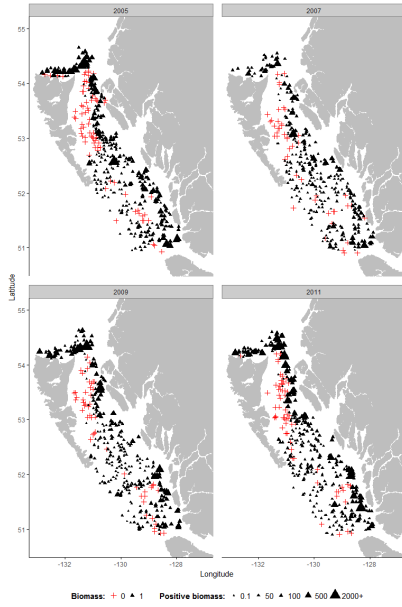
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## Appendices

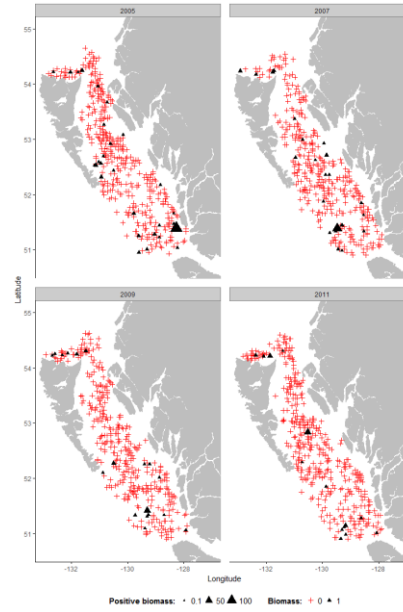
Appendix 1: Locations and quantities (kg) of catch biomass for each year in the study area.

Locations and quantities (kg) of catch biomass for each year in the study area. Red crosses represent zero catch. Black triangles represent positive catch.

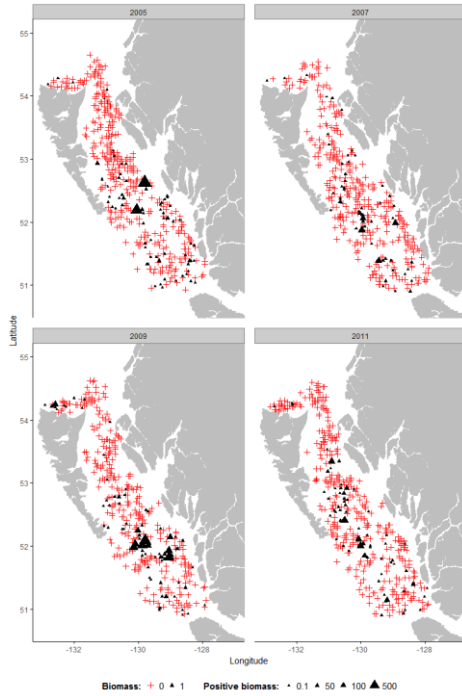
A1- 1 Arrowtooth Flounder



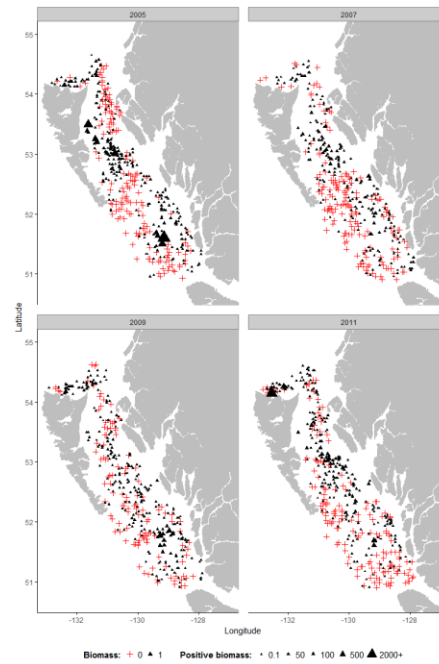
A1- 2 Bocaccio



A1- 3 Canary Rockfish

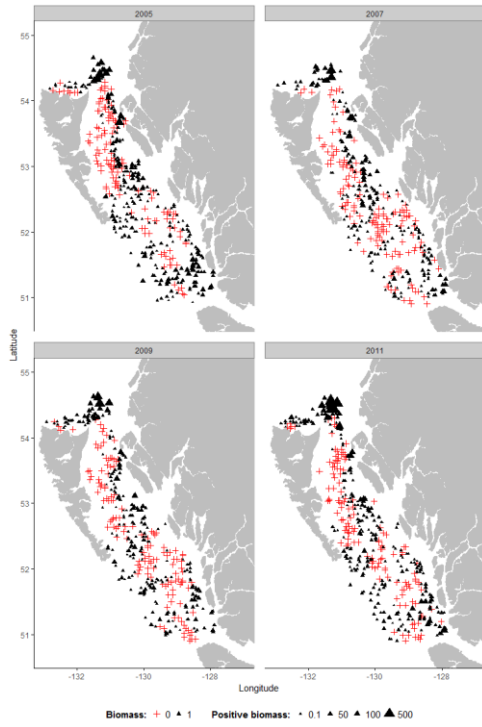


A1-4 Dogfish

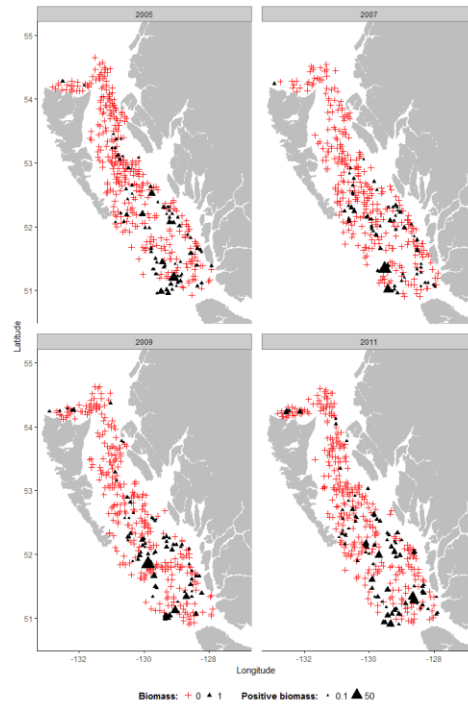




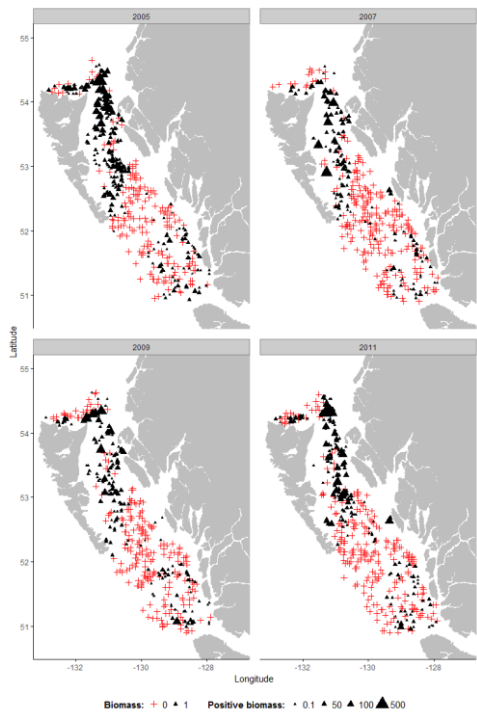
A1-5 Dover sole



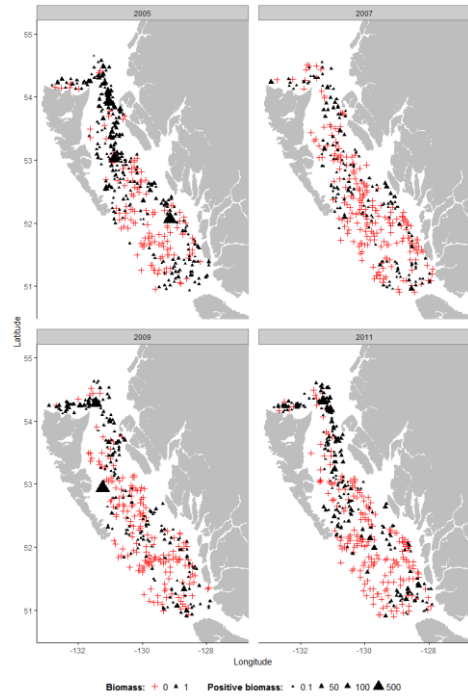
A1-6 Greenstripe rockfish



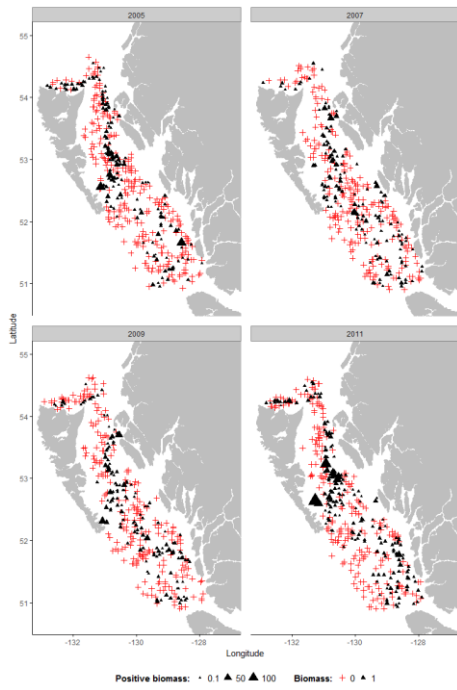
A1-7 English sole



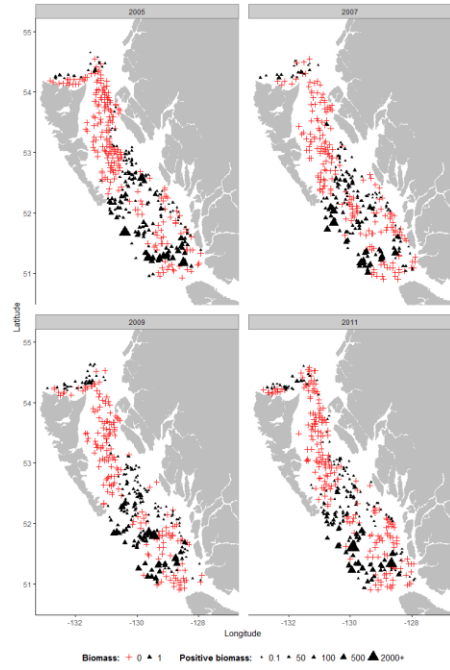
A1-8 Pacific cod



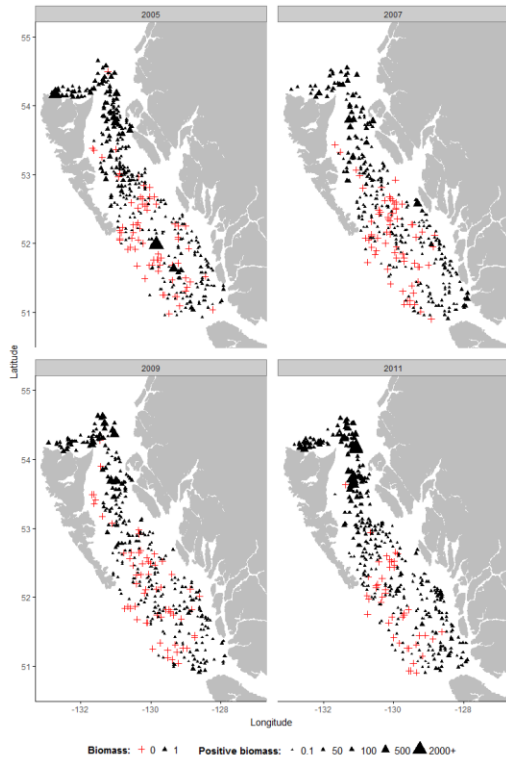
A1 - 9 *Petrale sole*



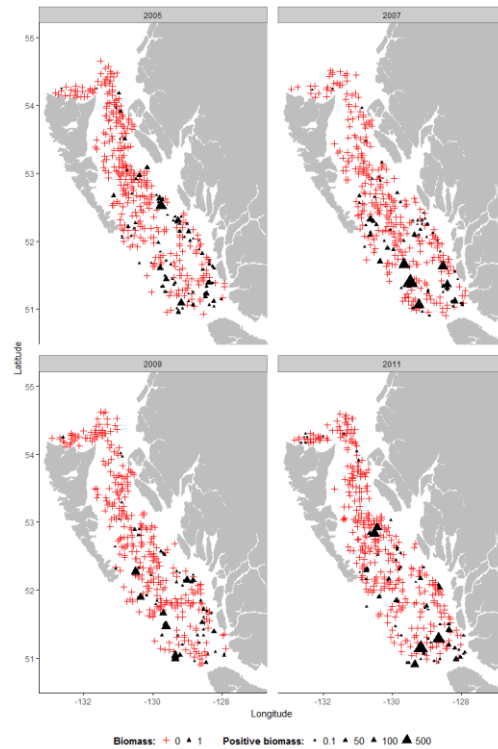
A1- 10 Pacific Ocean perch



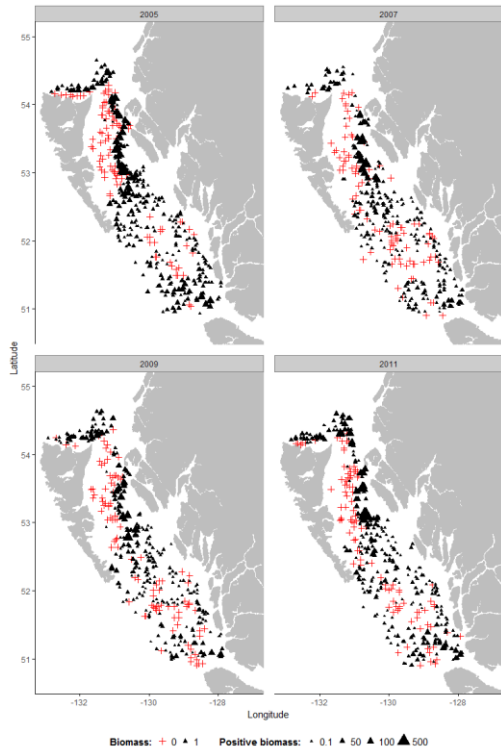
A1- 11 *Spotted ratfish*



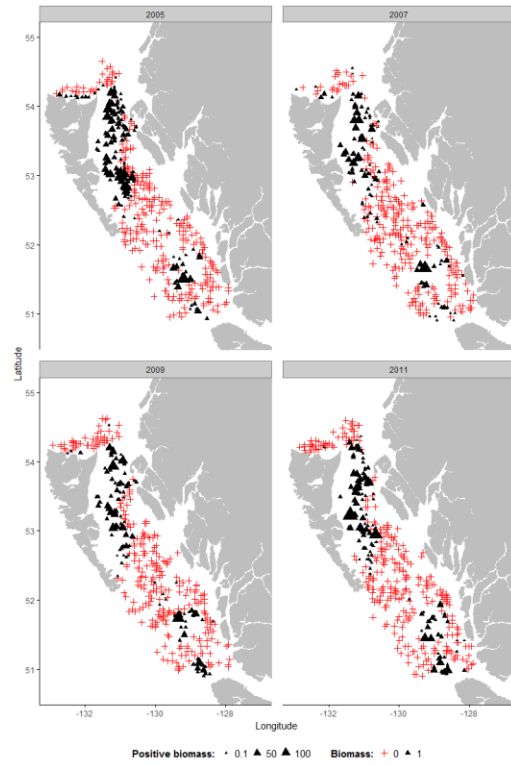
A1- 12 Redstripe rockfish



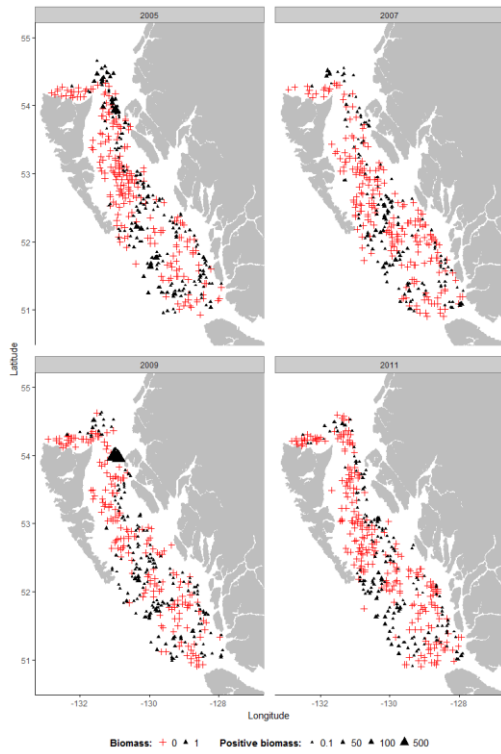
A1- 13 Rex sole



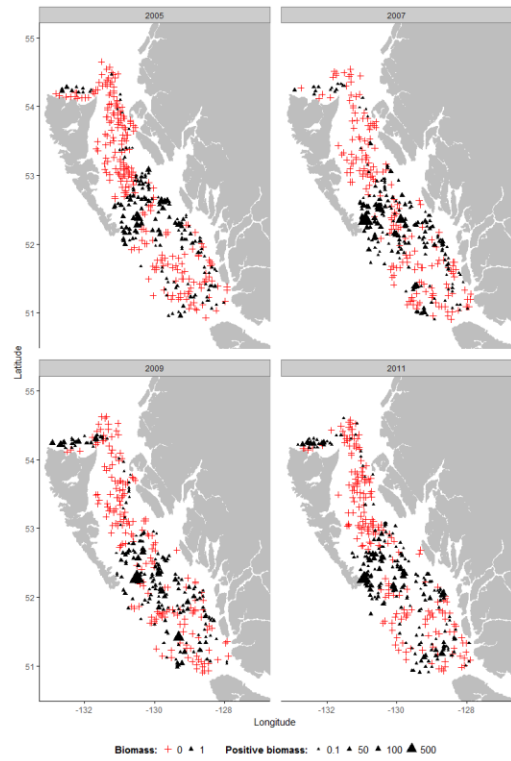
A1- 14 Rock sole



A1- 15 Sablefish

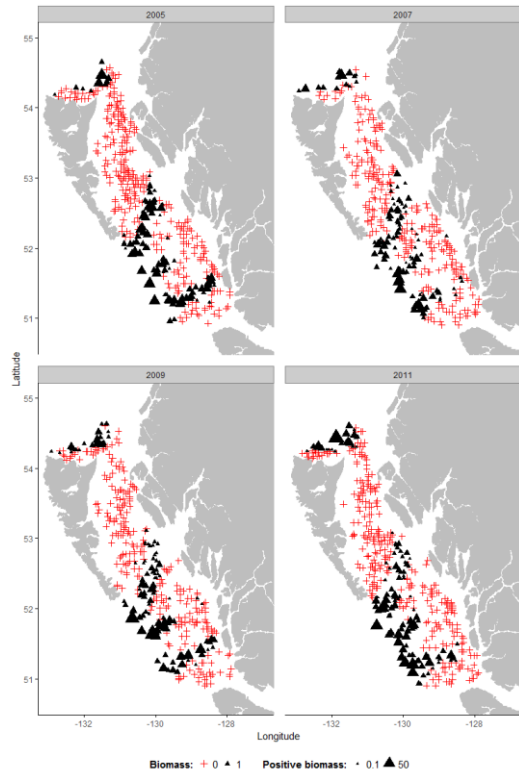


16 Silvergray rockfish

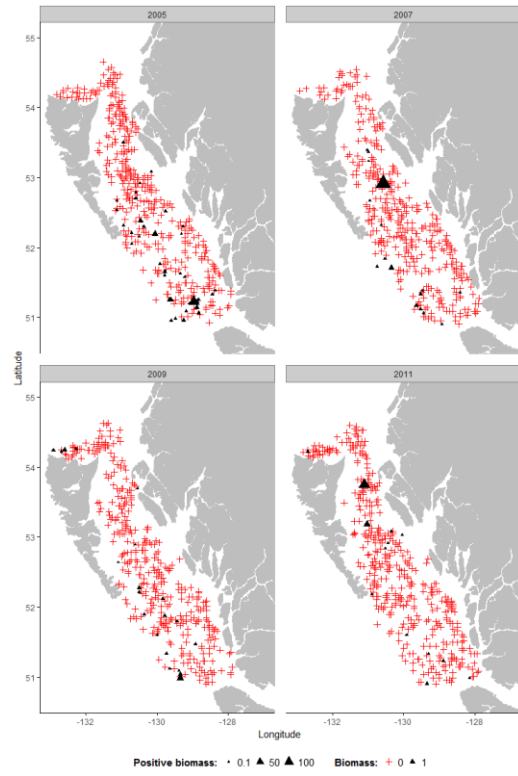


A1-

A1- 17 Shortspine thornyhead



A1- 18 Widow rockfish



## Appendix 2: Sample Nimble code

```
substitute({

  for (s in 1:n_obs){

    lambda[s] <- exp(mu + beta_year[Year[s]] + beta_temp*temp[s] + beta_depth*depth[s] )

    lambda_std[s] <- lambda[s]*SV[s]

  }

  for ( s in 1:n_pres){

    ngis[s] ~ dpois(lambda_std[pres[s]])

    Y[pres[s]] ~ dgamma(shape = a * ngis[s], rate = b)

  }

  for ( s in 1:n_abs){

    proba[s] <- 1 - exp(-lambda_std[abs[s]])

    Y[abs[s]] ~ dbern(proba[s])

  }

  ### Prior

  a ~ dgamma(shape = 0.1, rate = 0.1)

  b ~ dgamma(shape = 0.1, rate = 0.1)

  mu ~ dnorm(0, sd =10)

  beta_temp ~ dnorm(0, sd =10)

  beta_depth ~ dnorm(0, sd =10)

  beta_year[1] <- 0

  for(year_id in 2:n_year){

    beta_year[year_id] ~ dnorm(0, sd =10)

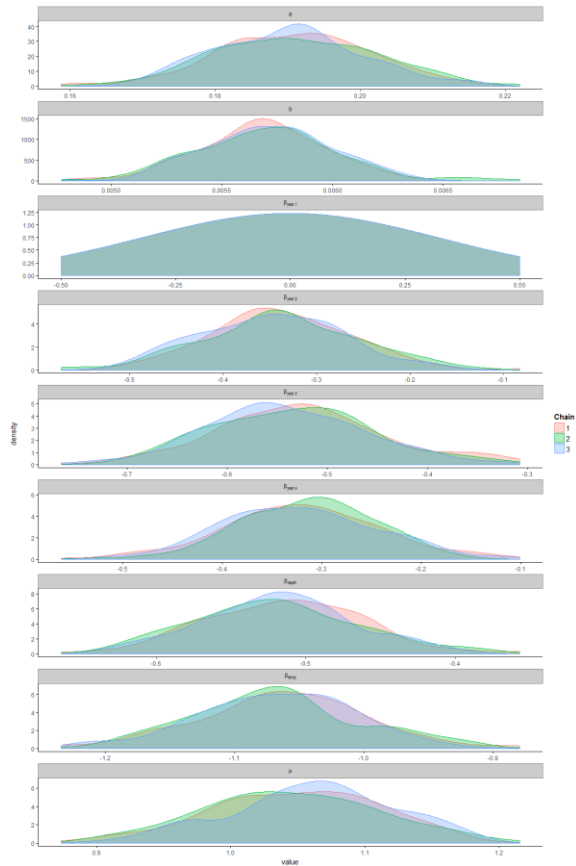
  }

})
```

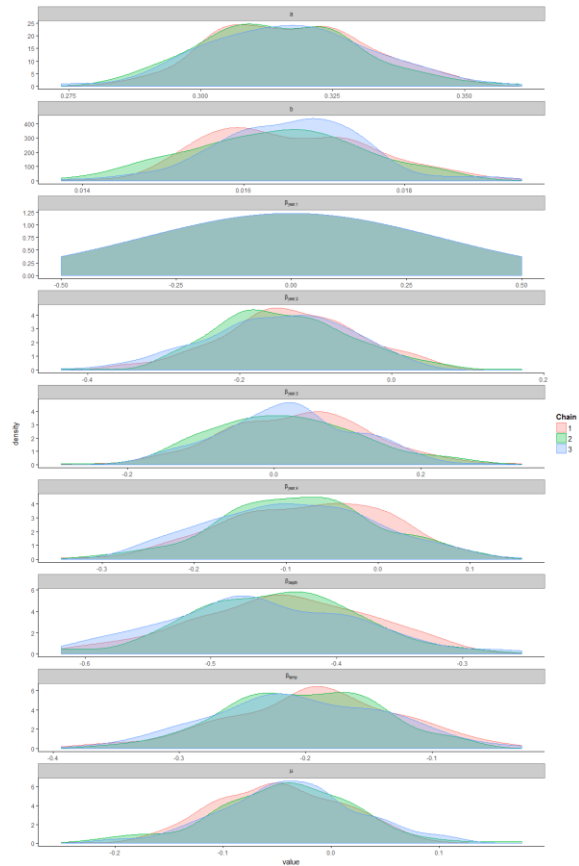
### Appendix 3: Posterior density distributions for each model parameter.

Posterior density distributions for each model parameter. Different coloured distributions represent chains of the Markov Chain Monte Carlo simulation. The overlay of density distributions from each chain serves as a visual representation of the model's convergence on the parameter's value.

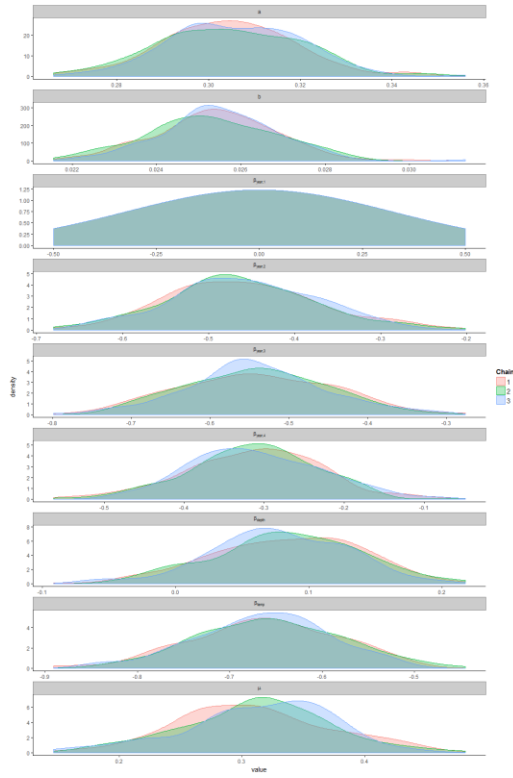
#### A3- 1 Arrowtooth Flounder



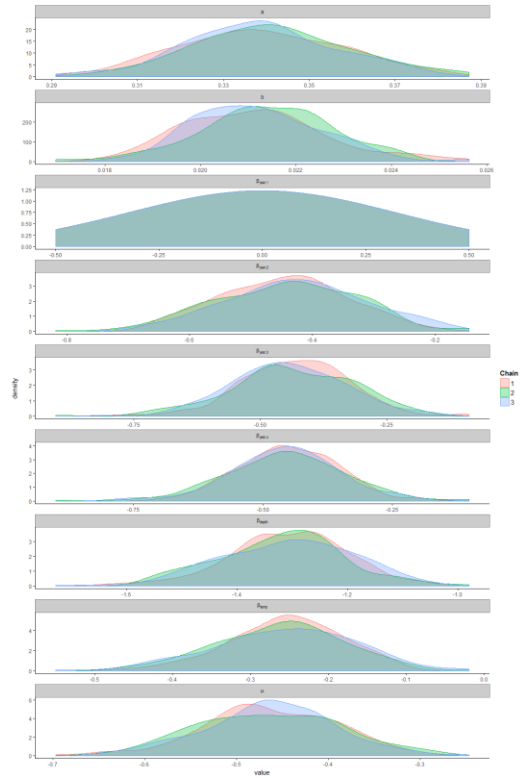
#### A3-2 Dogfish



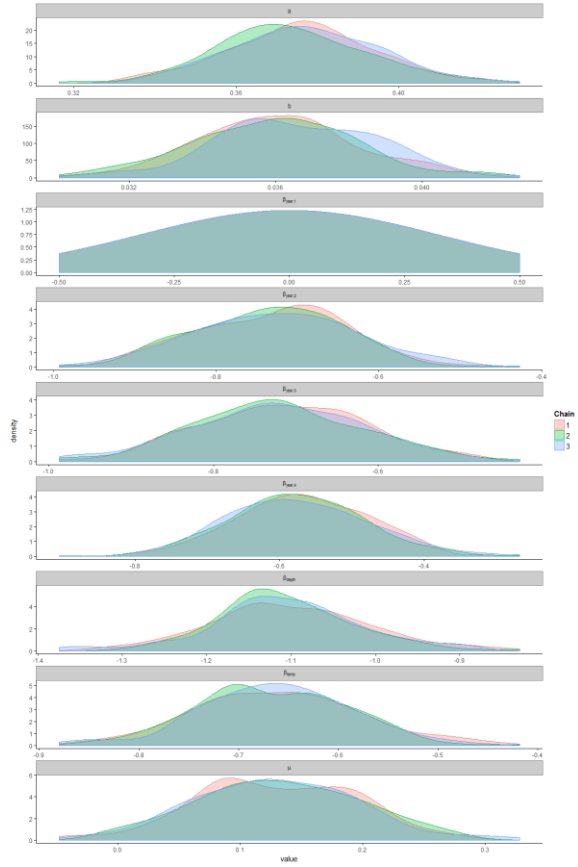
### A3 - 3 Dover sole



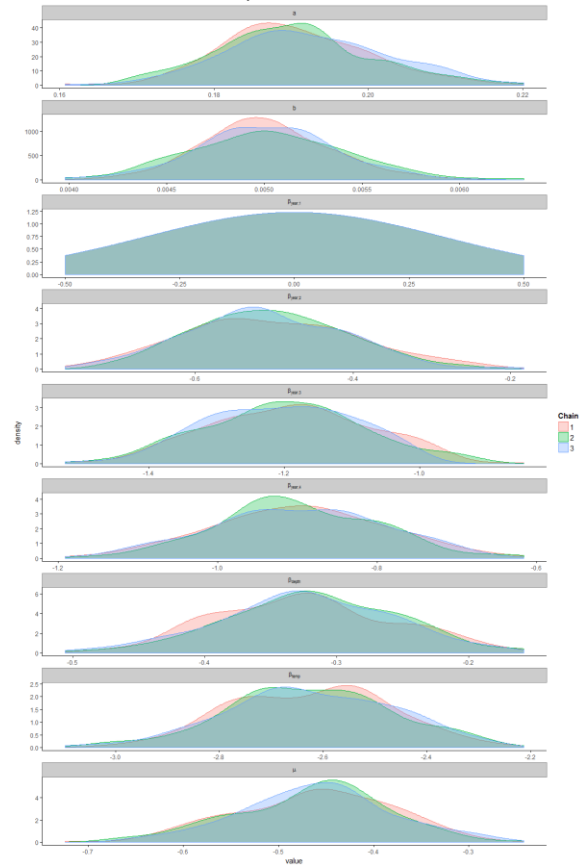
### A3- 4 English sole



### A3- 5 Pacific cod

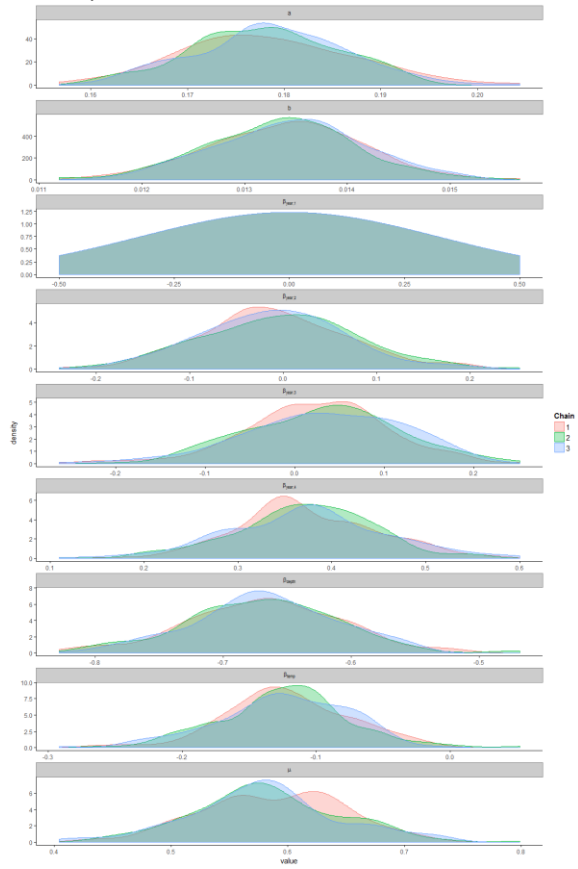


### A3- 6 Pacific Ocean perch

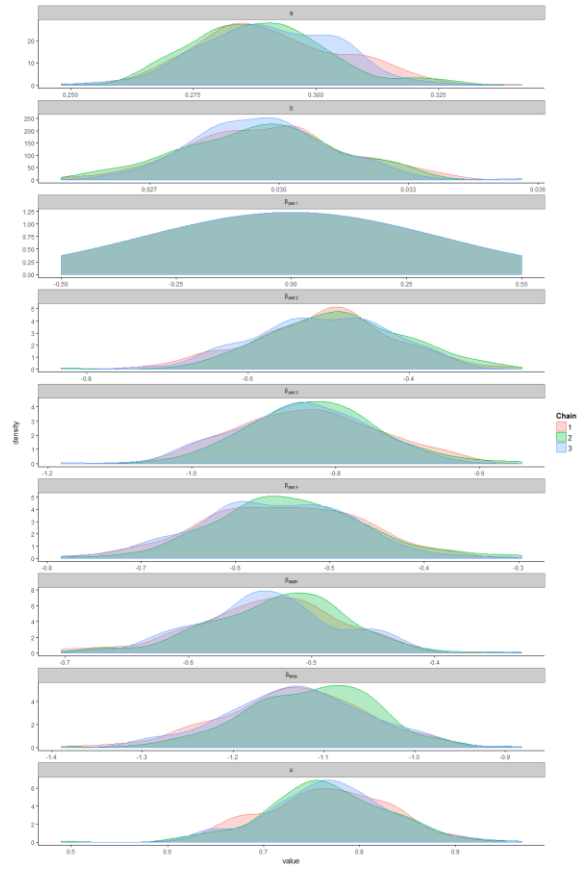




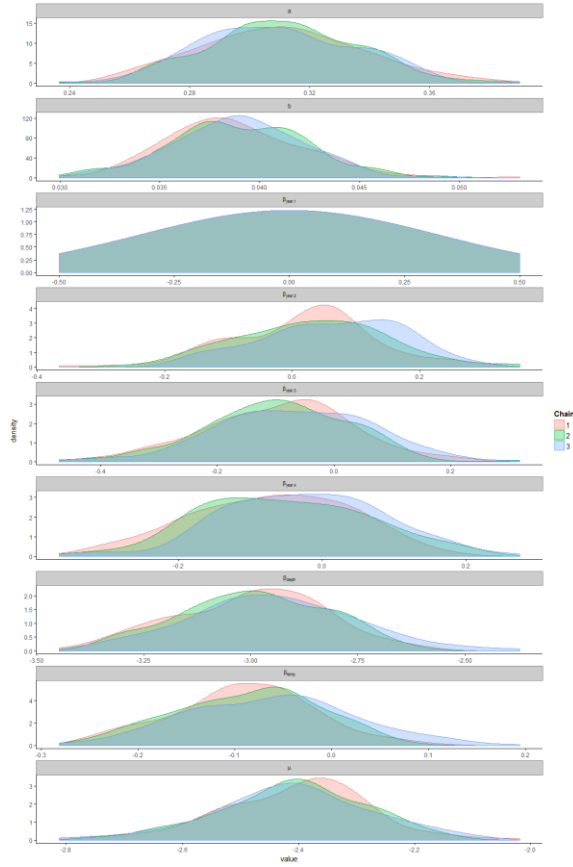
### A3- 7 Spotted ratfish



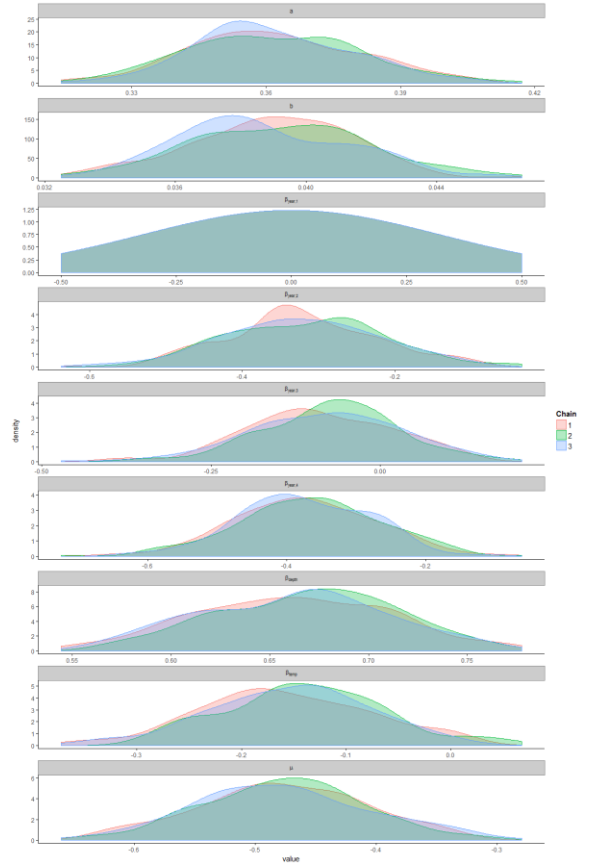
### A3- 8 Rex sole



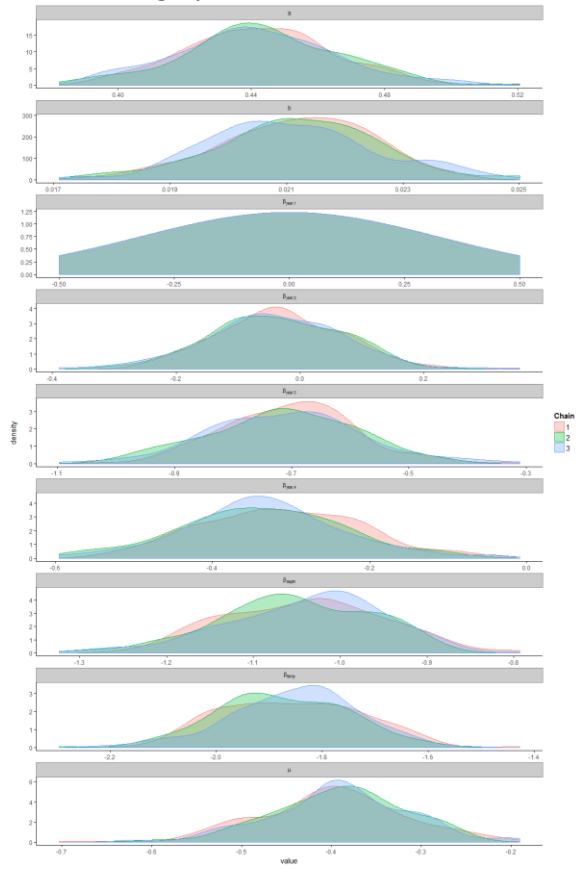
### A3-9 Rock sole



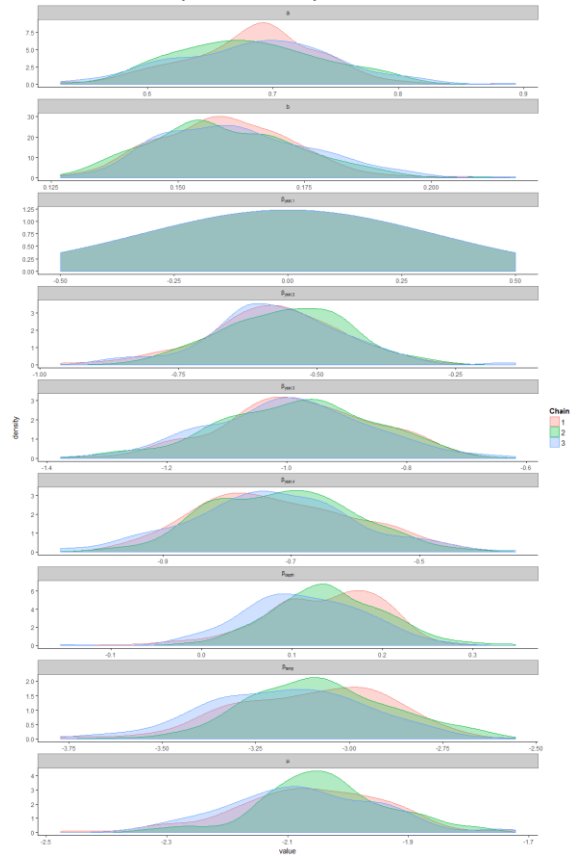
### A3-10 Sablefish



### A3- 11 Silvergray rockfish



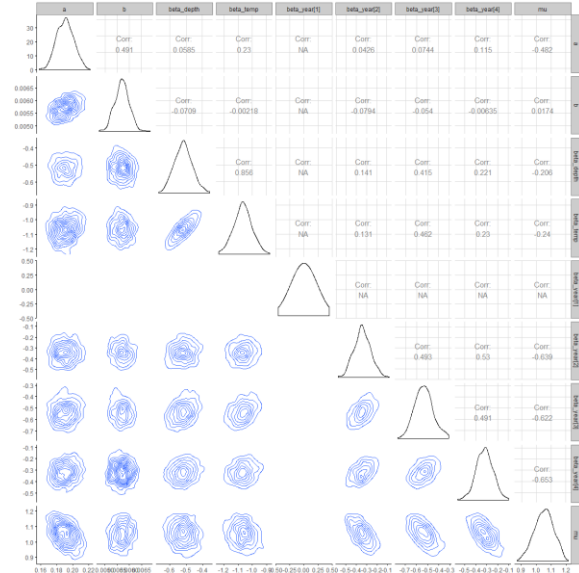
### A3 – 12 Shortspine Thornyhead



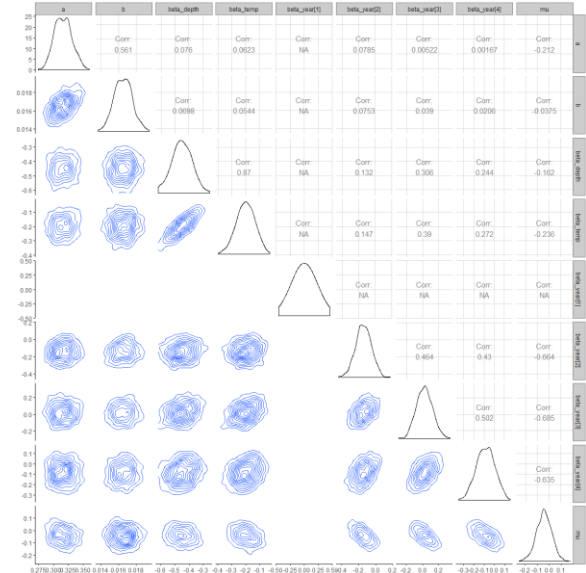
Appendix 4: Pairs plot of model parameters generated from posterior distributions.

Pairs plot of model parameters generated from posterior distributions. Diagonals show the marginal distributional density of each parameter. Above the diagonal are the correlation coefficients of the intersecting parameters. Below the diagonal shows topographic density plots of the intersecting parameters.

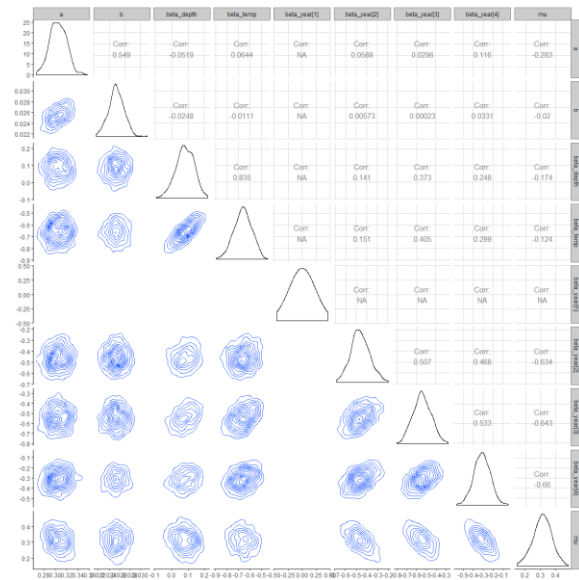
A4- 1 Arrowtooth Flounder



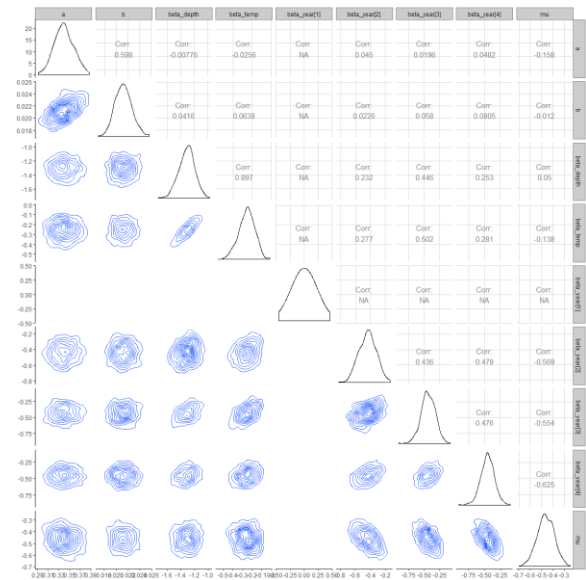
A4 -2 Dogfish



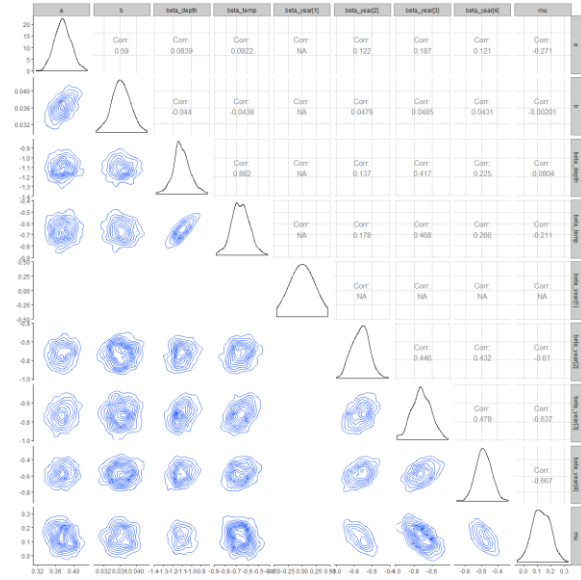
A4 -3 Dover sole



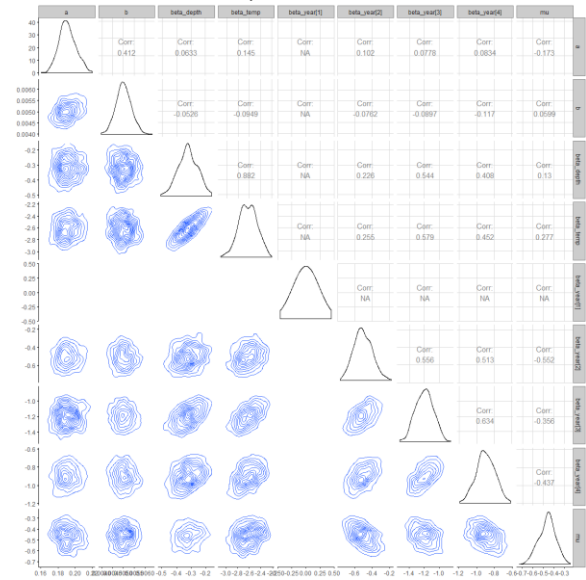
A4 - 4 English sole



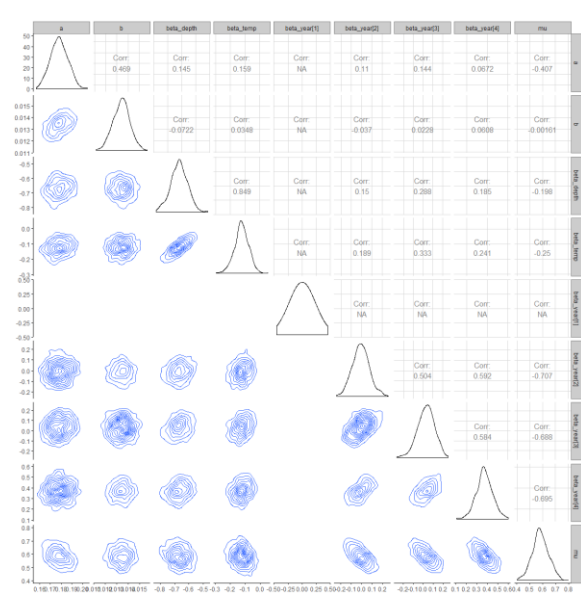
### A4- 5 Pacific cod



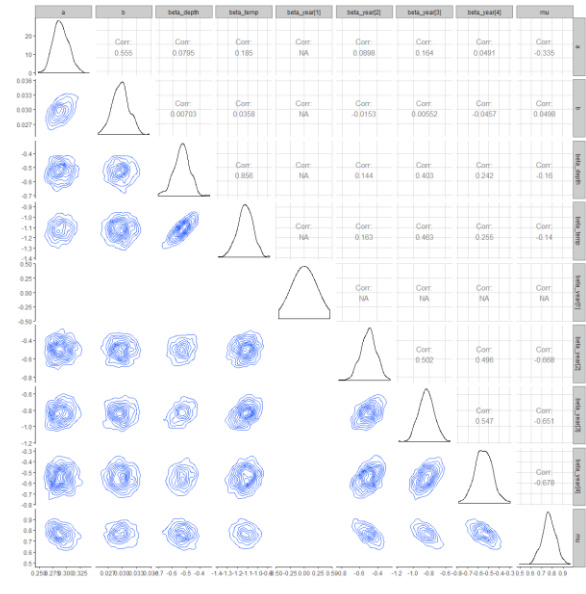
### A4-6 Pacific Ocean perch



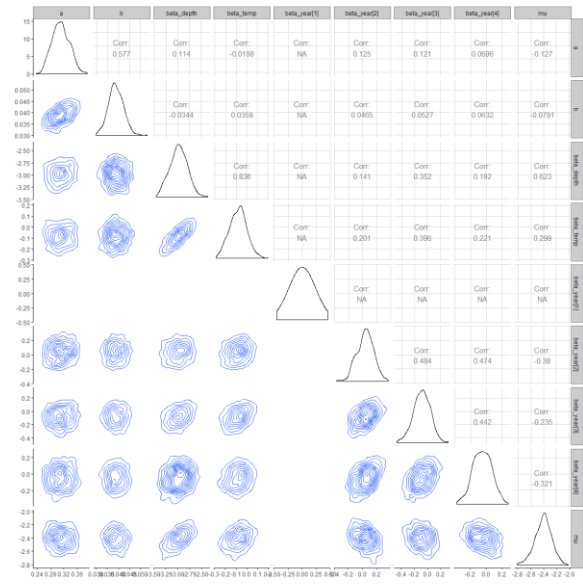
### A4- 7 Spotted ratfish



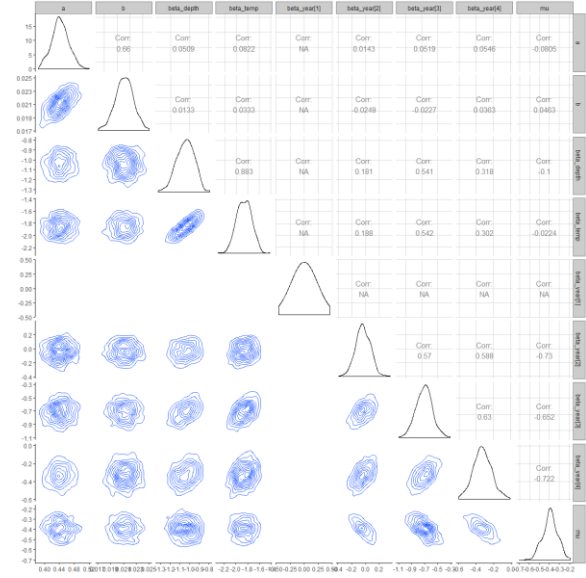
### A4- 9 Rex sole



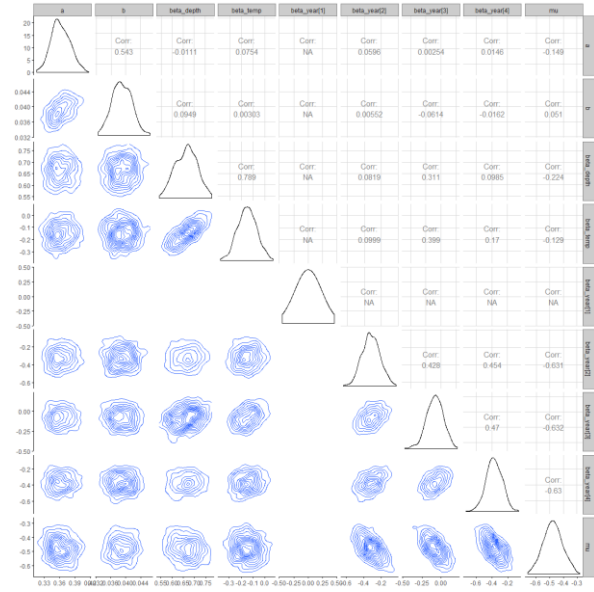
### A4- 8 Rock sole



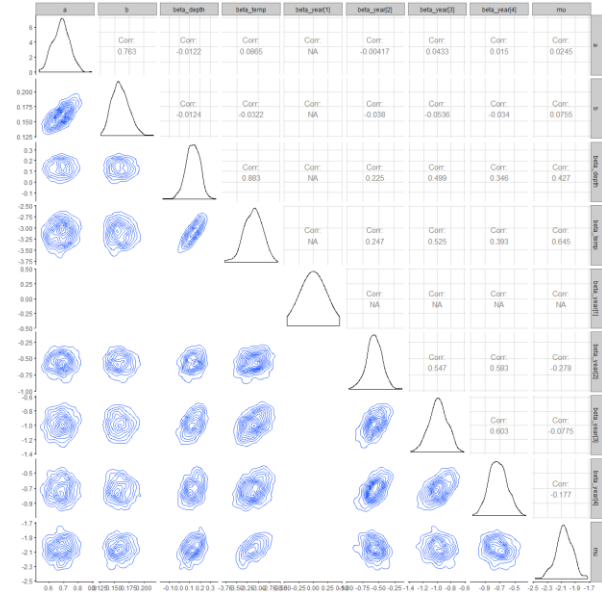
### A4- 11 Silvergray rockfish



### A4 - 10 Sablefish



### A4 - 12 Shortspine Thornyhead



## Appendix 5: Estimated model parameters

Model parameters and summary statistics of their posterior distributions for each species. Mean, standard deviation (sd), quantile at 2.5% (q2.5), median and quantile at 97.5% (q97.5).

### A5 – 1 Arrowtooth flounder

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.191	0.011	0.171	0.191	0.212
$b$	0.006	0.000	0.005	0.006	0.006
$\beta_{depth}$	-0.517	0.053	-0.620	-0.517	-0.404
$\beta_{temp}$	-1.066	0.064	-1.193	-1.068	-0.945
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.341	0.078	-0.482	-0.344	-0.186
$\beta_{year,3}$	-0.533	0.082	-0.680	-0.534	-0.354
$\beta_{year,4}$	-0.319	0.075	-0.473	-0.320	-0.173
$\mu$	1.051	0.063	0.926	1.053	1.164

### A5- 2 Dogfish

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.316	0.015	0.290	0.316	0.345
$b$	0.017	0.001	0.015	0.017	0.018
$\beta_{depth}$	-0.451	0.070	-0.598	-0.452	-0.318
$\beta_{temp}$	-0.200	0.066	-0.330	-0.199	-0.076
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.142	0.090	-0.315	-0.142	0.028
$\beta_{year,3}$	0.024	0.097	-0.156	0.024	0.217
$\beta_{year,4}$	-0.085	0.087	-0.249	-0.086	0.078
$\mu$	-0.043	0.063	-0.175	-0.042	0.078

### A5- 3 Dover sole

Parameter	mean	sd	q2.5	median	q97.5
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$a$	0.305	0.015	0.277	0.305	0.332
$b$	0.025	0.001	0.023	0.025	0.028
$\beta_{depth}$	0.082	0.053	-0.029	0.081	0.180
$\beta_{temp}$	-0.661	0.076	-0.815	-0.659	-0.520
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.460	0.086	-0.622	-0.463	-0.283
$\beta_{year,3}$	-0.541	0.091	-0.714	-0.544	-0.362
$\beta_{year,4}$	-0.312	0.081	-0.469	-0.313	-0.157
$\mu$	0.312	0.061	0.187	0.313	0.431

#### A5- 4 English sole

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.340	0.018	0.305	0.339	0.376
$b$	0.021	0.001	0.019	0.021	0.024
$\beta_{depth}$	-1.312	0.113	-1.536	-1.305	-1.102
$\beta_{temp}$	-0.257	0.082	-0.425	-0.253	-0.111
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.438	0.110	-0.647	-0.436	-0.228
$\beta_{year,3}$	-0.437	0.114	-0.662	-0.441	-0.213
$\beta_{year,4}$	-0.454	0.107	-0.661	-0.455	-0.245
$\mu$	-0.464	0.073	-0.607	-0.464	-0.316

#### A5- 5 Pacific cod

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.376	0.018	0.341	0.375	0.413
$b$	0.036	0.002	0.032	0.036	0.041
$\beta_{depth}$	-1.105	0.089	-1.278	-1.113	-0.904



$\beta_{temp}$	-0.663	0.078	-0.821	-0.663	-0.503
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.731	0.094	-0.903	-0.725	-0.544
$\beta_{year,3}$	-0.719	0.102	-0.914	-0.721	-0.518
$\beta_{year,4}$	-0.573	0.094	-0.749	-0.574	-0.391
$\mu$	0.130	0.066	0.003	0.129	0.255

#### A5- 6 Pacific Ocean perch

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.191	0.010	0.173	0.190	0.211
$b$	0.005	0.000	0.004	0.005	0.006
$\beta_{depth}$	-0.322	0.065	-0.444	-0.322	-0.200
$\beta_{temp}$	-2.624	0.157	-2.919	-2.618	-2.325
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.506	0.102	-0.694	-0.512	-0.298
$\beta_{year,3}$	-1.198	0.115	-1.404	-1.196	-0.983
$\beta_{year,4}$	-0.898	0.105	-1.100	-0.902	-0.692
$\mu$	-0.462	0.080	-0.624	-0.459	-0.313

#### A5- 7 Spotted ratfish

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.178	0.008	0.163	0.178	0.194
$b$	0.013	0.001	0.012	0.013	0.015
$\beta_{depth}$	-0.668	0.058	-0.791	-0.667	-0.559
$\beta_{temp}$	-0.123	0.048	-0.224	-0.123	-0.030
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.008	0.080	-0.159	-0.009	0.161

$\beta_{year,3}$	0.030	0.084	-0.144	0.035	0.180
$\beta_{year,4}$	0.373	0.077	0.218	0.372	0.533
$\mu$	0.584	0.062	0.461	0.581	0.707

#### A5- 8 Rock sole

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.311	0.026	0.264	0.311	0.361
$b$	0.039	0.003	0.032	0.039	0.046
$\beta_{depth}$	-2.980	0.180	-3.317	-2.976	-2.643
$\beta_{temp}$	-0.080	0.079	-0.228	-0.076	0.076
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	0.038	0.115	-0.169	0.045	0.254
$\beta_{year,3}$	-0.086	0.128	-0.339	-0.082	0.152
$\beta_{year,4}$	-0.050	0.115	-0.281	-0.052	0.172
$\mu$	-2.409	0.131	-2.689	-2.402	-2.158

#### A5- 9 Rex sole

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.290	0.014	0.266	0.289	0.319
$b$	0.030	0.002	0.026	0.030	0.033
$\beta_{depth}$	-0.532	0.058	-0.660	-0.529	-0.430
$\beta_{temp}$	-1.125	0.077	-1.278	-1.123	-0.980
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.501	0.085	-0.663	-0.498	-0.344
$\beta_{year,3}$	-0.838	0.094	-1.007	-0.840	-0.647
$\beta_{year,4}$	-0.550	0.081	-0.708	-0.550	-0.386
$\mu$	0.767	0.064	0.643	0.766	0.895

### A5- 10 Sablefish

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.362	0.018	0.326	0.360	0.401
$b$	0.039	0.003	0.034	0.039	0.044
$\beta_{depth}$	0.664	0.047	0.575	0.667	0.755
$\beta_{temp}$	-0.150	0.079	-0.302	-0.150	0.001
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.320	0.101	-0.510	-0.323	-0.125
$\beta_{year,3}$	-0.081	0.108	-0.299	-0.077	0.120
$\beta_{year,4}$	-0.372	0.100	-0.568	-0.374	-0.184
$\mu$	-0.477	0.069	-0.611	-0.476	-0.339

### A5- 11 Silvergrey rockfish

Parameter	mean	sd	q2.5	median	q97.5
$a$	0.442	0.023	0.397	0.441	0.487
$b$	0.021	0.001	0.018	0.021	0.024
$\beta_{depth}$	-1.044	0.090	-1.217	-1.039	-0.888
$\beta_{temp}$	-1.861	0.126	-2.102	-1.861	-1.629
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.036	0.105	-0.242	-0.039	0.152
$\beta_{year,3}$	-0.709	0.124	-0.946	-0.704	-0.460
$\beta_{year,4}$	-0.327	0.103	-0.529	-0.330	-0.111
$\mu$	-0.394	0.077	-0.549	-0.393	-0.253

### A5-12 Shortspine Thornyhead

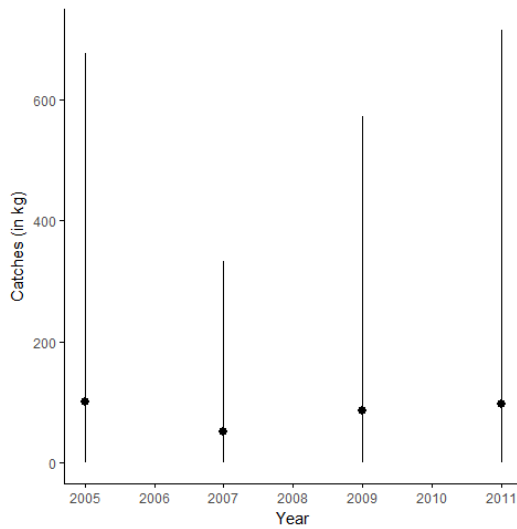
Parameter	mean	sd	q2.5	median	q97.5
$a$	0.684	0.058	0.579	0.686	0.796
$b$	0.160	0.014	0.136	0.159	0.190
$\beta_{depth}$	0.129	0.065	-0.007	0.132	0.252

$\beta_{temp}$	-3.117	0.207	-3.530	-3.110	-2.730
$\beta_{year,1}$	0.000	0.000	0.000	0.000	0.000
$\beta_{year,2}$	-0.568	0.119	-0.812	-0.567	-0.344
$\beta_{year,3}$	-0.986	0.129	-1.238	-0.985	-0.758
$\beta_{year,4}$	-0.723	0.119	-0.946	-0.731	-0.479
$\mu$	-2.058	0.119	-2.301	-2.061	-1.833

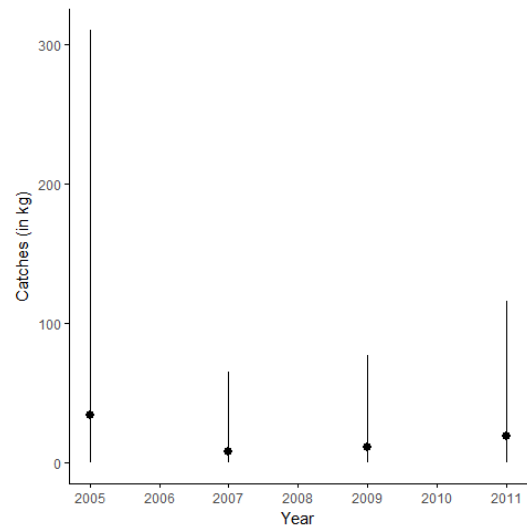
## Appendix 6: Estimated mean catch biomass

Mean catch biomass per year predicted from the full posterior distribution. Dots represent mean catch biomass per year with their associated 95% credible interval of the catches. Predictions were only made for 2005, 2007, 2009, and 2011 as these were the survey years included in the model fitting.

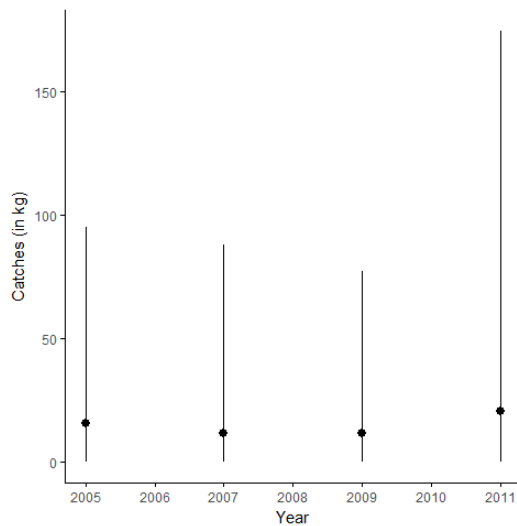
### A6-1 Arrowtooth Flounder



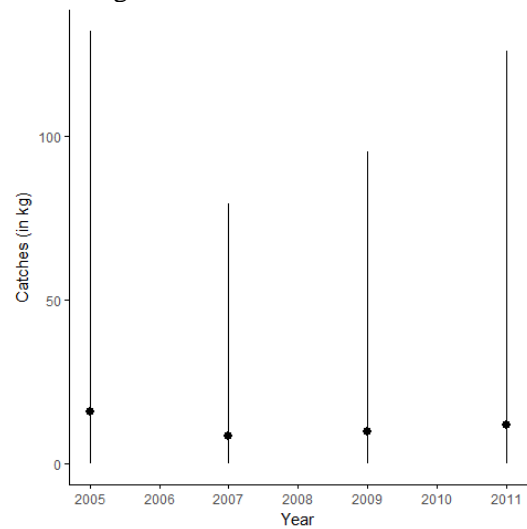
### A6-2 Dogfish



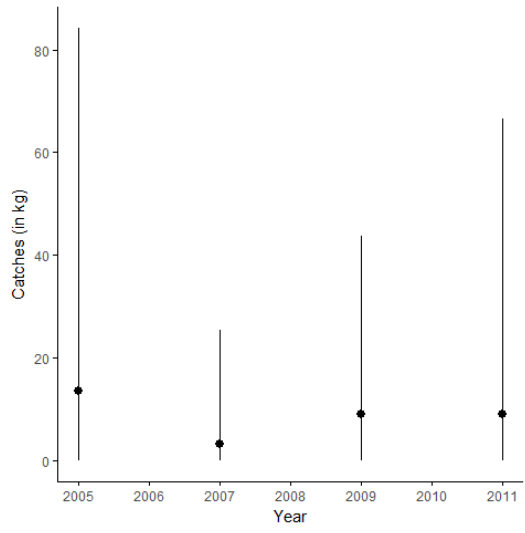
### A6-3 Dover sole



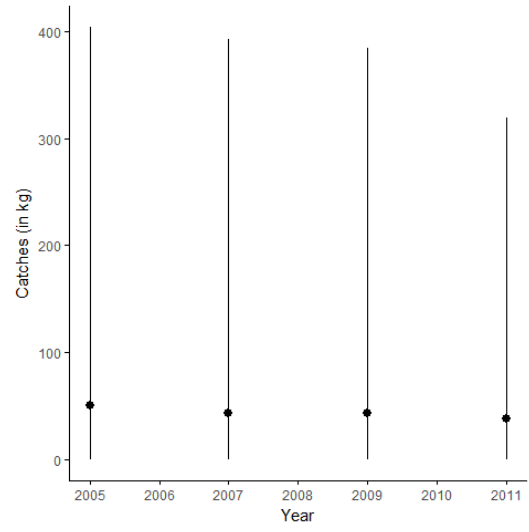
### A6-4 English sole



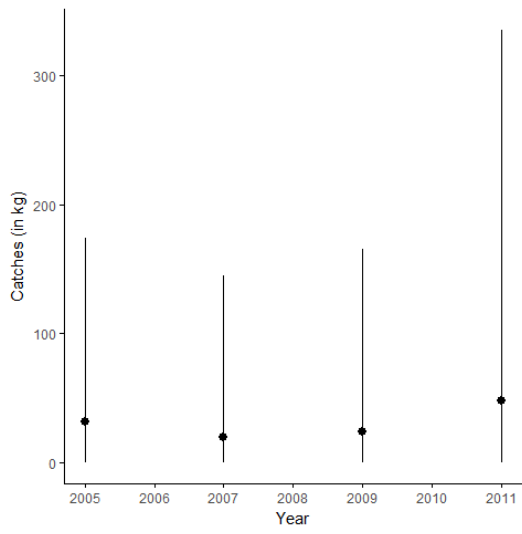
A6- 5 Pacific cod



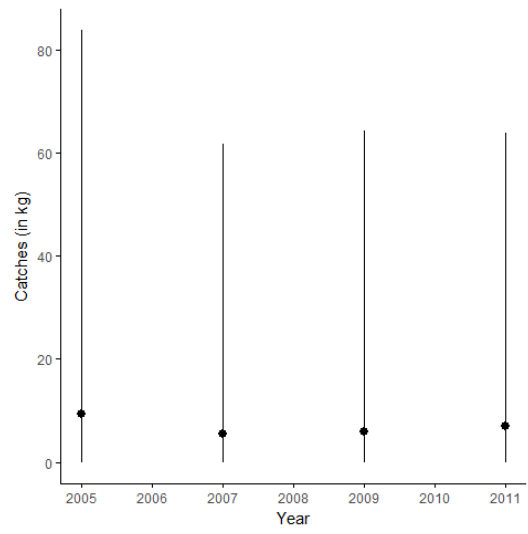
A6- 6 Pacific Ocean perch



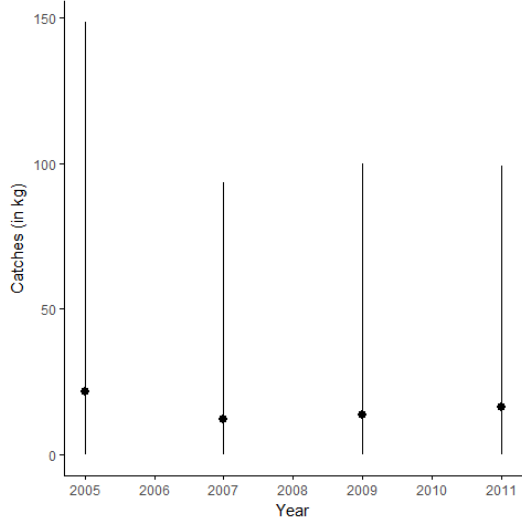
A6- 7 Spotted ratfish



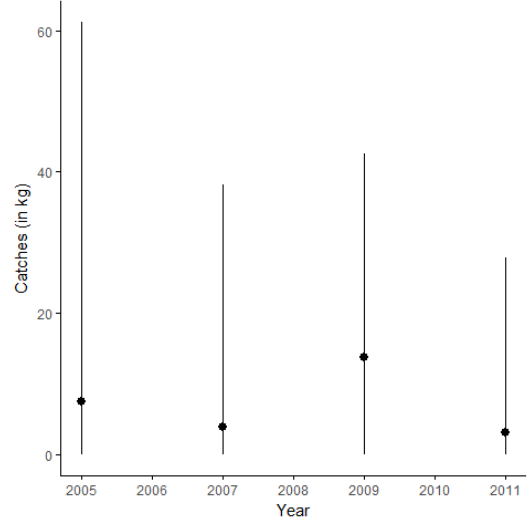
A6- 8 Rock sole



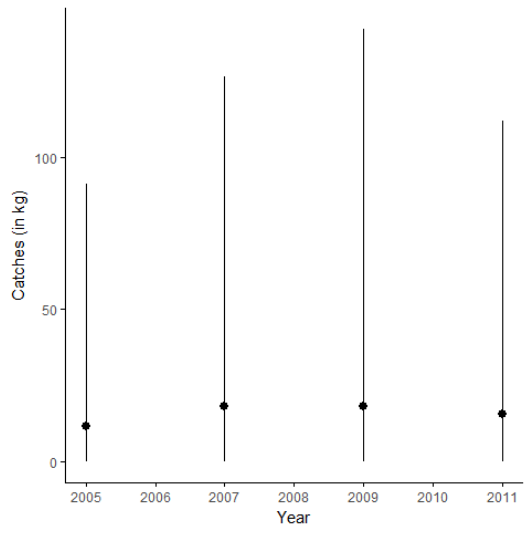
A6- 9: Rex sole



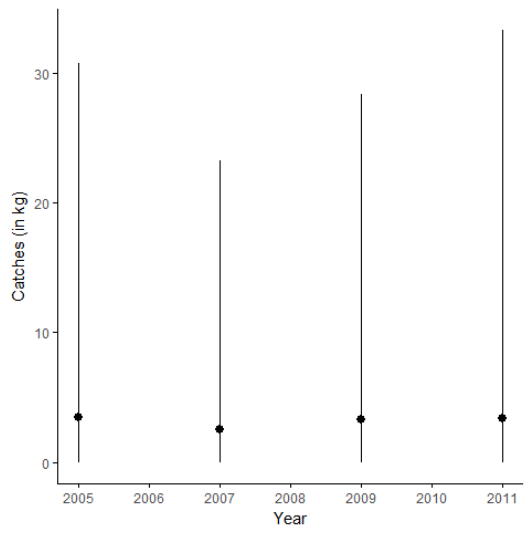
A6- 10: Sablefish



A6- 11: Silvergray rockfish



A6- 12 Shortspine Thornyhead

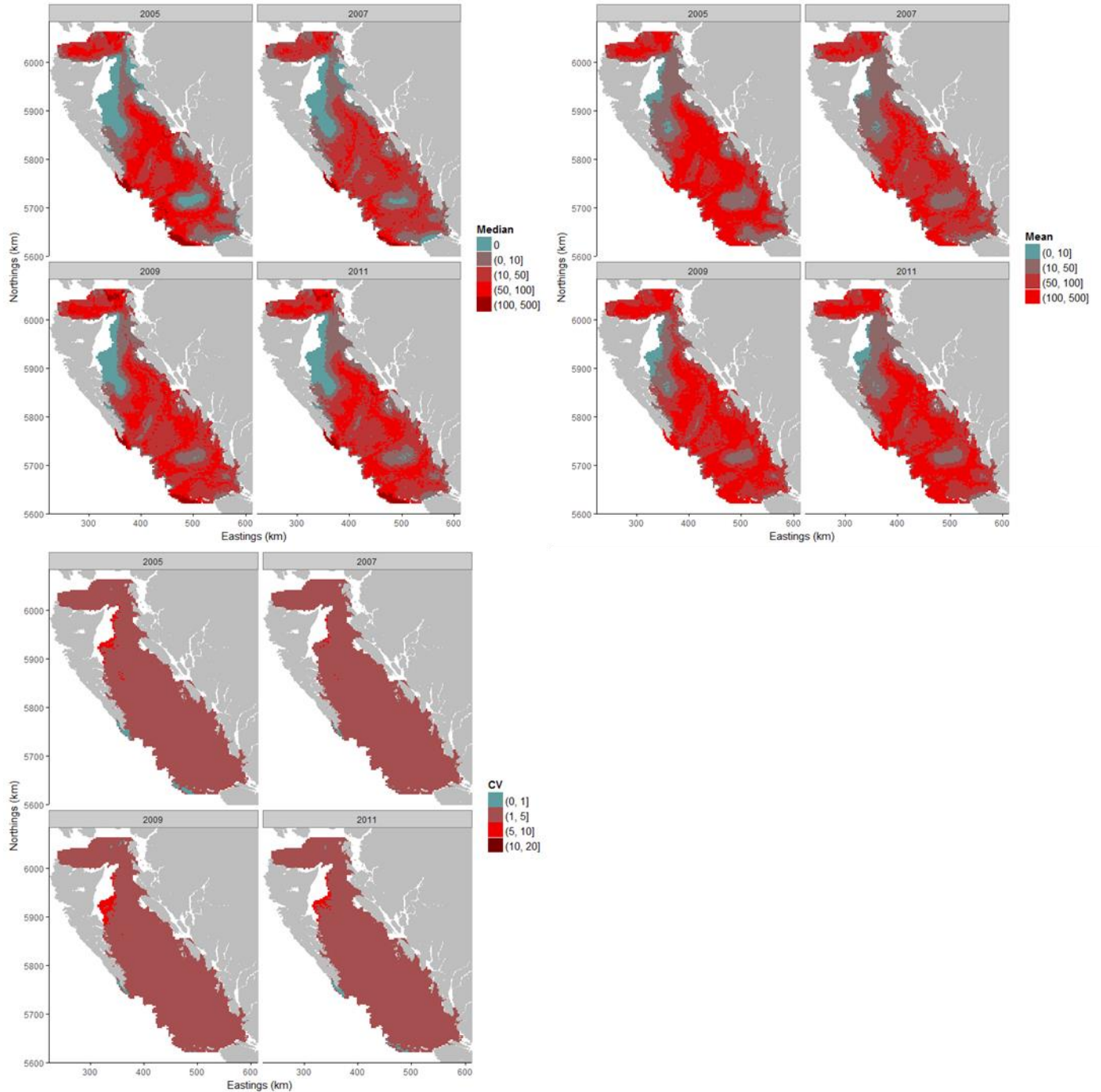




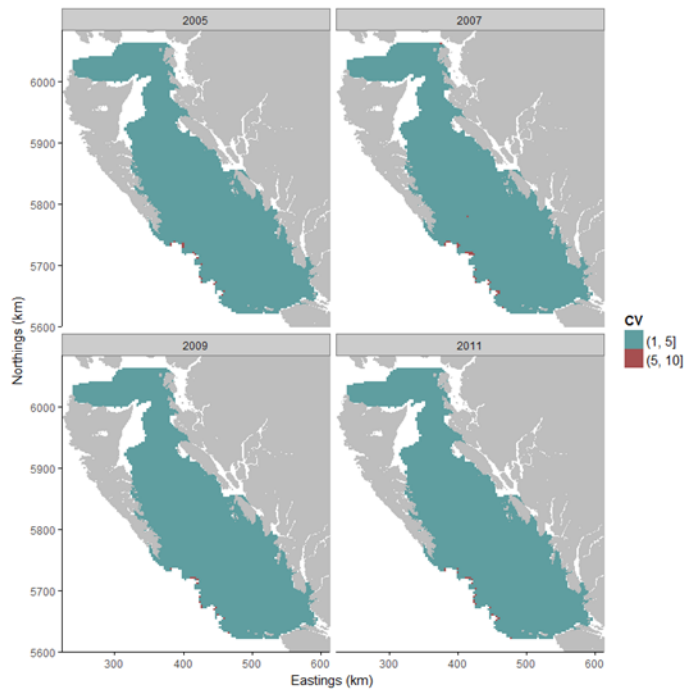
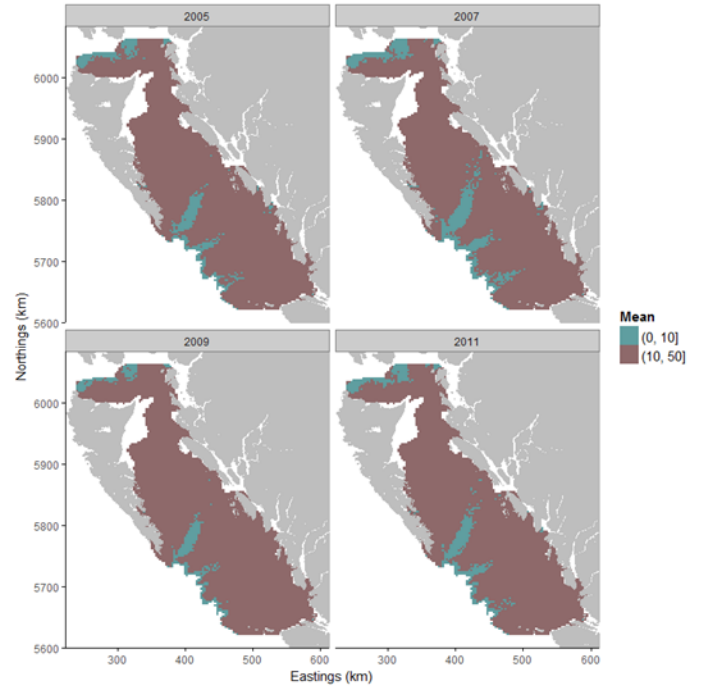
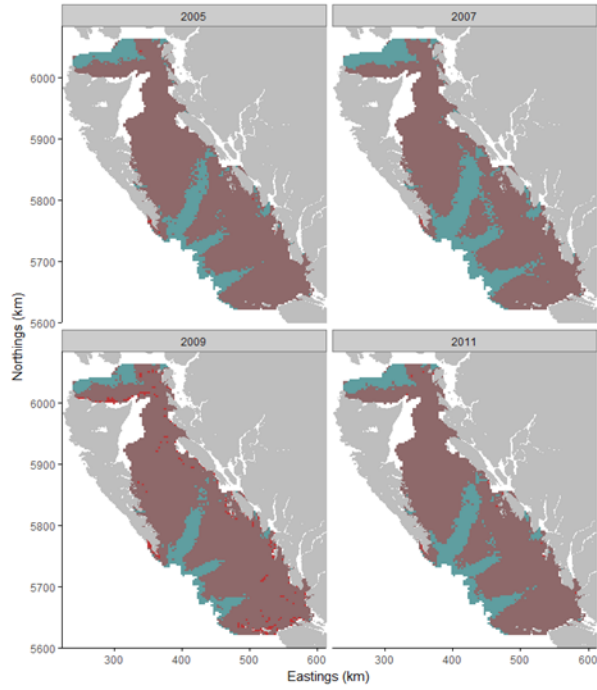
## Appendix 7: Predicted median and mean biomass for each survey year

Predicted median and mean biomass for each survey year. Predictions were calculated from the posterior predictive distribution and temperature, depth, and year values at each grid cell of the study area.

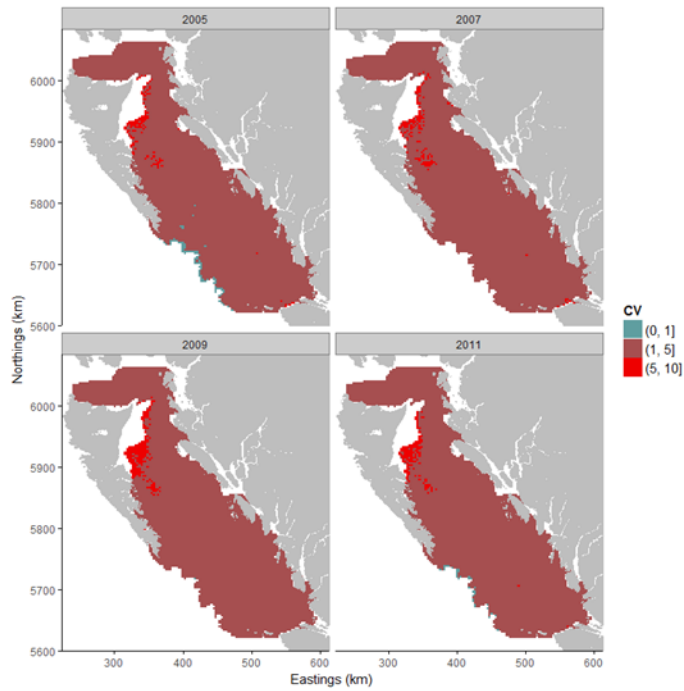
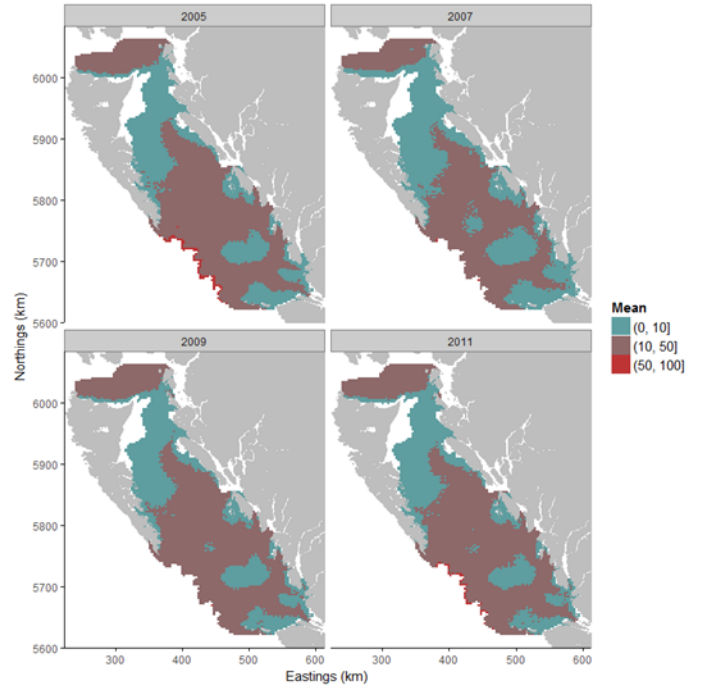
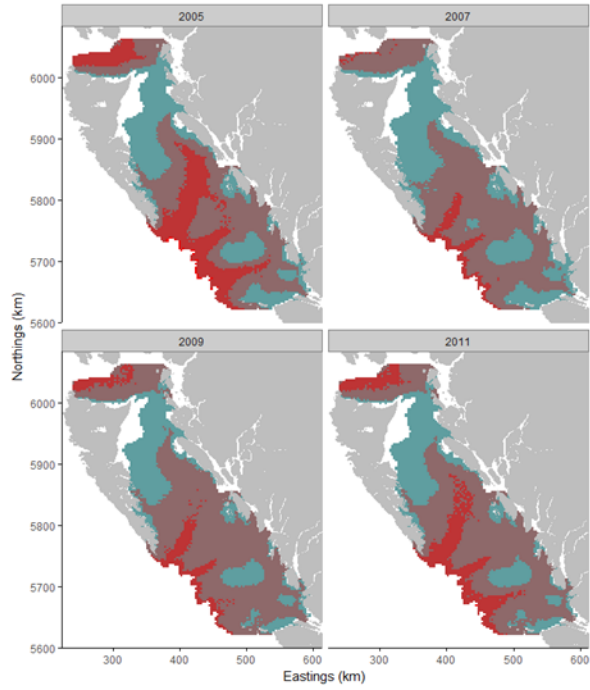
### A7-1. Arrowtooth Flounder



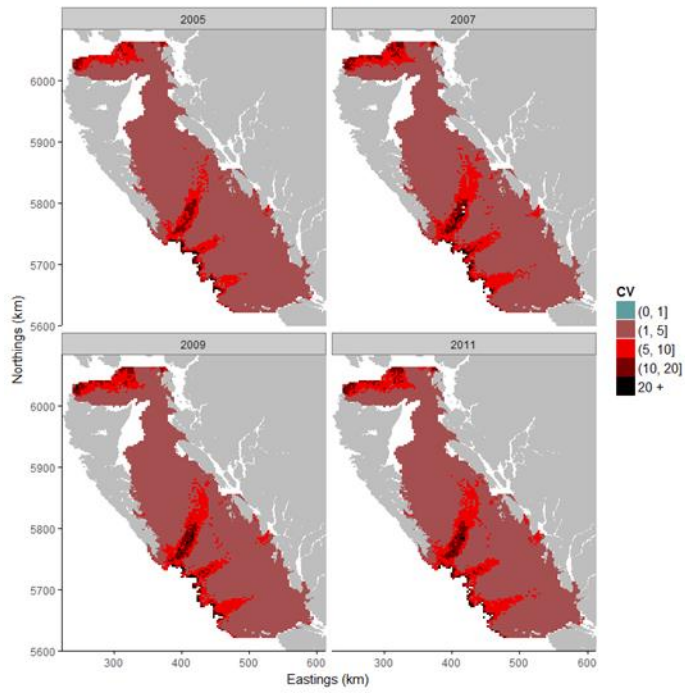
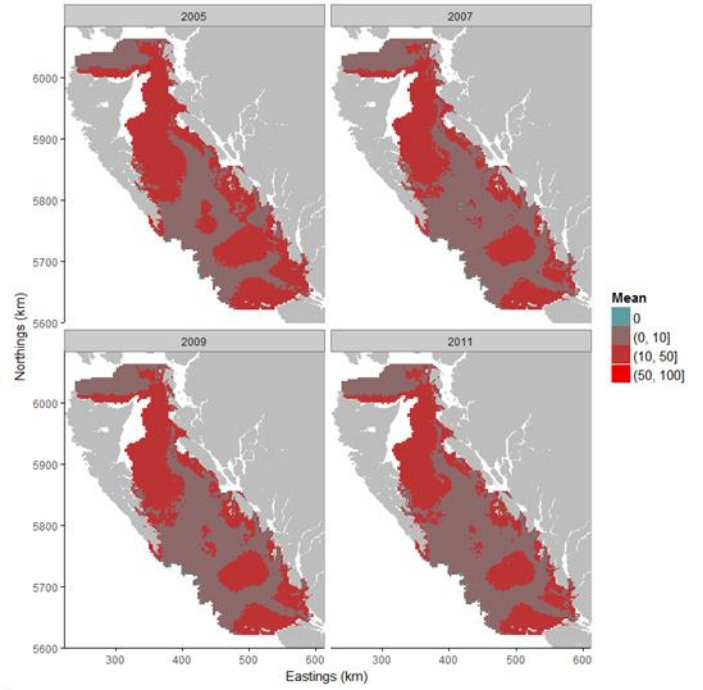
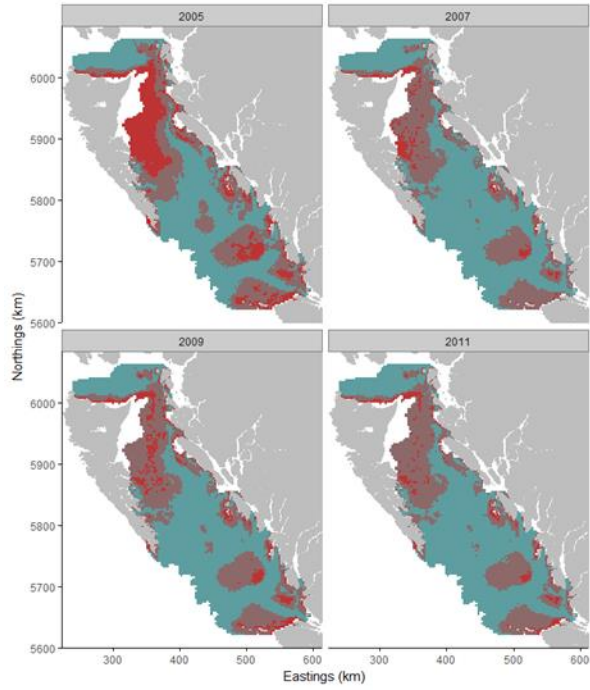
## A7-2. Spiny Dogfish



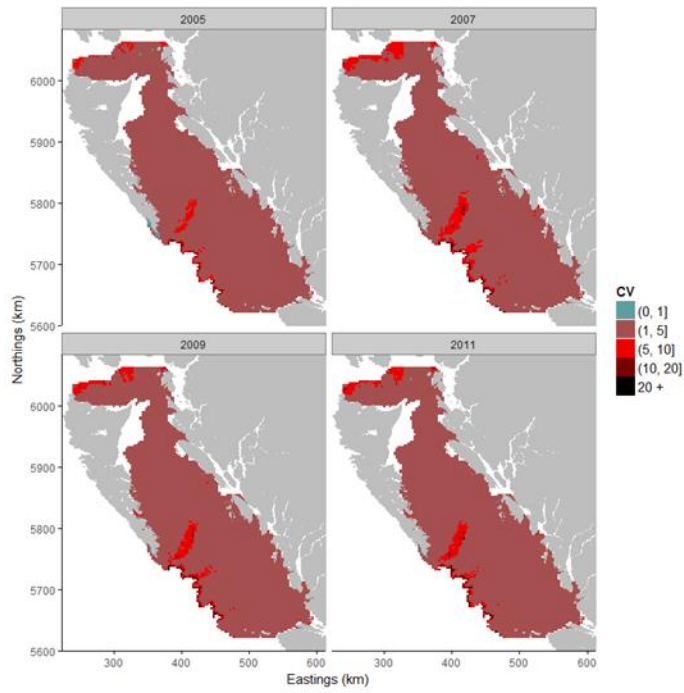
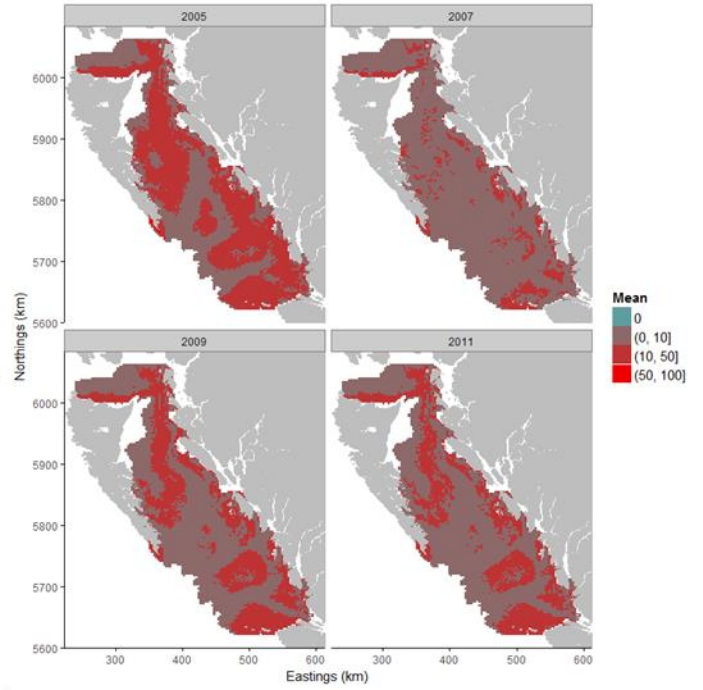
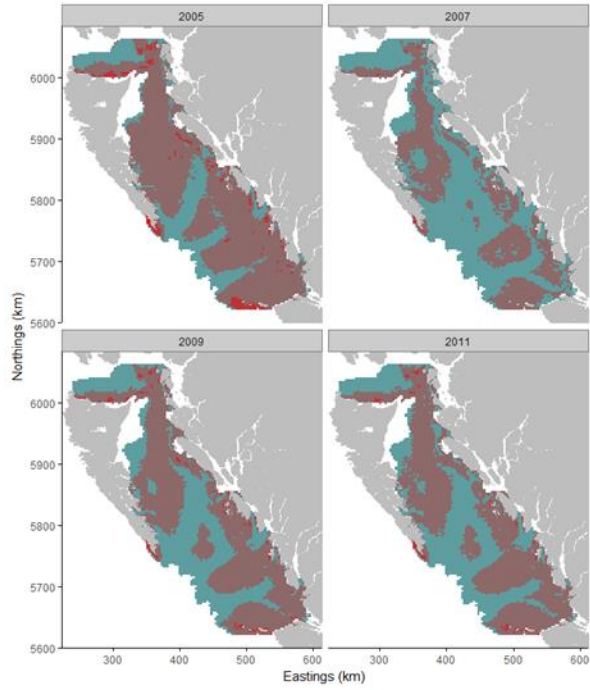
### A7-3. Dover Sole



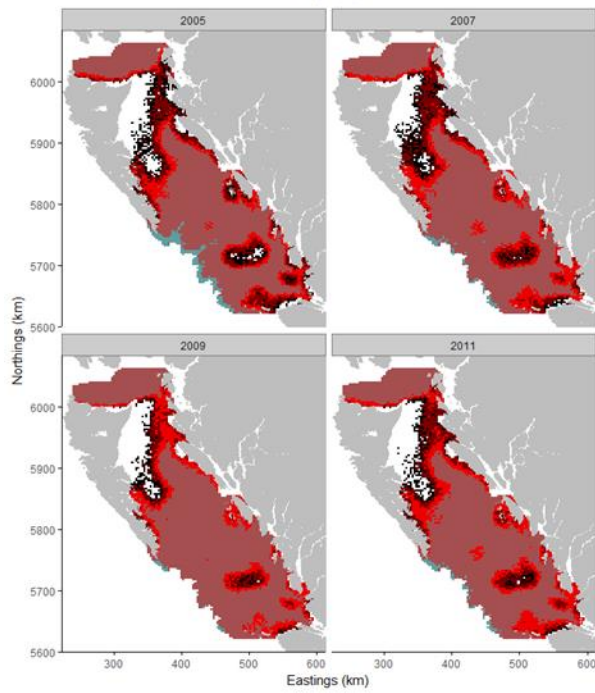
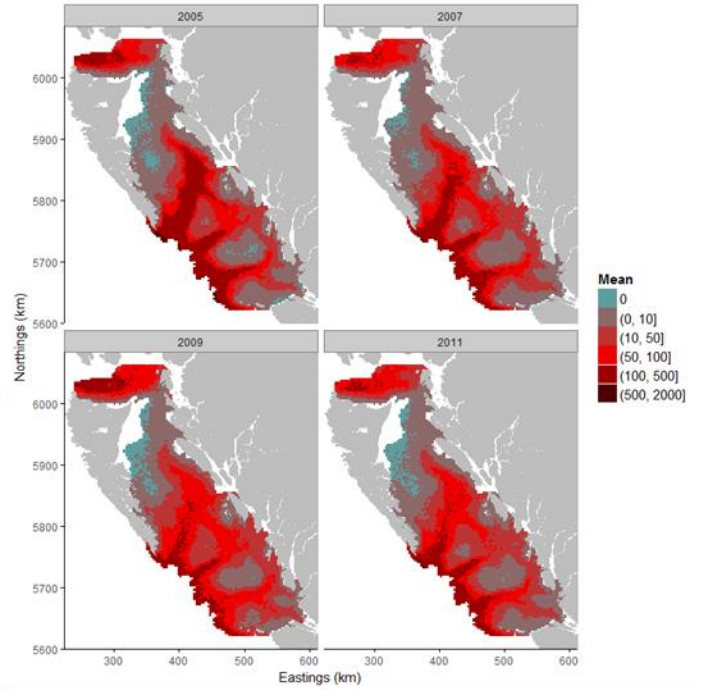
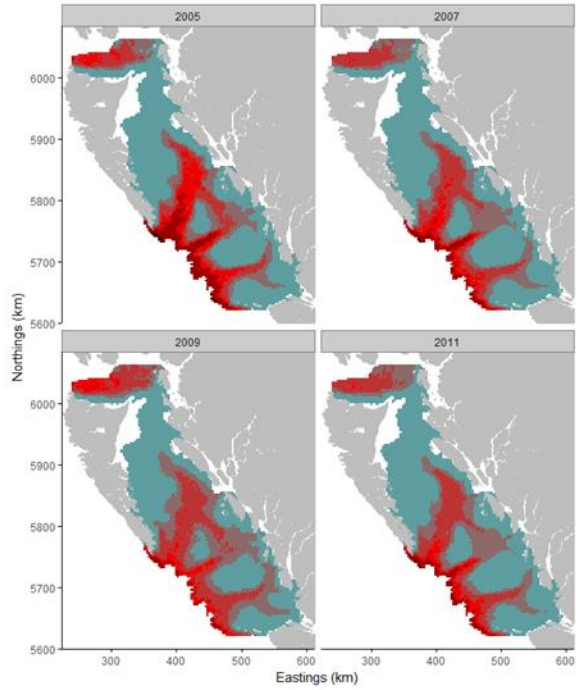
#### A7-4. English Sole



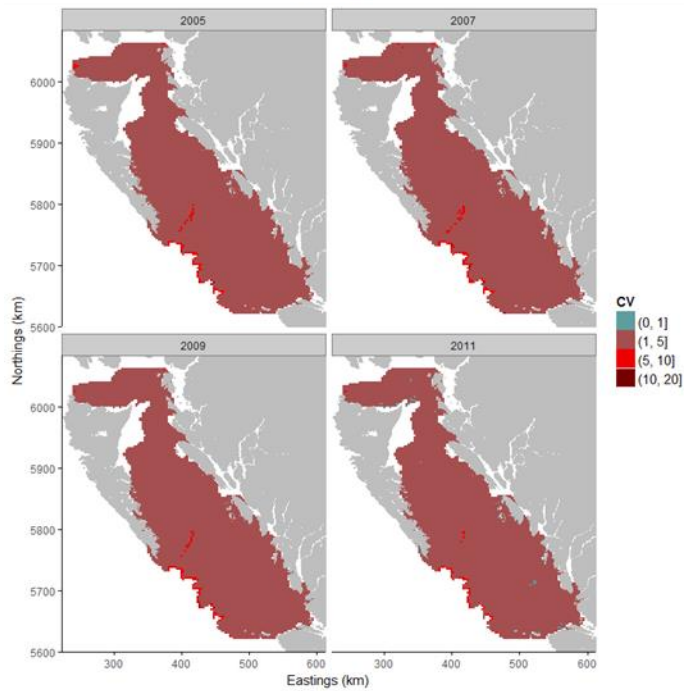
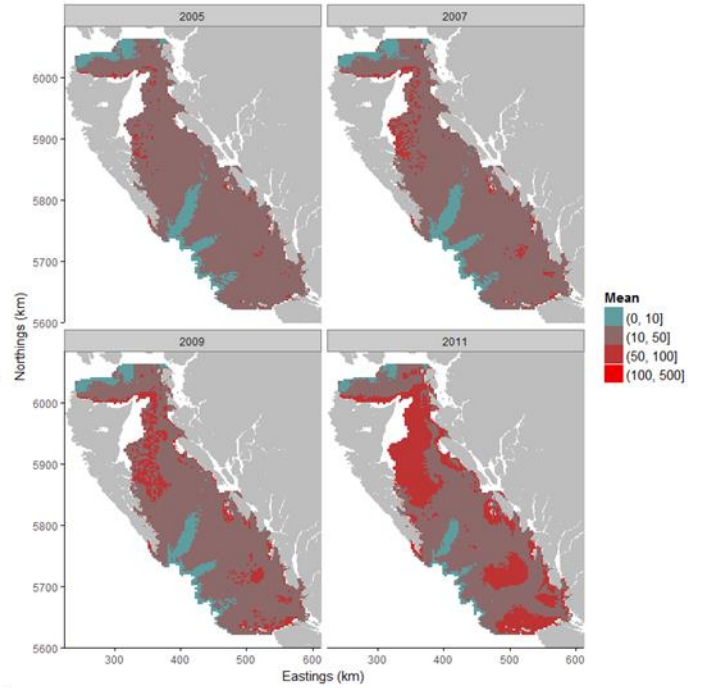
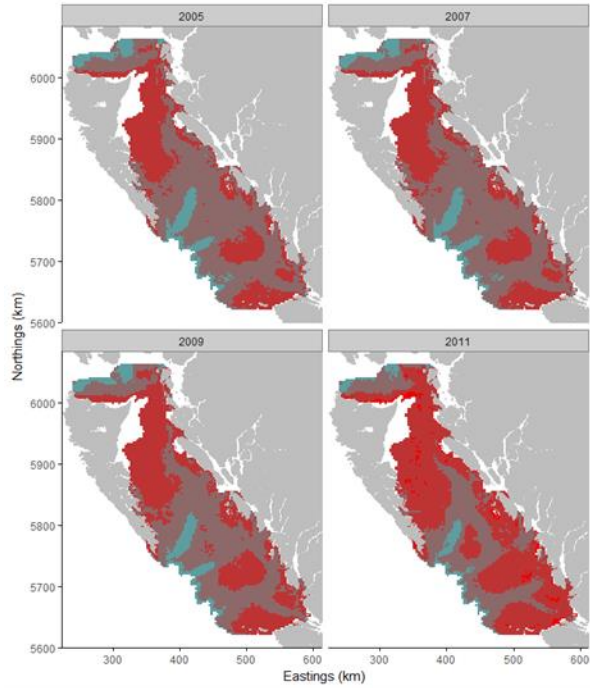
### A7-5. Pacific Cod



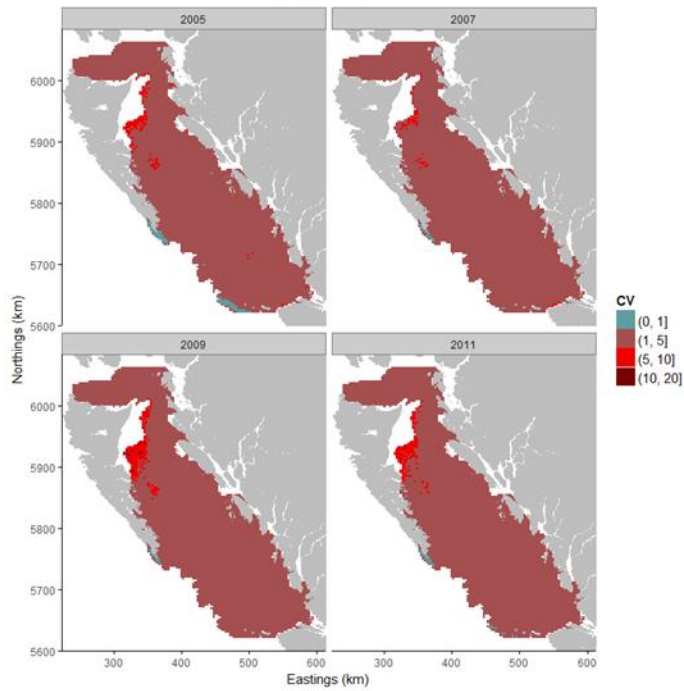
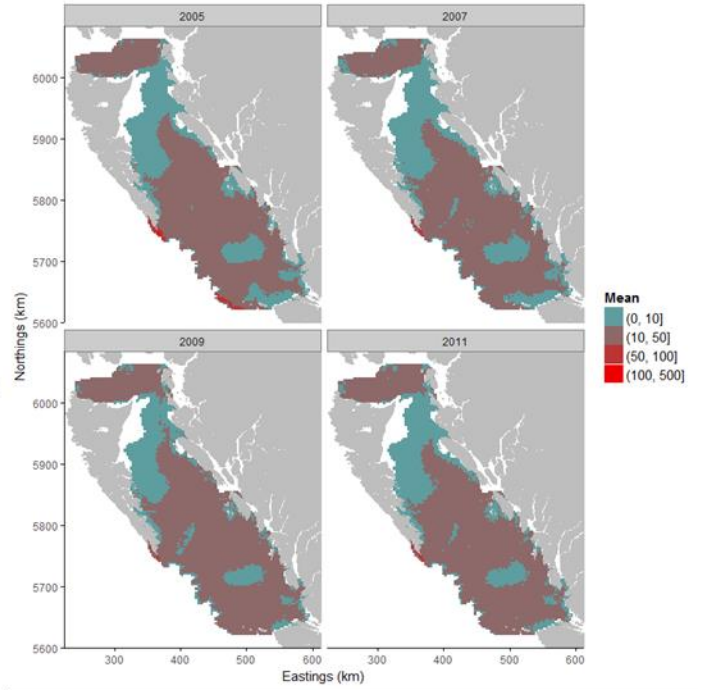
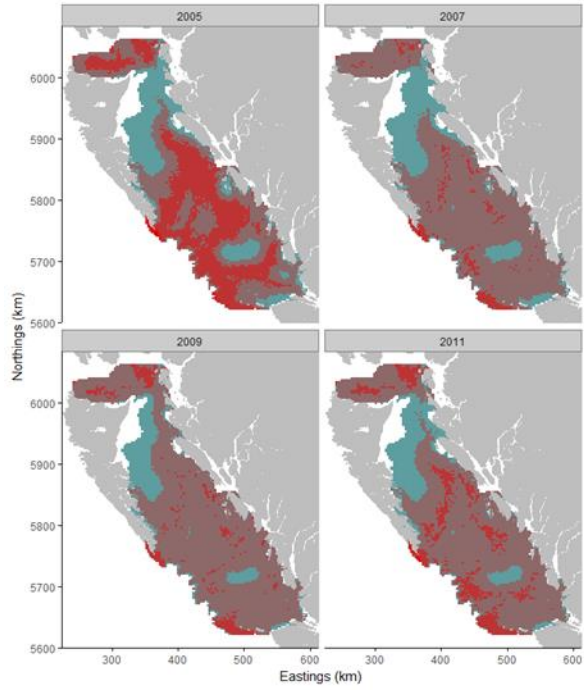
A7-6. Pacific Ocean Perch



### A7-7. Spotted Ratfish

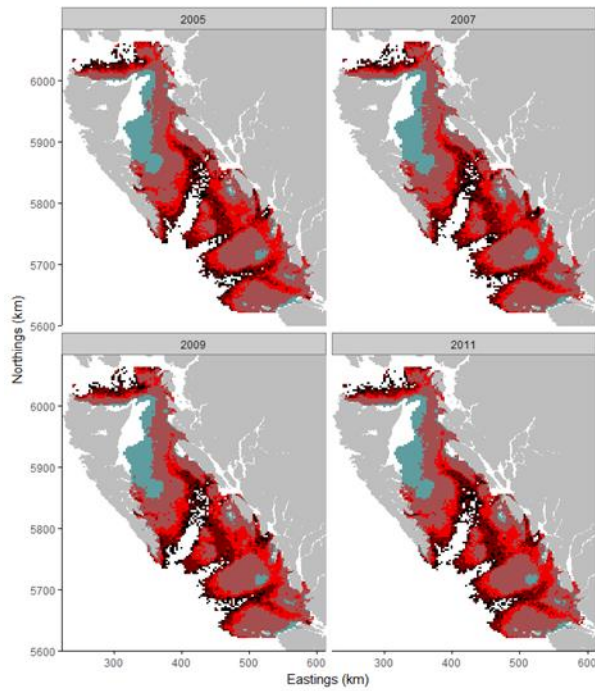
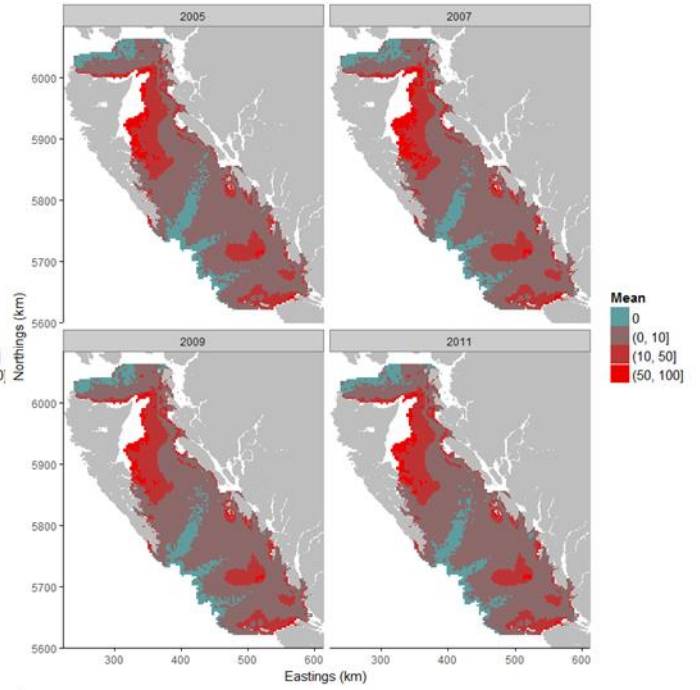
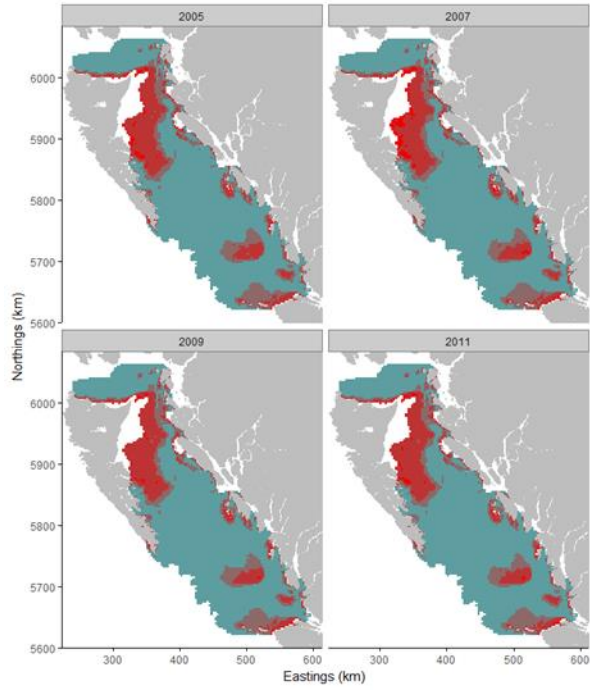


A7-8. Rex Sole

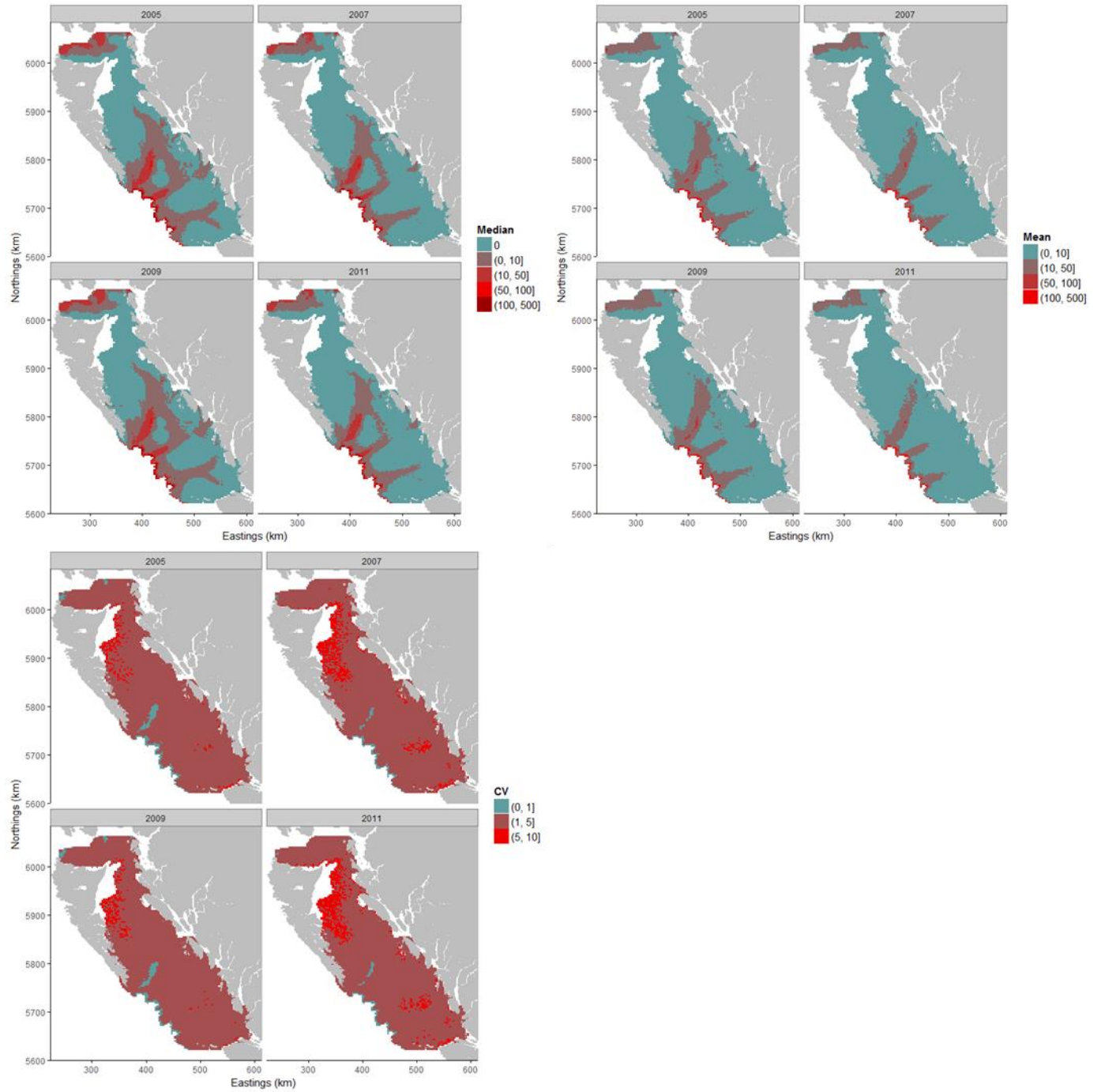




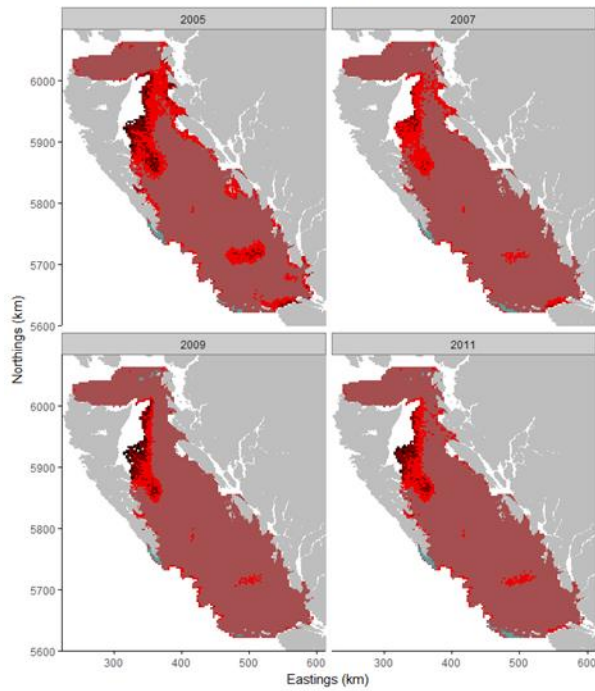
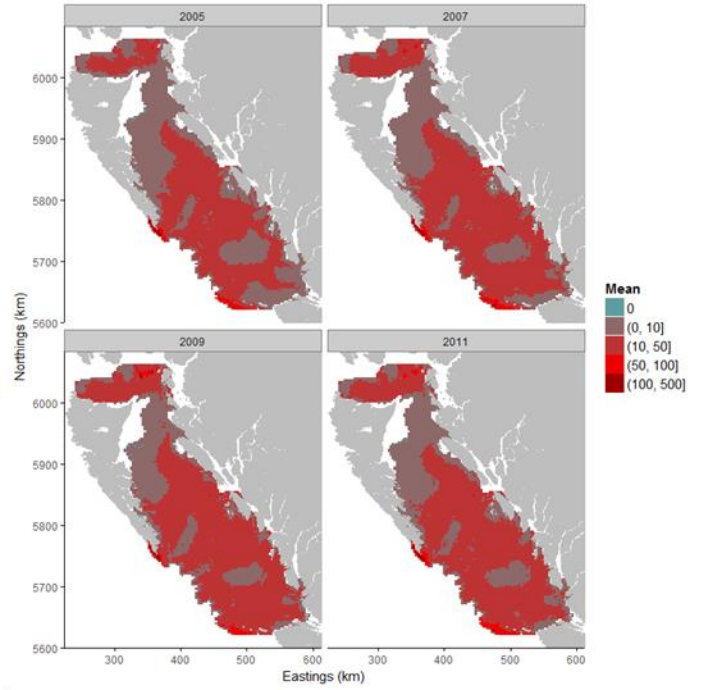
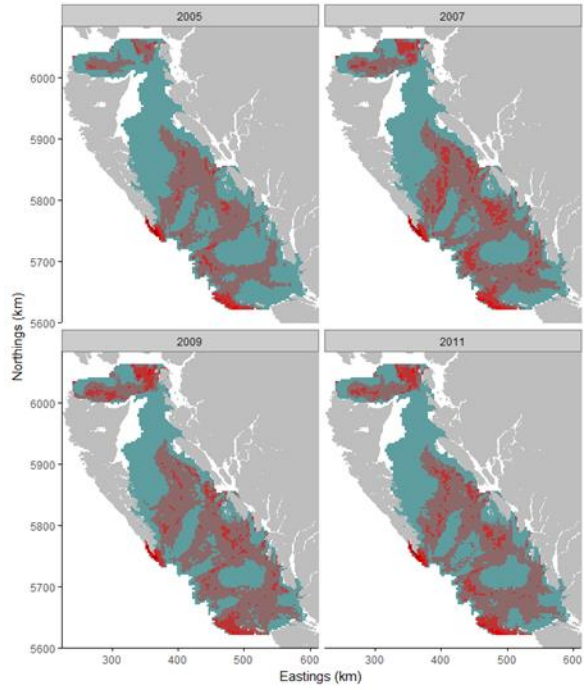
A7-9. Rock Sole



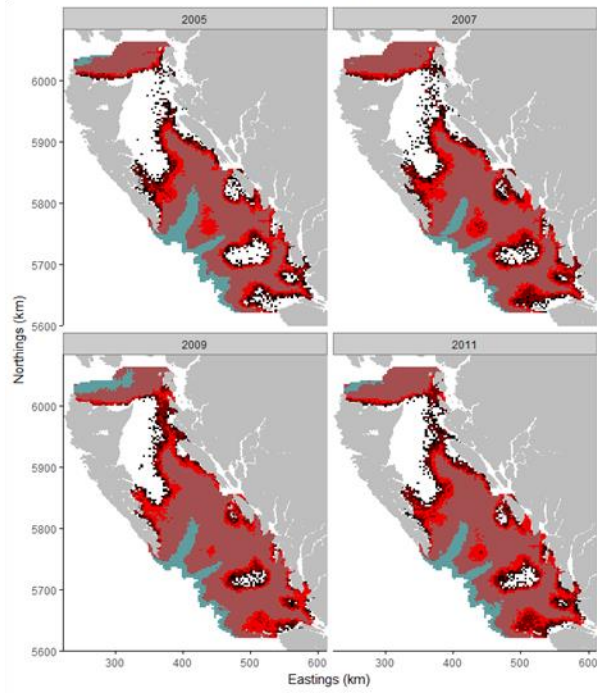
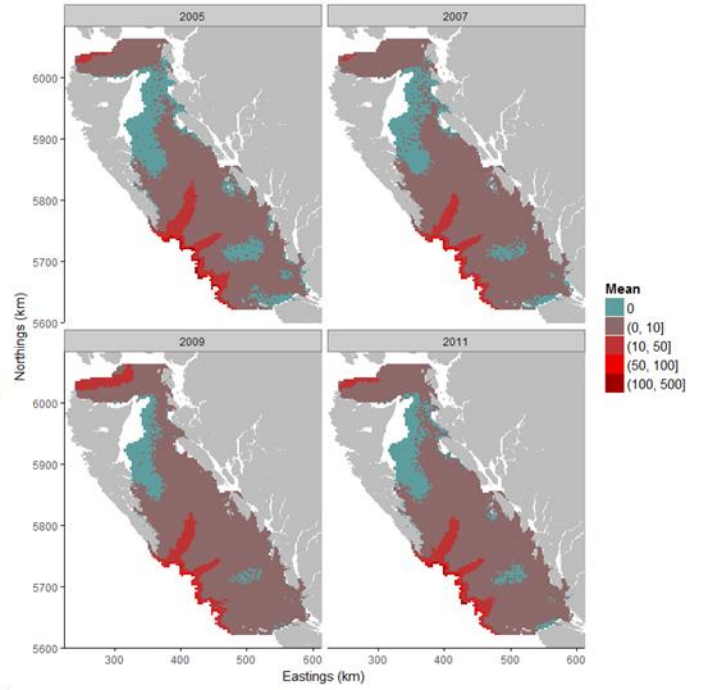
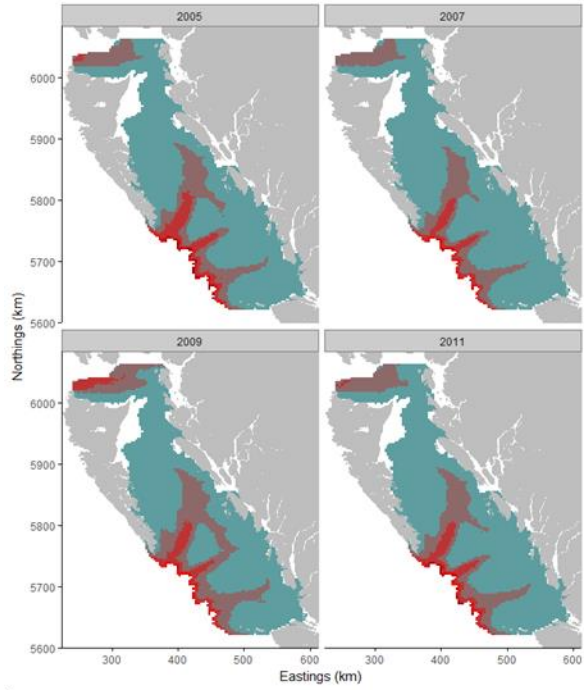
## A7-10. Sablefish



A7-11. Silvergrey Rockfish

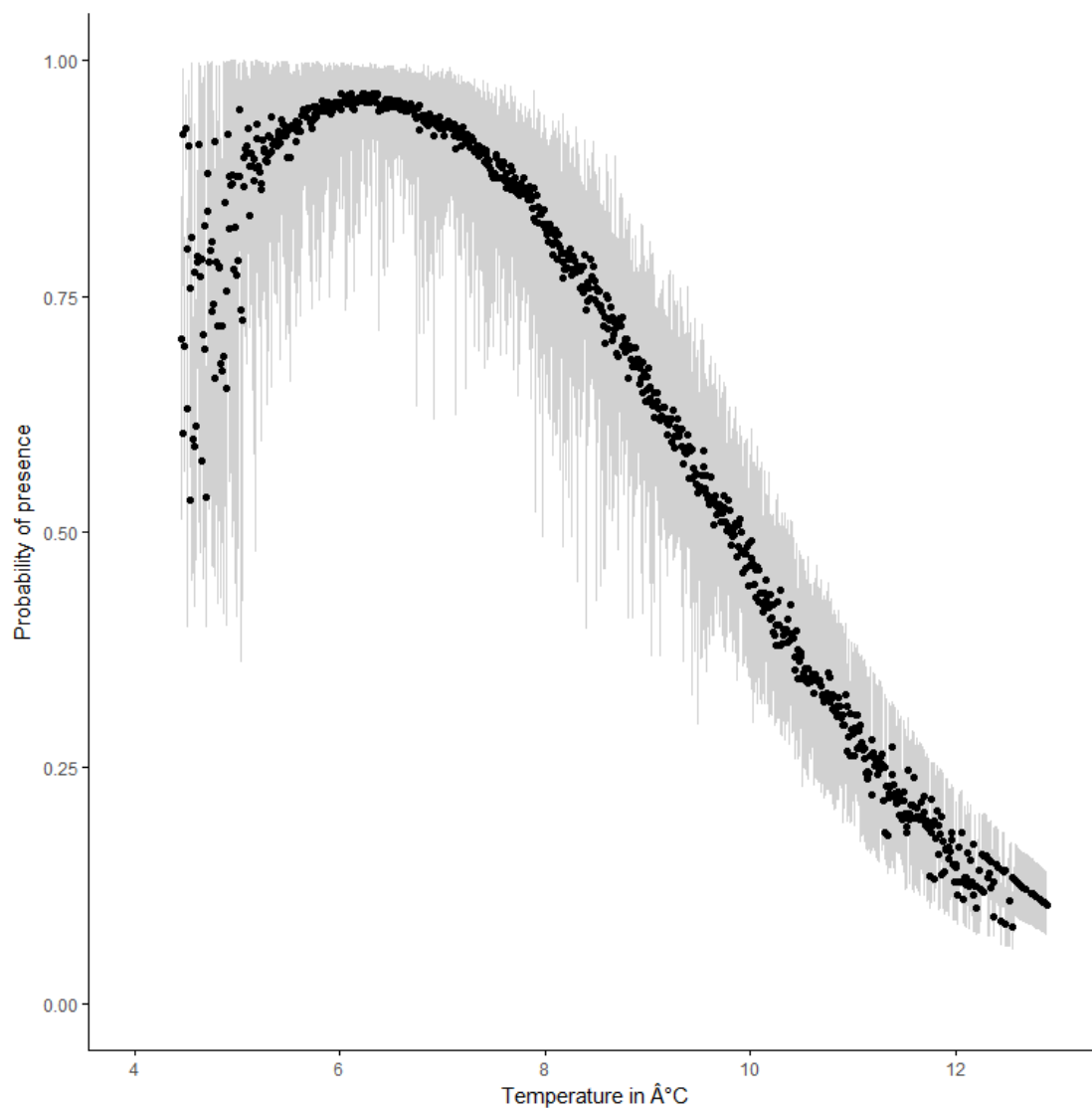


A7-12. Short Spine Thornyhead

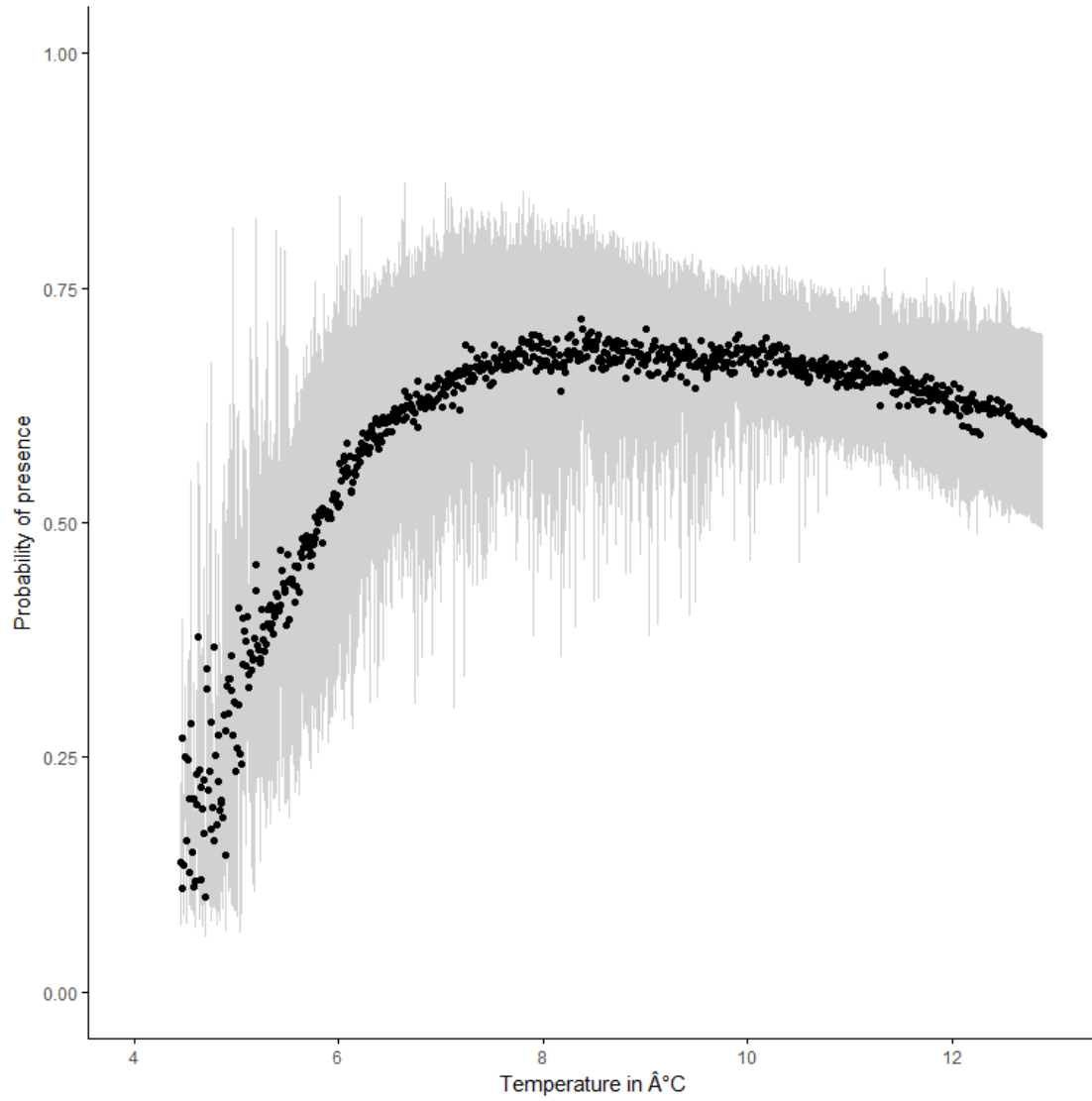


## Appendix 8: Probability of Presence Across Temperature

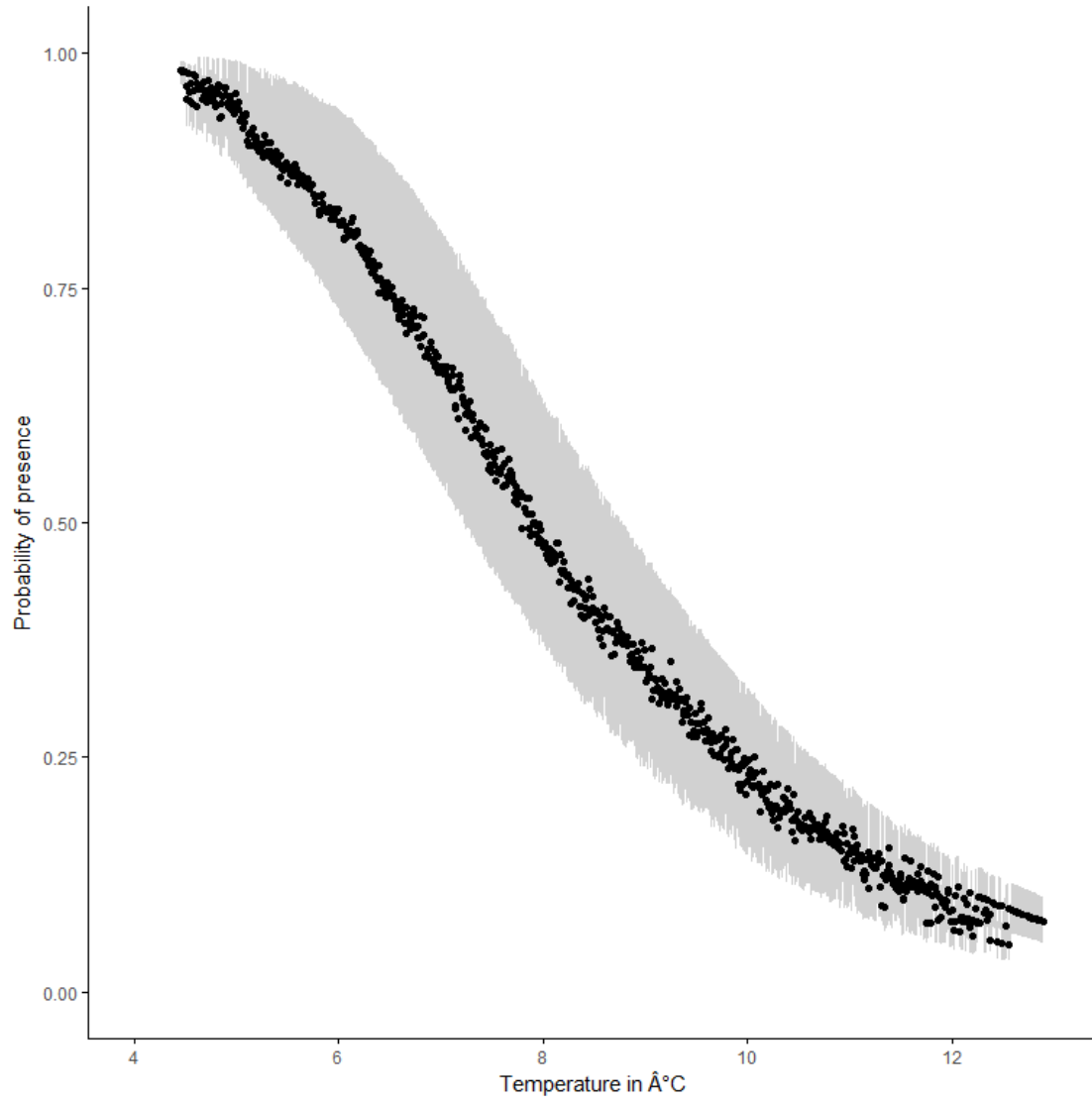
Probability of Presence Across Temperature. Probabilities are derived from the probability of positive biomass (presence) in the posterior predictive distribution in each grid cell of the study area, averaged across all survey years. The probabilities are mapped to ROMS temperature values at the respective grid cell. Temperature range is truncated to the observed temperature range of the trawl surveys.



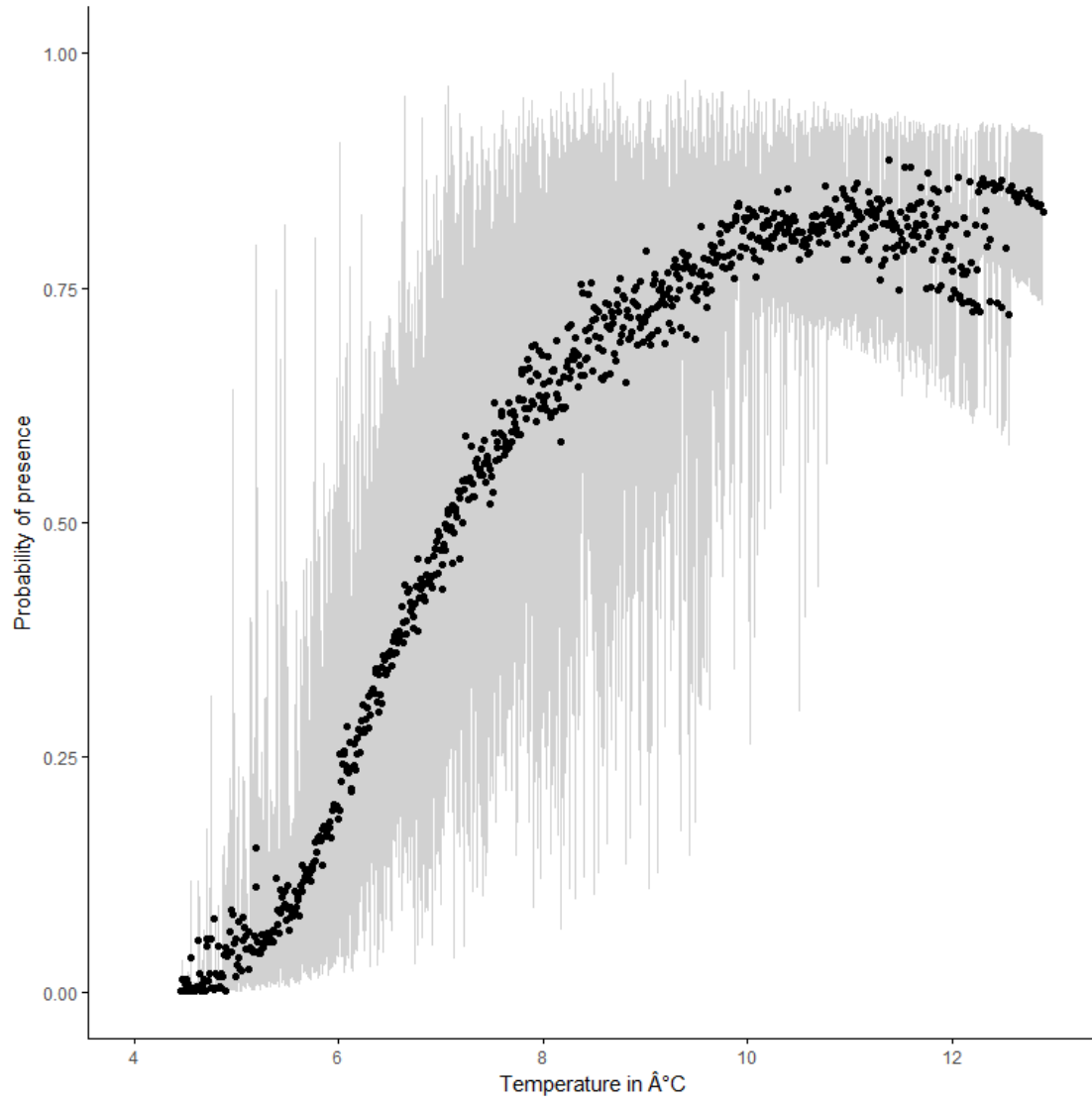
A8-1 Arrowtooth Flounder



A8-2 Spiny Dogfish

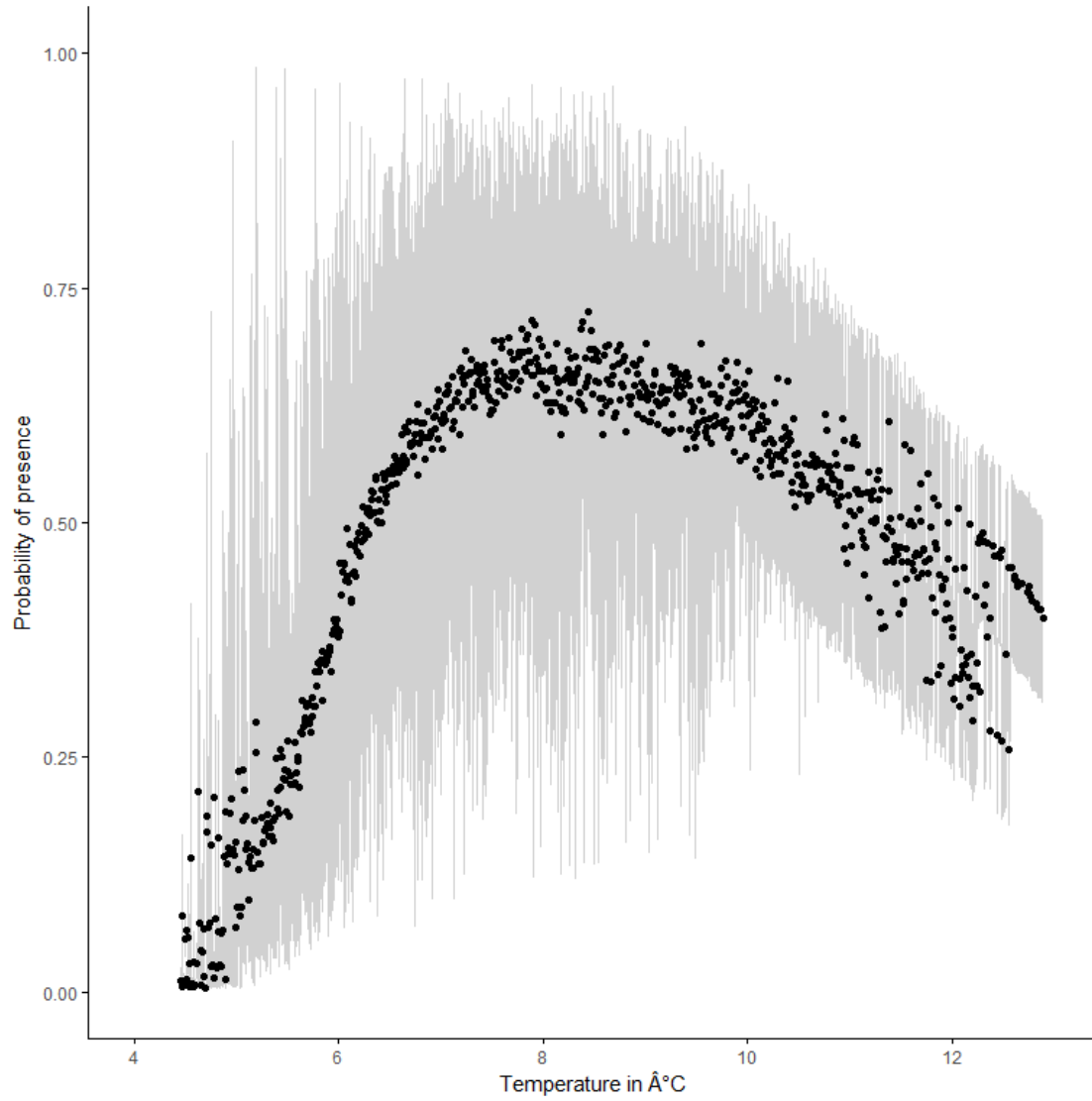


A8-3 Dover Sole

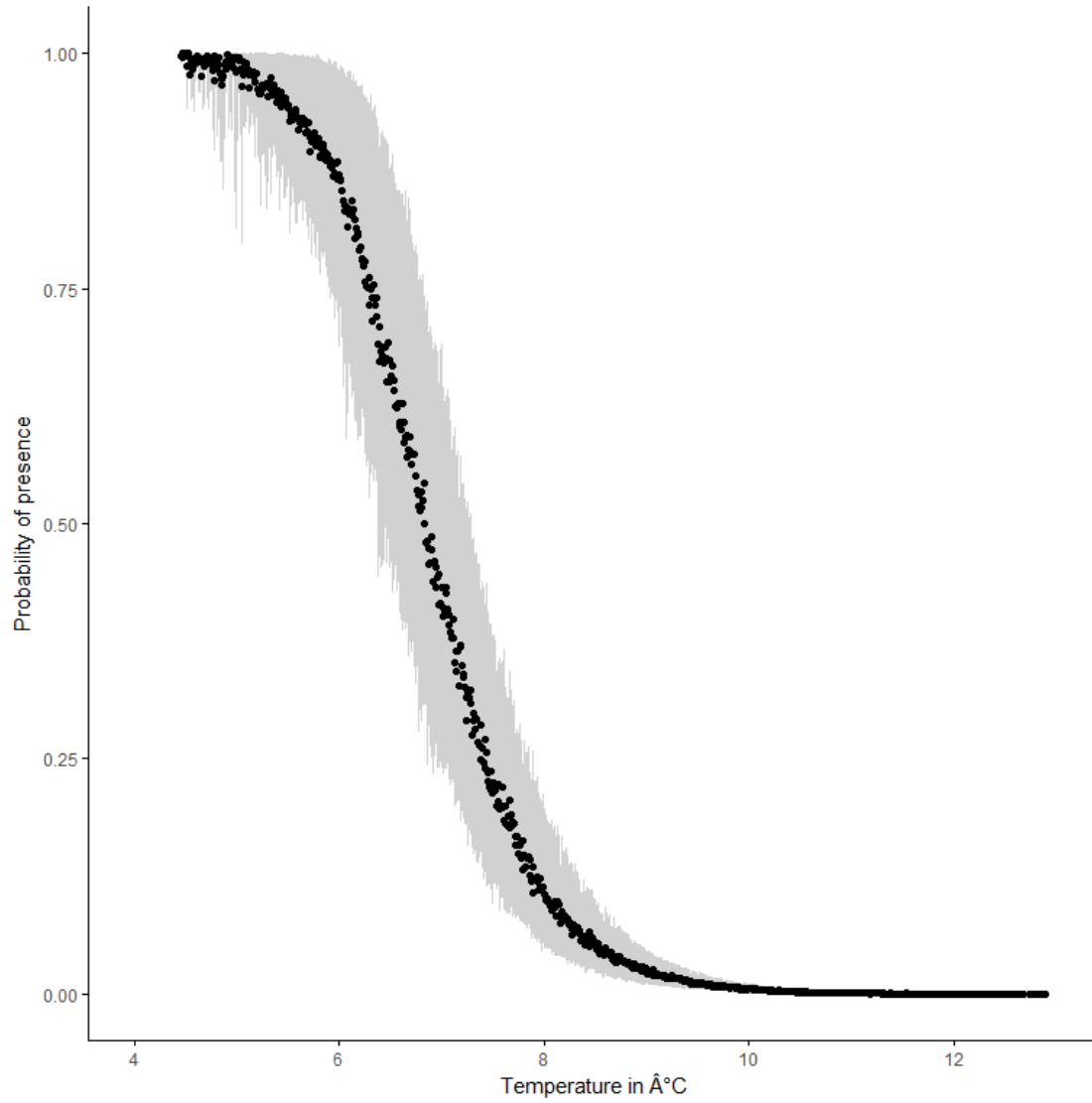


A8-4 English Sole

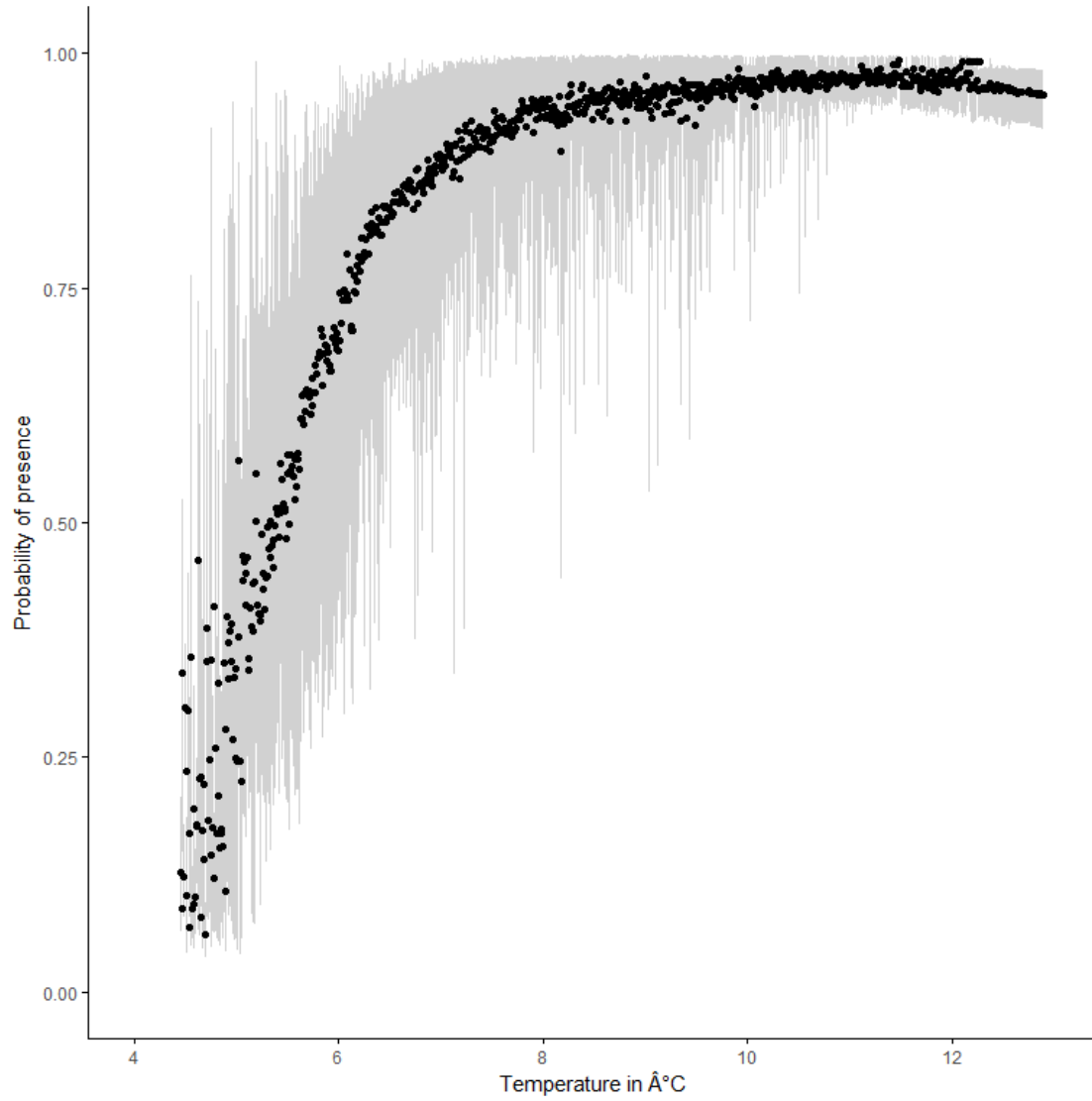




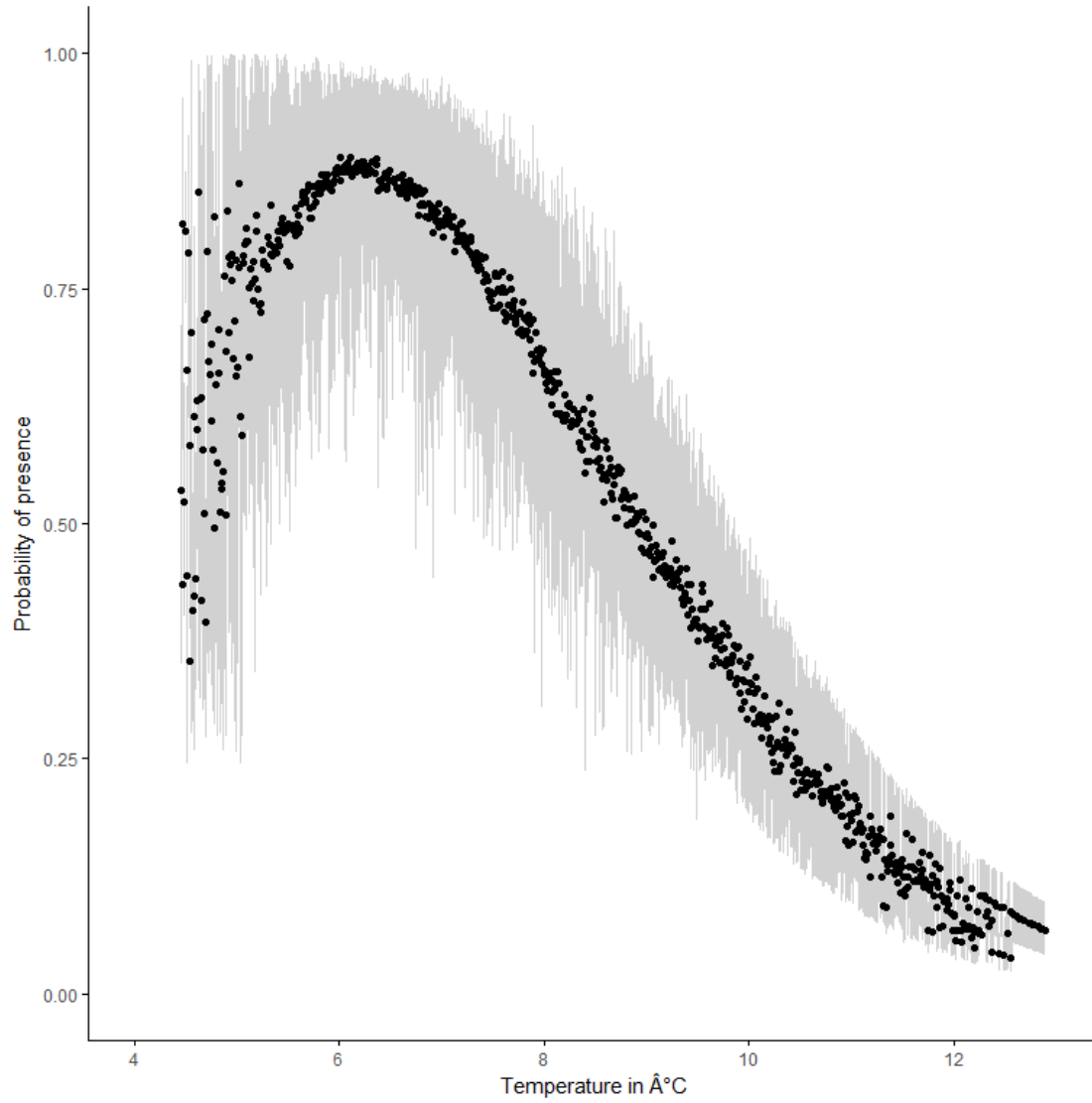
A8-5 Pacific Cod



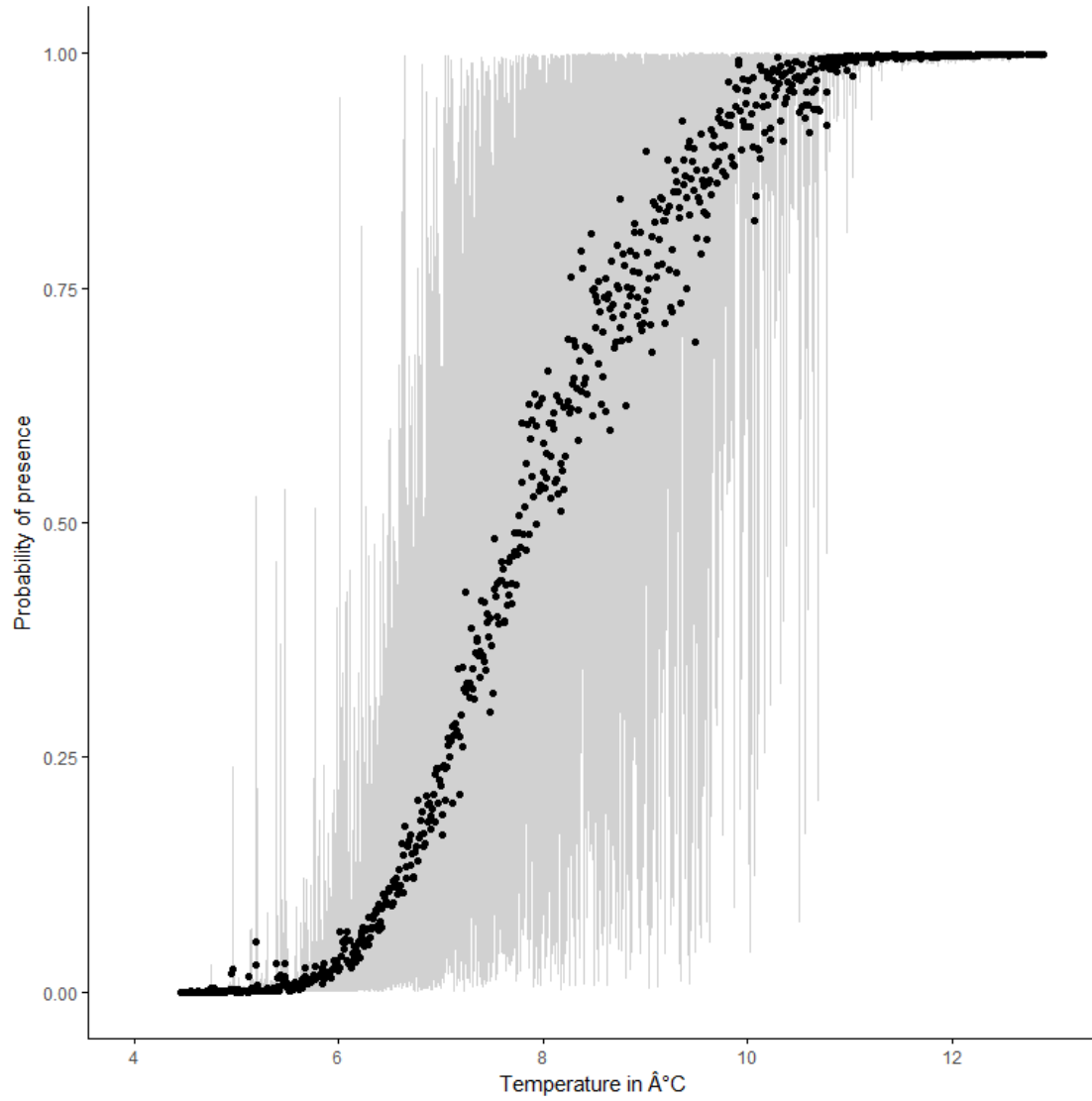
A8-6. Pacific Ocean Perch



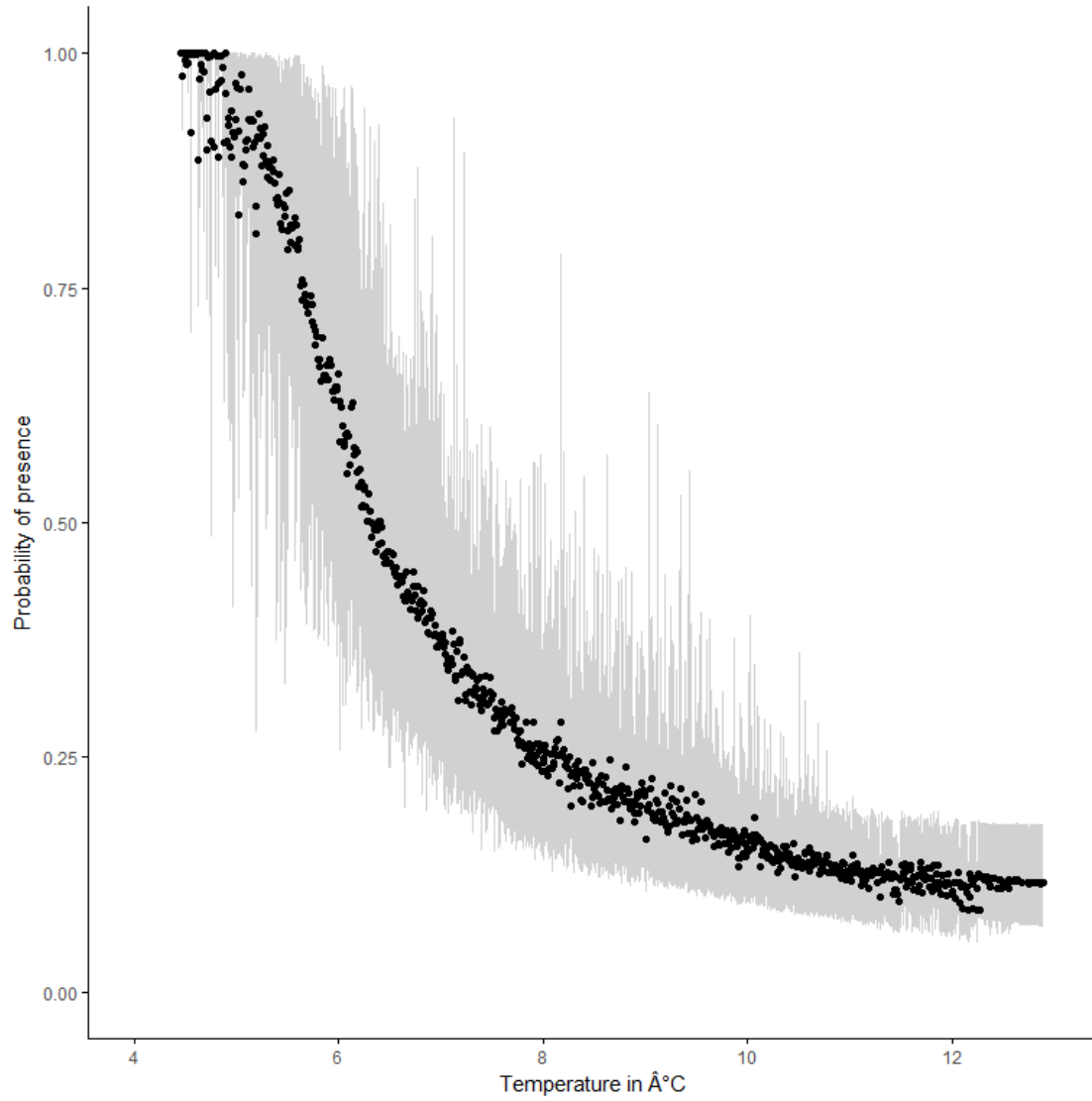
A8-7. Spotted Ratfish



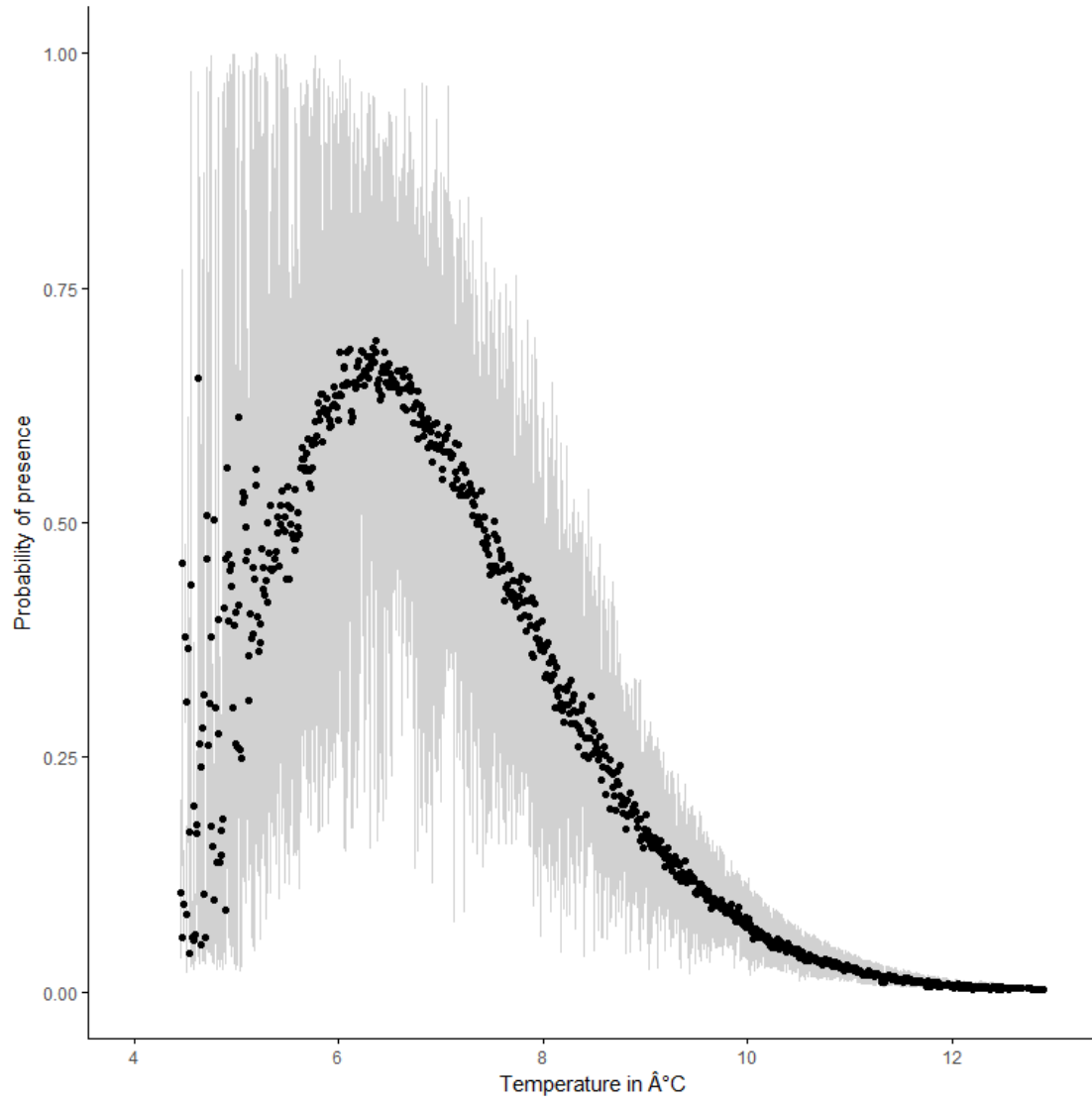
A8-8. Rex Sole



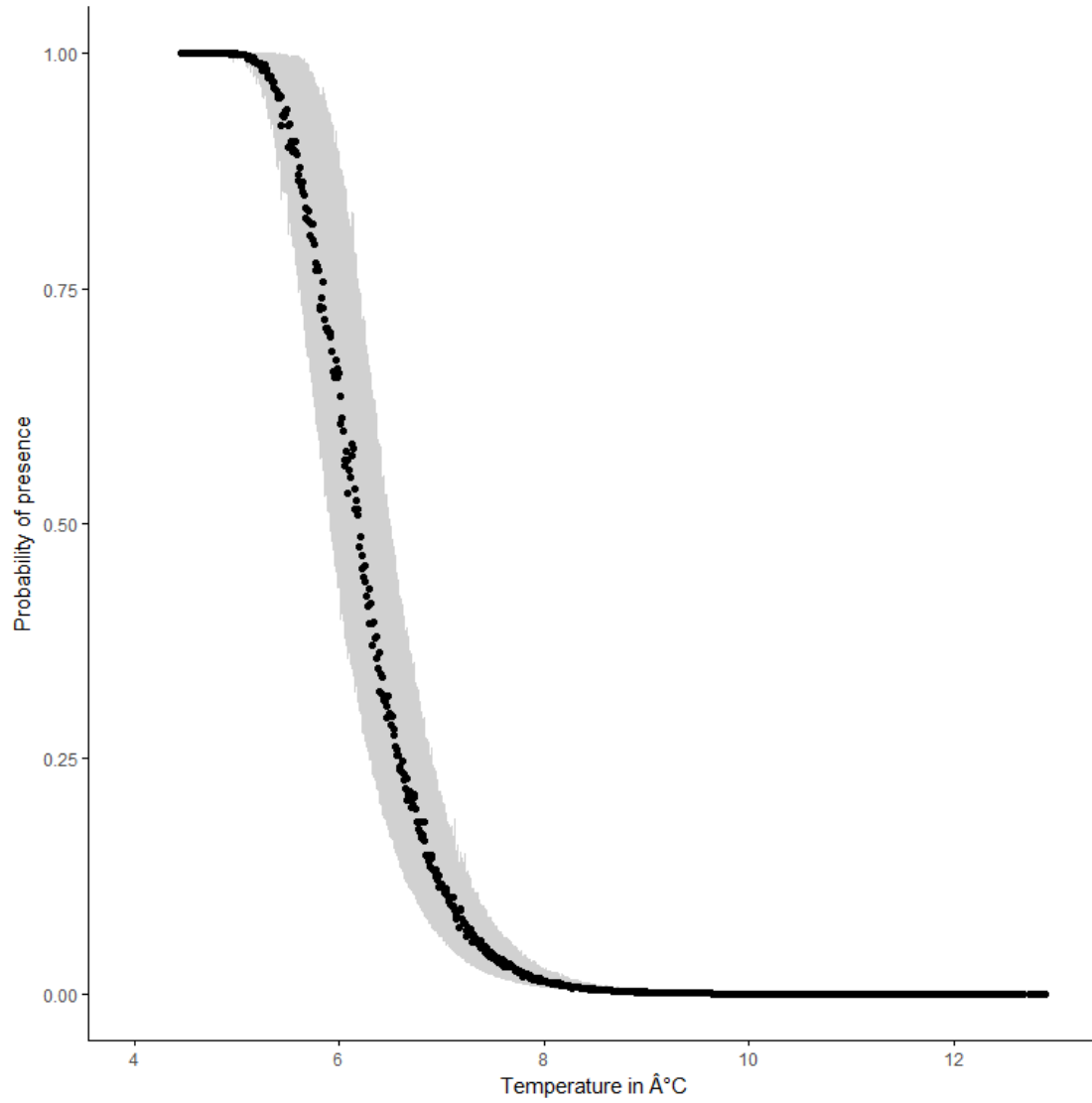
A8-9. Rock Sole



A8-10. Sablefish



A8-11. Silvergrey Rockfish



A8-12. Shortspine Thornyhead