Estimating climate-driven phenology shifts and survey availability using fishery-dependent data

Maxime Olmos[1,2,3*], James Ianelli[3], Lorenzo Ciannelli[2], Ingrid Spies[3], Carey R. McGilliard[3*], James T. Thorson[3*]

[1]*Present address:* DECOD (Ecosystem Dynamics and Sustainability), IFREMER, INRAE, Institut Agro, ZI Pointe du Diable, Plouzane F-29280, France

[2]College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

[3]Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

* Corresponding authors

maxime.olmos@ifremer.fr

carey.mcgilliard@noaa.gov

james.thorson@noaa.gov

HIGHLIGHTS

- Climate-driven phenology shifts has been inferred using seasonal spatio-temporal models and fishery-dependent data
- Spawning movement phenology occurs earlier during warm years than cold years
- Spatial distribution is more constrained, and biomass is lower during cold years than warm years
- Fish were more available to the summer survey during warm years than cold years because of earlier spawning migration during warm years
- Phenology differed by sex with males staying longer on the spawning grounds than females.
- Fishery-dependent data can be used to compute a catchability covariate within the yellowfin stock assessment.

ABSTRACT

Environmental changes are predicted to impact fish ecology; specifically, the phenology of spawning and larval settlement, resulting adult and larval movement, and ultimately seasonal habitat utilization. Hence, warm or cold environmental conditions may cause early or late seasonal movement among habitats. However, resource surveys are typically designed to occur at approximately the same time each year, and this mismatch in timing between survey sampling and fish movement can cause a different proportion of population biomass to be available to the survey in different years. In this study, we demonstrate an application to minimize such impacts using yellowfin sole (*Limanda aspera*) in the eastern Bering Sea as a case study. We employed fishery-dependent catch-and-effort (also called catch per unit effort (CPUE)) data collected by observers on commercial vessels, which covered the months of March-October (whereas survey data were limited to June-August). We built a seasonal spatio-temporal model so that seasonal distribution could be used to better explain summer survey availability and movement timing as impacted by interannual temperature changes. Our results highlight (i) spawning movement phenology occurs earlier during warm years than cold years, (ii) spatial distribution is more constrained and biomass is lower during cold years than warm years, (iii) fish were more available to the summer survey during warm years than cold years, and (iv) phenology differed by sex with males staying longer on the spawning grounds than females. Finally, we computed an overlap index between the survey area and fishery CPUE data to be used as a catchability covariate within the yellowfin sole stock assessment. This index confirmed the changes in relative availability of this species by year as presently used in the assessment.

Keywords: movement phenology, climate-driven phenology shifts, seasonal spatiotemporal model, fishery-dependent data, spatial availability, catchability, yellowfin sole.

I. INTRODUCTION

Rapid environmental changes to fish habitat present several major challenges to fisheries ecology and management. In response to a changing climate, marine organisms can adapt to the new conditions within their current geographical range, can track their climatic niches in time and/or in space or can become locally extinct (García Molinos et al., 2016). This can lead to changes in the ecosystem structure and functioning across space and time. To track their niche in space and time, marine organisms have to adapt by changing the seasonal timing of many biological processes (termed "phenology"), including the timing of spawning and larval settlement, resulting adult and larval movement, and ultimately seasonal habitat utilization (Rogers and Dougherty, 2019).

Accounting for such spatial and temporal aspects of climate responses can be critical to successfully manage fisheries. Previous studies have shown that spawning phenology, particularly spawning migration phenology, is sensitive to temperature in fish species conducting ontogenetic migration (McQueen and Marshall, 2017; Sims et al., 2004). For example, climate-induced changes in spawning phenology has been shown for striped bass *(Morone saxatilis)* (Peer and Miller 2014) in Chesapeake Bay, which led to higher than anticipated fishing mortality on spawning fish during cold years. Resource surveys for use in stock assessments are typically designed to occur at approximately the same time each year (NRC, 2000). However, warm or cold temperature conditions may cause early or late movement (Asch, 2015) into or out of the survey area causing differential "availability" of the resource (Staudinger et al., 2019). The ability to detect such climate impacts requires models that can use additional data and handle seasonal, interannual, and spatial processes, and these are rare (Sydeman et al., 2015; Thorson et al., 2020). Some movement phenology studies have focused on anadromous fish because of easier access to their spawning grounds and juvenile habitats in rivers (Kovach et al., 2015; Otero et al., 2014). For oceanic conditions, habitat and seasonal coverages are challenging. Fishery-dependent data can expand our "snapshot" survey data and improve understanding of essential fish habitat (Dambrine et al., 2021; Murray et al., 2013). The expanded seasonal and spatial coverage can then be useful to explore biological processes such as spawning within a large spatial domain (Neidetcher et al., 2014). But fishery-dependent data present some limits (Maunder et al., 2006) because those data might confound changes in fishing behavior with trends in abundance. Considering fishing behavior is then important to avoid biased estimates of biomass and distribution. Nevertheless, fishery-dependent have been widely used to provide inside about fishery ecosystems functioning (Pauly et al., 1998) and to characterize seasonal distribution and habitat use (Kneebone et al., 2020). Indeed, previous studies highlighted that fishery-dependent and independent data might provide very similar patterns in term of fish spatio-temporal distributions (Pennino et al., 2016). With respect to spatio-temporal models, previous authors have included seasonal variation in isolation (Grieve et al., 2017; Thorson et al., 2016) or included both changes in spatial distribution among years and among seasons (Akia et al., 2021; Bourdaud et al., 2017; Kai et al., 2017; Kanamori et al., 2019). In particular, (Thorson et al., 2020) built seasonally explicit spatiotemporal models that included annual and seasonal variation in spatial distribution and density to identify interannual changes in phenology. Those models can be useful to identify climate-driven shifts in the seasonal timing of fish movement and ecosystem productivity but are expensive in terms of parametrization, and computation time. Spatio-temporal models that account for seasons when fit to fishery data may suffer from unbalanced designs and a lack of parsimony. In this study, we resolve this problem by an alternative approach accounting for seasonality

implicitly, using spatially varying catchability to represent seasonality. This allows us to explore migration timing and how interannual temperature changes impact seasonal migrations.

We implemented this approach on yellowfin sole (*Limanda aspera*) from the eastern Bering Sea (EBS). This stock represents the largest flatfish fishery in the world by landed weight (Spies et al., 2019). Adults exhibit a benthic lifestyle and occupy separate spawning areas (in summer) and feeding areas (in late summer) on the eastern Bering Sea shelf. From over-wintering grounds near the shelf margins, adults begin a migration onto the inner shelf in spring each year for spawning and feeding (Nichol, 1995; Wakabayashi, 1989; Wilderbuer et al., 1992) (Fig.1). The directed fishery historically occurs from winter through autumn, and NMFS research surveys take place during the summer months (Wilderbuer et al., 1992). The availability of this stock has been shown to vary within the survey area (Nichol, 1998; Nichol et al., 2019) due to spawning migrations. Presently, the stock assessment model used for setting catch advice includes a temperature coefficient that impacts the availability of the stock to the survey gear (Wilderbuer et al., 2019).

As with other flatfish stocks where males remain on the spawning grounds longer than females (Arnold and Metcalfe, 1996; Hirose and Minami, 2007; Rijnsdorp, 1989; Solmundsson et al., 2003), Nichol et al., (2019) also showed that male yellowfin sole remained on the spawning grounds longer than females and highlighted positive correlations between the proportion of females relative to male and annual estimated survey biomass. However, all those conclusions rely on data collected from scientific surveys designed to occur at the same time each year within the same restrained spatial domain, which precludes our understanding of changes in timing of spawning migration. No seasonal or interannual processes have been inferred to better understand the impact of interannual temperature changes on yellowfin sole movement phenology. In this paper, using fishery-dependent catch per unit effort data (CPUE), we propose to extend these previous findings (Nichol et al., 2019) by inferring seasonal movement and relationships between movement and interannual temperature changes. Because spatially explicit fishery CPUE data are available throughout multiple seasons and years, it can be used to build a model on a sub-seasonal interval to capture seasonal movement within a wide spatial domain. We developed a model which accounts for seasonality implicitly and explored how migration timing and interannual temperature changes can impact the spatiotemporal distribution of CPUE data. To this end, we estimated spatially varying catchability coefficients linking density, seasons, and interannual temperature changes. We specifically define early (March 19-May 21), intermediate (May 22-July 30), and late (August 1-September 24) fishing seasons for yellowfin sole. These seasons include 33.2%, 32.7%, 32.6% respectively of the total fishery landings from 2001 and 2019. This study's period (March 19-September 24) corresponds to high fishing effort that brackets spawning timing and migration of yellowfin sole in the Bering Sea and includes the fishery-independent survey timing occurring during the intermediate season.

We address four key questions:

[Q1] Does the timing of migration and progression of spawning impact the fishery CPUE and is the progression of spawning dependent on temperature changes in the EBS?

During warm years, we expect migrations to start earlier, with high CPUE in the middle shelf during the early season, and then again in the middle and outer shelf during the late season when back migration is more progressed (Fig. 2, second row). Inversely, during cold years, we expect

migration to be delayed with high CPUE in the inner shelf and in the middle shelf during the intermediate and late season respectively, when back migration to wintering areas is delayed (Fig. 2, second row).

[Q2] Does fish availability to survey change between warm and cold years?

During warm years, because migrations are more progressed, we expect substantial overlap between survey area and fisheries CPUE during the intermediate season (i.e. during the survey timing). By contrast during cold years, fish are expected to be in shallower water during the intermediate season and not available to the survey, so we expect lower overlap between survey area and fisheries CPUE during the intermediate season, while we expect a strong overlap during the late season when fish starts leaving spawning grounds to wintering areas (Fig. 2).

[Q3] Does phenology, that is the timing of spawning migration, change with sex?

We expect male yellowfin sole remain on the spawning grounds longer than females, because females appear to migrate out of the spawning areas earlier than males, based on analyses from survey data (Nichol et al., 2019).

[Q4] Can we use fishery CPUE to account for change in availability to the survey to improve the yellowfin stock assessment?

The yellowfin stock assessment (Spies et al., 2019) includes the survey mean bottom temperature and survey timing across stations as covariates affecting survey catchability. We evaluate how an "overlap index" computed from seasonal fishery CPUE (derived from [Q2]) might improve the assessment of yellowfin sole in the eastern Bering Sea.

II. MATERIALS AND METHODS

In this section, we will first present the spatiotemporal models in a general way so that it can be applied to other cases of study, then the data specific to our case study, and then the specific methodologies to address the questions posed above.

II.1. Spatio-temporal model accounting implicitly for seasonal variations

We developed spatiotemporal models which estimate the expected fisheries CPUE $b(s_i, t_i)$ (in biomass per tow duration) for each sample i, occurring at location s_i and year t_i.

To define the spatial resolution of the model, we adopted the SPDE (Stochastic Partial Differential Equation) spatial framework which represents continuous Gaussian fields as a discrete Gaussian Markov random field (Lindgren, 2012). The number of knots determines the spatial resolution of the model (and is specified by the user as a trade-off between the accuracy of the Gaussian Markov random fields representation and computational cost). We used a k-means algorithm to identify the location of knots to minimize the total distance between the location of knots and extrapolation-grid cells (Fig. S1). The SPDE approximation involves generating a triangulated mesh that has a vertex of a triangle at each knot (here we used the package *R-INLA* (Lindgren, 2012)). Then spatial variables at location s, are interpolated from knots to extrapolation grid using this triangulated

mesh (Fig. S1) (Grüss et al., 2020). Concerning the temporal resolution of the model, year t_i is defined as an integer {2001, 2002, …, 2019}. We calculate $b(s_i, t_i)$ using a Generalized Linear Mixed Model (GLMM) while including random effects to describe additional variability from covariates not included in the process error terms (spatial and spatiotemporal variations, more details below in equation (1)). We specifically define a linear predictor that is then transformed via an inverse-link function. In the following we used a log-link function, so that all effects are additive in their impact on predicted fisheries log-CPUE, which also simplifies interpretation of covariate effects.

The model is a log-linked linear predictor as follows:

$$log\,[b(s_i, t_i)] = \beta(t_i) + \sum_{k=1}^{n_k}\left(\left(\lambda(k) + \varphi(s_i, k)\right) q(i, k)\right) + \omega(s_i) + \varepsilon(s_i, t_i)\,, \qquad (1)$$

where $\beta(t_i)$ is the intercept for year t_i, $\omega(s_i)$ and $\varepsilon(s_i, t_i)$ represent, respectively, spatial, and spatiotemporal variation in fishery CPUE; and $q(i, k)$ is an element of matrix q composed of n_k measured catchability covariates that explain variation in catchability, $\lambda(k)$ is the estimated impact of catchability covariates for this linear predictor, $\varphi(s_i, k)$ is zero-centered spatial variation in that slope term. The model was designed to predict fishery CPUE as a function of temporal variation, spatial variation, and spatiotemporal variation effects, as well as catchability covariates. It accounts for these spatio-temporal dynamics as follows:

1. Spatial variation: the spatial variation terms, ω(s), in Equation (1) represent unmeasured spatial variation in the linear predictor that is stable over time;
2. Spatio-temporal variation: the spatiotemporal variation terms ε(s,t), represent unmeasured spatial variations in the linear predictors that changes between years;
3. Temperature-mediated drivers represented as catchability: $\varphi(s, k)$ in Equation (1) encompasses the spatially varying effect of covariates on fisheries CPUE. A part of the spatial variation is then attributed to catchability covariates. For each catchability covariate (indexed by k) tested, we implemented corner constraints only for the linear effect $\lambda(k)$, and not for the spatially varying effect $\varphi(s_i, k)$.

These spatial and spatio-temporal terms can be modelled as random effects following a multivariate normal distribution (Gaussian random fields):

$$\begin{aligned} \boldsymbol{\omega} &\sim MVN(\mathbf{0}, \sigma_\omega^2 \mathbf{R}_\omega) \\ \boldsymbol{\varepsilon}(t) &\sim MVN(0, \sigma_\varepsilon^2 \mathbf{R}_\varepsilon) \\ \boldsymbol{\varphi}(k) &\sim MVN\left(0, \sigma_\varphi^2 \mathbf{R}_\varepsilon\right) \end{aligned} \qquad (2)$$

where σ_ω^2 is the estimated pointwise variances of the spatial variation in CPUE; σ_ε^2 is the estimated pointwise variances of the spatio-temporal variation in CPUE; σ_φ^2 is the estimated pointwise variances of the spatial effect for each covariate k; $\mathbf{R}(s_1, s_2)$ is the correlation between location s_1 and location s_2 for spatial and spatiotemporal terms and is approximated as following a Matern function:

$$\mathbf{R}(\mathrm{s}_1, \mathrm{s}_2) = \frac{1}{2^{\nu-1}\Gamma(\nu)} \times (\kappa|(s_1 - s_2)\mathbf{H}|)^\nu \times K_\nu(\kappa|(s_1 - s_2)\mathbf{H}|) \qquad (3)$$

where **H** is a two-dimensional linear transformation representing geometric anisotropy, ν is the Matern smoothness (fixed at 1.0), and κ governs the decorrelation distance.

Finally, in this study, we analyzed fisheries dependent data, in particular those CPUE data that did not include zeros, and we assumed CPUE by location to be lognormally distributed. Code for model M3 is available online on Github (https://github.com/MaxOlmos/Flat_fish_2021).

II. 2. Data

Fishery-dependent catch-and-effort (CPUE)

We used catch (biomass in kg) and effort (tow duration) data collected by observers on Bering Sea-Aleutian Islands commercial bottom trawl vessels from 2001 to 2019 between March 19-September 24. For each commercial catch, observers record geographical position (longitude and latitude) and total catch of yellowfin sole, extrapolated from a sample. Sample locations are defined as the centroid of one of 105 polygons defined by the Alaska Department of Fish and Game (called ADFG cells, one degree of longitude by half degree latitude), where these cells encompass the spatial domain of yellowfin sole fishery in the eastern Bering Sea (Suppl. Mat. Fig. S2, S3). We aggregated all observed sets within a given year, season (early/intermediate/late), and ADFG spatial cell to a single observation. We aggregated from observed sets to unique year-cell-season combinations in two ways:

1. Average ratio: We present results based on this method by calculating the ratio of catch and effort for each observed set, and then averaged across these. This "average ratio" has also been done in model-based analyses and allows to correct for effects of changes in the distribution of fishing fleets and activity (Walters, 2003; Walters and Hilborn, 2005)
2. Ratio estimator: As a sensitivity analysis, we separately summed the catch and effort for all observed sets, and then taking the ratio of these sums (Swain and Wade, 2003). This is conceptually similar to "ratio estimators" (Myers and Worm, 2003);

In practice, we found that results were not highly sensitive to the choice of aggregation method (Suppl. Mat. Fig. S5, S6) so the spatio-temporal model was fit to these aggregated data (using the average ratio method). Also, this aggregating process is designed to mitigate the potential bias arising from preferential sampling (Alglave et al., 2022; Conn et al., 2017), by ensuring that areas with a disproportionately higher CPUE of observed sets are still aggregated to a single fitted observation. As a preliminary check and as suggested by Alglave et al. (2022), we explored the relationship between sampling intensity and biomass to diagnose any potential strong preferential sampling. Our results suggested that preferential sampling is low (Suppl. Mat. Fig. S4), so we did not account for any preferential sampling in our model.

Catchability covariates

We sought to understand how the spatiotemporal distribution of CPUE changed depending on warm or cold temperature years. Thorson, (2019a) has assessed the impact of temperature and cold pool on yellowfin sole. But this study relied on survey data that are only defined for the intermediate season. Unfortunately, no temperature associated with fishery CPUE samples are available. So, based on Nichol et al. (2019) and the time variation in cold pool extent (Suppl. Mat. Fig. S7, *akgfmaps* package (https://github.com/afsc-gap-products) we approximated interannual temperature changes in the Bering Sea using temperature as a discrete variable with two levels: nine cold years (2006-2013, 2017) and ten warm years (2001-2005, 2014-2016, 2018, and 2019).

We encourage future work using other covariates to approximate interannual temperature changes in the Bering Sea such as temperature (continuous variable, yearly or seasonally defined) and cold pool extent.

The *season* covariate is discrete with three levels which were based on the migration ecology of yellowfin sole (Nichol, 1998; Spies et al., 2019; Wilderbuer et al., 1992): early (March 19-May 21), intermediate (May 22-July 30), and late seasons (August 1-September 24), where these seasons include 33.2% , 32.7% and 32.6%, respectively of the total fishery landings between 2001 and 2019, and the survey occurs during the intermediate season (between 2001 and 2019, more than 99.9% of the survey tows occurs during the intermediate season).

To implicitly estimate changes in movement phenology depending on temperature changesin the EBS we considered the combined effect of *interannual temperature changes* and *season* on fishery CPUE data.

Different models for the spatiotemporal variation of fishery CPUE were tested (Table 1). In the reference model M3, we inferred whether the timing of migration (i.e., season) changes with different environmental conditions (i.e., for years with warm or cold years). Three models of lower complexity were also considered (M0, M1, M2, Table 1) to test if accounting implicitly for seasonal movement (i.e., season and temperature effects) better explains the spatiotemporal variations in fishery CPUE data. We used Akaike's Information Criterion (AIC) for model selection as a measure of model parsimony to identify the level of complexity that likely minimizes the combination of bias (Akaike, 1974).

Male and female data

Fisheries CPUE were apportioned into male and female categories using female proportion data from observer data. For some locations, female proportions do not exist (17% of the locations). In this case we attributed to this location the value of the closest neighbor for a given year and a given combination of covariates (i.e., all combinations of levels constituting the *seasons* covariates) (Suppl. Mat. Fig.S8).

II.3. Estimation and model fitting

Parameters are estimated using release 3.8.2 of the Vector Autoregressive Spatio-Temporal (VAST) package (Thorson, 2019), which is publicly available online (https://github.com/James-Thorson/VAST) and runs within the R statistical environment (R Core Team, 2017). Spatial terms were estimated using the SPDE approximation (Lindgren et al. 2011), such that we estimate the value of each spatial variable at a set of knots.

The marginal log likelihood was computed using the Laplace approximation implemented by the R package 'TMB' (Kristensen et al., 2016) through an approximation of the integral across all random effects. Finally, VAST employs the generalized delta method implemented in TMB to calculate the standard errors of all the fixed and random effects, as well as the standard errors of the derived quantities (Kass & Steffey 1989). In some cases, we also calculated standard errors (SEs) for entire vectors of output (e.g., $se\left(\varphi(s,k)\right)$ for the spatially varying term $\boldsymbol{\varphi}$). In these cases, we extracted the joint precision matrix (e.g., matrix of 2nd derivatives) of fixed and random

effects evaluated at their maximum likelihood estimates and conditional upon the data. We then generated 250 samples from this joint precision matrix, recompute all quantities for each sample, and then calculate the standard error as the standard deviation of these samples. This approximation had lower accuracy than the generalized delta method but is computationally efficient when calculating standard errors for quantities calculated as a nonstandard function of parameters.

II.4. Model validation and evaluation

We assessed model convergence by checking that the gradient of the marginal log-likelihood is less than 0.0001 for all fixed effects, and that the Hessian matrix of second derivatives of the negative log-likelihood is positive definite. We checked model residuals and validated the model using the DHARMA framework (Hartig, 2022) within VAST by computing QQ-plot residuals (Suppl. Mat. Fig. S10), plotting how residuals vary with magnitude of the predictions (Suppl. Mat. Fig. S10), and spatial map of quantile residuals (Suppl. Mat. Fig. S11). None of our diagnostics highlight any strong patterns in residuals and does not indicate any strong inconsistencies between the models and the data.

Model M3, which accounts for changes in movement phenology in response to interannual temperature changes has the lowest AIC value so appears to be the best descriptor to represent spatiotemporal variations in CPUE and was therefore retained in the subsequent analyses (Table 1).

II.5. Derived quantities and model specifications

Here we describe the methodology used to find evidence in support of each of our fundamental questions, using results from fitting the model (Eq. 1, model M3) to the data, as described above.

[Q1] Does the timing of migration and progression of spawning impact the fishery CPUE and is the progression of spawning dependent on interannual temperature changes in the EBS?

We compared spatial distribution of fishery CPUE between cold and warm years. We first calculated the average predicted biomass CPUE for each season (u) in warm vs. cold years $v(t)$:

$$b(s,t,u) \equiv b(s,t) \times \varphi\left(s, k_{u,v(t)}\right) \tag{4}$$

$$b(s,u,v^*) = \frac{\sum_{t=1}^{n_t} I(v(t)=v^*) b(s,t,u)}{\sum_{t=1}^{n_t} I(v(t)=v^*)} \tag{5}$$

where $k_{u,v}$ is the covariate associated with season u and temperature v, $v(t)$ is the temperature for each year t, and $I(v(t)=v^*)$ is an indicator function that equals 1 when year t is associated with temperature v^* and 0 otherwise. So, $b(s,t,u)$ is the predicted fishery CPUE for each knot location s, in year t within *season* u, and $b(s,u,v^*)$ is the average fishery CPUE in season u for all years with temperature v. Then, for a given season and a given temperature, we generated and compared

cumulative maps of biomass (kg.min^{-1}) by identifying the areas that encompassed the top 95th percentile of total biomass across the modeled spatial domain.

Additionally, we assessed the significance of the spatial effect $\varphi_{u,v,s}$ for each location *s*, season *u*, and temperature *v*, by computing a two-sided Wald test of significance. We computed the p-value assuming that the ratio $\frac{\varphi(s,k_{u,v})^2}{se\left(\varphi(s,k_{u,v})\right)^2}$ follows a Chi-squared distribution with one degree of freedom (Wald Chi-Squared test). We consider the effect significant if p-value <0.05.

[Q2] Does fish availability to survey change between warm and cold years?

We investigated how the spatial distribution of fisheries CPUE overlap with the survey area depending on seasons and temperature. We computed an overlap index $OI(t,u)$ for each year t, each season *u* and each temperature *v(t)*. This overlap index $OI(t,u)$ is defined by calculating the predicted fisheries biomass for all locations in the survey area ($s \in A_{Tot}$), and the predicted biomass in the entire fished area ($s \in A_{EBS}$), and then calculating their ratio:

$$OI(t,u) = \frac{\sum_{s \in A_{Tot}} b(s,t) \times \varphi\left(s, k_{u,v(t)}\right)}{\sum_{s \in A_{EBS}} b(s,t) \times \varphi\left(s, k_{u,v(t)}\right)} \quad (6)$$

Because the predicted biomass $b(s,t,u)$ accounts for interannual variation via parameter $\beta(t)$ (see Eq. 1) we also derived an overlap index from the expected spatial main effect (i.e. defined as the product between $\omega(s)$ and $\varphi\left(s, k_{u,v}\right)$), as a sensitivity analysis (Suppl. Mat. Fig.S9):

$$OI_{\omega}(u,v) = \frac{\sum_{s \in A_{Tot}} \omega(s) \times \varphi\left(s, k_{u,v}\right)}{\sum_{s \in A_{EBS}} \omega(s) \times \varphi\left(s, k_{u,v}\right)} \quad (7)$$

This sensitivity shows that the overlap index is not sensitive to the choice of Eqs. 6 or 7, so in the following analysis we calculated it from $b(s,t)$ (Eq. 6).

[Q3] Does phenology, i.e the timing of spawning migration, change with sex?

We used the modelling framework defined in section II.1 (M3) to run two independent spatiotemporal models, one for males and one for females. We extracted the predicted average fishery CPUE, $b(s,u,v)$, in season u for all years with temperature $v(t)$, for both males and females, to investigate if movement phenology changes between males and females depending on temperature. We also extracted $OI(t,u)$ for both males and females to investigate if availability to the survey changes with sex.

[Q4] Can we use CPUE (results from [Q1], [Q2] and [Q3]) to account for change in availability to the survey to improve the yellowfin stock assessment.

We evaluated the overlap index relative to current covariates used to model survey "availability" in the operational stock assessment used for management (Nichol et al., 2019). The yellowfin stock

assessment (Spies et al., 2019) includes the survey mean bottom temperature and survey timing across stations as covariates on survey catchability, q:

$$q = e^{-\alpha + \beta_1 T + \beta_2 S + \beta_3 TS} \quad (8)$$

where T is survey mean bottom temperature, S is survey timing, and TS is the interaction of T and S. The parameter α is the estimated intercept and $\beta_1, \beta_2 and\ \beta_3$ are the estimated coefficients of the effect of temperature, survey timing and the interaction of temperature and survey timing on catchability, respectively.

Presently, the assessment model code requires a covariate for every survey year. The 2021 base accepted model was modified such that the current covariate anomaly values from 1982-2019, and 2021 were set to zero (no anomaly) except for the same years from the overlap index: 2001-2019. Each covariate was normalized for the period where the overlap index is available. Three stock assessment model (SAM) configurations were deemed reasonable to show for the evaluation:

SAM.1: Temperature, survey timing, and their interaction as covariates on catchability (Eq. 8).

SAM.2: Overlap index during the survey season, $OI(t, u = Int.)$, as a covariate on catchability (Eq. 6).

We ran MCMC sampling from the posterior distribution using the ADNUTS R package (Monnahan et al., 2019; Monnahan and Kristensen, 2018).

III. RESULTS

[Q1] Does the timing of migration and progression of spawning impact the fishery CPUE and is the progression of spawning dependent on temperature in the EBS?

The model can predict the spatial distribution of fisheries CPUE for each year and each season (Fig. 3, Suppl. Mat. Fig.S12). Our results highlight that CPUE is affected by the season and progression of spawning migration. The model estimates a strong effect of seasons on the spatial distribution of yellowfin sole CPUE (Fig.3, 4, 5). During the early season, CPUE are mostly distributed across all EBS, whereas during the Intermediate season, CPUE are distributed in the Inner Shelf, close to the spawning areas (Fig. 3). Finally, during the late season, CPUE are more distributed across the inner and middle shelf where yellowfin soles have started their migration back to the wintering areas in the outer shelf.

Additionally, our results highlight that the seasonal distribution of CPUE is dependent on temperature. The spatiotemporal model estimates the effect of seasonality and temperature on fisheries CPUE (Fig. 4, see Suppl. Mat. Fig. S13 for the significant effects). During the early season, cold temperature conditions show elevated CPUE in a broad band of the outer and southern middle domain while warm years show elevated CPUE in a small hotspot in the outer domain. During the intermediate and late seasons, cold temperature conditions are associated with elevated CPUE in the shallowest waters of the inner shelf (intermediate) or the middle domain (late), while warm temperature conditions show less association with inner-domain CPUE (Fig. 4).

Seasonal distribution of CPUE is then different during warm and cold years (Fig. 5). The most significant differences appear during the intermediate seasons, where yellowfin soles are concentrated in the shallowest water in the inner shelf close to the spawning areas during cold years, while they are less constrained and distributed in the middle shelf during warm years.

Collectively, our results show that spawning movement phenology is more progressed during warm years than cold years. Specifically, biomass hotspots are confined to shallow waters during the Intermediate season (and to a lesser degree the Late season) during cold compared with warm years (Fig. 5, see middle and right panels).

[Q2] Does fish availability to survey change between warm and cold years?

Our results highlight that movement phenology in relation to interannual temperature changesin the EBS affects availability of these species to the survey. During the intermediate season (which corresponds to the survey season), the spatial distribution of fisheries CPUE is significantly different between cold and warm years (Fig. 5). During cold years, CPUE are in the shallowest water of the inner shelf close the spawning areas, mostly outside of the survey area, whereas during the warm years, CPUE are found in both middle and inner shelf within the survey area.

Our result also suggest that yellowfin sole are more available to the survey during warm years than in cold years (Fig. 6). Interannual temperature changes in the EBS impact the overlap between fisheries CPUE and the survey grid, the strongest difference between warm and cold years occurring during the Intermediate season (i.e., the survey season). During the survey season, warm years are associated with high overlap values (~0.73 on average) whereas cold years are associated with lower overlap (~0.68 in average). Finally, during late season, Fig. 6 also shows that overlap is stronger during cold years suggesting that yellowfin sole has migrated back to the middle/outer shelf from the inner shelf.

[Q3] Does phenology, that is the timing of spawning migration, change with sex?

In terms of total biomass, female biomass is larger than male biomass across the time-series (except in 2013, Suppl. Mat Fig. S14). Both males and females present a seasonal pattern in their spawning migration. (Fig. 7). Our results also highlight some differences. During the intermediate season, males are concentrated in the spawning grounds, so very few males are available to the survey, whereas females are more distributed across the inner and middle shelf, so more available to the survey than males (Fig. 7). Overlap with the survey area is more important for females than males for all seasons (Fig. 8), males staying longer in the inner shelf that females (Fig. 7, 2nd row, columns 2 and 3).

Both males and females movement phenology is impacted by temperature (Fig. 7). In particular, during the intermediate seasons, fish were more aggregated in the inner shelf during cold years than warm years. Also, temperature impacted the overlap index for both males and females but with approximately the same magnitude. Indeed, both males and females present a higher overlap index during warm than cold years, but the difference between male and female overlap index does not change with warm or cold years (Fig. 8). Standard deviations are higher in cold years due to temporal variability in temperatures and cold pool extend; with some years being

colder than other (i.e 2012, 2013 are colder than 2011, 2017, Figure S7), which could generate greater variability in terms of overlap within cold years (Fig. 5 and Fig. 7).

[Q4] Can we use fishery CPUE to account for change in availability to the survey to improve the yellowfin stock assessment?

We evaluated the overlap index relative to currently used covariates (mean bottom temperature, survey timing, and their interaction). For model SAM.1, both main coefficients were greater than zero indicating that when the temperatures were warmer and the survey start date later, the relative abundance as indexed by the standard survey area covered a greater fraction of the resource (Fig. 9a). This also demonstrates that the coefficient of the interaction term (of temperature and timing) was negative; this would reduce the value for catchability in years where waters were warm, and migration was later than normal. When we applied the overlap index alone as a covariate (SAM.2), the coefficient was also significantly greater than zero which is consistent with the notion that the YFS resource distribution overlaps with the survey area (Fig. 9b).

IV. DISCUSSION

In this study, we inferred movement phenology and relationships between movement and interannual temperature changesusing spatially explicit, year-round fishery dependent CPUE data. We fit a novel spatiotemporal model that included a sub-seasonal component to these data, which allowed for us to infer seasonal movement patterns. Applying this model to yellowfin sole in the Bering Sea as an example, our results highlight evidence for shifts in movement phenology based on seasonal temperature conditions, where spawning migration occurred earlier in warm conditions. We also demonstrated these climate-related shifts in movement phenology can have notable impacts on interpretation of other data sources used in stock assessment modeling (e.g., survey data) and specification of catch limits. For yellowfin sole, this was demonstrated by computing an index of overlap at the time of the summer survey and using this index as a catchability covariate to improve the assessment. The use of a sub-seasonal spatio-temporal modeling approach fit to year-round, spatially-explicit fishery dependent data could be used to explore other aspects of climate-related phenology that may be occurring for many species worldwide.

Consequences of climate-driven shifts in phenology on harvested populations

As climate change has been impacting all ecosystems on the globe (Hoegh-Guldberg and Bruno, 2010; Parmesan and Yohe, 2003; Poloczanska et al., 2013) climate-driven shifts in phenology are an essential concern in fisheries ecology. There is a need to account for environmental changes that impact the phenology of migration to provide effective management measures. First as highlighted in this study, shifts in phenology impact the fishery independent survey, designed to occur at approximately the same time each year and to provide annual indices of abundance for stock assessments. So, any climate-driven mismatch in timing between the survey and seasonal movement dynamics can cause a different proportion of population biomass to be available to the survey in different years. Long-term warming of the Bering Sea is likely to cause directional shifts in seasonal movement, in turn causing long-term changes in availability to surveys. Based on our

results, we urge stock assessment scientists to investigate if drastic changes in stock abundance represent sustained population conditions, or instead signal changes in timing of ecological events, such as spawning migration.

Secondly, ignoring climate-driven changes in phenology when managing fisheries might lead to potential overharvesting or missed harvesting opportunities. Such changes in phenology might strongly impact the reproductive success of some stocks. A shift in spawning migration induced by changes in temperature conditions can lead fisheries to catch adults before they could spawn leading to unanticipated changes in fishing mortality (Peer and Miller, 2014). For anadromous fish, accounting for phenology shifts is critical because fisheries management for those species rely on expected time of fish arrival in harvested areas (Mundy and Evenson, 2011). However, warm conditions lead to early migration which might be mistaken as large abundance and could, in turn, lead to overharvesting. Climate-driven shifts in phenology are leading to incorporation of temperature conditions in defining closed areas and fishing seasons. Zacher et al. (2018) highlighted how important it is to account for the differences in red king crab (*Paralithodes camtschaticus)* distribution with temperature regime to evaluate the effectiveness of a closed area to protect crab from bycatch in trawl fisheries. Crabs were aggregated within closed areas during warm years and outside closed areas during cold years, and therefore more susceptible as bycatch during cold years (Zacher et al., 2018). For Pacific halibut (*Hippoglossus stenolepis*), mortality applied during spawning and feeding migrations might impact biomass distribution. Changing environmental conditions is altering the timing of those migrations and current fishing season might be too short to protect those periods. As a consequence, allowing harvesting by seasonal interception fisheries too early might impact the spawning success and the stock productivity (Loher, 2011).

Mechanisms underlying changes in spawning movement phenology, spatial constraints and biomass

By further examining the mechanisms underlying the yellowfin sole example, we argue that our study provides insight into other species whose spatial distribution phenology may be affected by climate. Our study highlights how interannual temperature changes impact the timing of spawning movement but also the location and biomass of fish. During warm years the yellowfin spawning migration occurs earlier with a less constrained distribution (Fig. 5) and high biomass (Fig. S14). Whereas during cold years, yellowfin movement occurs later, the spatial distribution is more constrained in the inner shelf, and total biomass is lower than during warmer years. Those results seem to be in accordance with previous studies (Bartolino et al., 2011; Nichol et al., 2019; Porter, 2022). Both density dependent and independent mechanisms can affect the biomass and distribution of bottom-fish (Spencer, 2008) and explain such patterns. Considering density-independent mechanisms, the difference in spatial extent of the spawning area related to temperature could be the result of yellowfin sole adults tracking the temperature of their preferred habitat (between 1 and 7 °C, Bartolino et al. (2011); Porter (2022)). So, when bottom temperatures are warm, the spawning area might extend to the western part of the inner shelf following favorable temperatures that extend to the middle shelf as the cold pool contracts. Whereas cold years may constrain yellowfin in shallow waters in the inner shelf (Nichol et al., 2019; Porter, 2022).

Our results also match patterns resulting from density-dependent mechanisms. According to the theory of density-dependent habitat selection, expansion of area occupied is expected to be the result of an increase in population size which reduces habitat suitability and increases competition

(Spencer, 2008). Our results suggest that the presence of density-dependent mechanisms seem to be dependent on temperature conditions, and occur mostly during warm years. When bottom temperatures are favorable (warm years), our results show an increase in density linked with an increase in area occupied during the intermediate season, resulting from an expansion to suitable habitats. Such mechanisms linking increase in density and spatial expansion are quite common for marine species and have been observed in many systems (Scotian Shelf juvenile haddock (Marshall and Frank, 1995), Atlantic cod in the southern Gulf of St. Lawrence (Swain and Wade, 1993), and walleye pollock (Bacheler et al., 2009)). Future studies could integrate density-dependent responses with the same modelling framework used here (Thorson, 2022).

In addition to density independent mechanisms, a decrease in total biomass and a more constrain distribution in the inner shelf during cold years can be explained by density-dependent mechanisms. Indeed, between warm and cold years prey availability for yellowfin sole can change in the EBS. During cold years, the cold pool extends over the middle shelf during the summer season, and thus acts as a physiological barrier. Yeung et al. (2013) showed that this thermal barrier displaces three flatfish species, flatfish yellowfin sole (*Limanda aspera*), Alaska plaice (*Pleuronectes quadrituberculatus*) and northern rock sole (*Lepidopsetta polyxystra*) in the inner shelf, intensifying competition for prey resources between those species during cold years.

Another potential mechanism to consider is the effect of local depletion on abundance. During warm years the fishing fleet is more diffuse (less sea ice and a greater portion of the shelf open for trawling), and there is less of an effect of local depletion. However, in cold years, when yellowfin are more aggregated, the fishing effort and fish vulnerability increase and then local scale harvesting might have a negative effect on local fish density (Bartolino et al., 2012).

Our results also highlight differences between males and females which are in accordance with previous studies (Bartolino et al., 2011; Nichol et al., 2019). First, female distribution is more expanded than male distribution and goes through the middle shelf. Then female biomass density is higher than male density. Such results are in accordance with the fact that for many flatfish species females grow to a larger size than males (van der Veer et al., 2001). So density-dependent habitat expansion for females might be more important because of their higher energetic requirements (Bartolino et al., 2011). In our study males also seem to stay longer in the spawning area (especially during the warm years) than females (Nichol et al., 2019) a phenomenon largely observed for flatfish (Rijnsdorp, 1989; Solmundsson et al., 2003) which results in higher overlap between the survey area and fisheries CPUE for females. This can be taken into account in the stock assessment by modeling sex-specific availability.

A step forward to combine fishery and survey CPUE within a seasonal time step

In this study, we developed a spatiotemporal model on a sub-seasonal interval to capture seasonal movement based on fishery CPUE data. CPUE fishery data are of great interest to understand key demographic processes and their relationship with environmental changes, and to characterize essential habitats (Dambrine et al., 2021), which survey data cannot do (Suppl. Mat. S15). Fishery CPUE is typically available over a large spatial domain and seasonal range, which allowed us to detect phenology and time-varying availability. Fishery CPUE data were important to infer spatiotemporal changes in spawning migration dynamics occurring outside the survey period. These data can also be extremely useful to assess populations occurring in untrawlable habitat, such as with many species of *Sebastes.* Untrawlable habitat can be a problem for estimating indices of abundance from bottom trawl surveys (Jones et al., 2012, 2021; Thorson et al., 2013;

Zimmermann, 2003). Through cooperative research using fishing industry and community knowledge of fish distribution and behavior, fishery CPUE data has the potential to improve interpretation of survey-based indices of abundance (Johnson, 2011; Ressler et al., 2009).

However, fishery CPUE can present some limits. Fishery CPUE data might confound changes in fishing behavior with trends in abundance and then are not proportional to the actual abundance. We did not explicitly account for fishing behavior in this study, but we made sure that preferential sampling of yellowfin fishery CPUE was low. We acknowledge that some bias might exist with the actual abundance due to difference in catchability. But the goal of this study is not to provide an unbiased index of abundance, rather to highlight how movement phenology, represented here as seasonal hotspots in wintering, spawning, and feeding areas might change depending on temperature. Accounting for scientific survey data within our approach could be complementary to CPUE fishery data and provide an additional data source to estimate unbiased fish spatial distribution and key demographic processes. Resource surveys for use in stock assessments are typically designed to occur at approximately the same time each year (NRC, 2000), and cover a large geographic area accounting for areas of few or null abundance. They also sample most of the life stages of the populations providing information for characterizing the age structure and population dynamics of the stocks. By using a standardized effort, they provide unbiased quantities on stocks. A spatio-temporal model fitted simultaneously to fishery and survey data could be used to create a joint abundance index. The joint abundance index could then be included in assessments; in the example of yellowfin sole, the joint index would be an alternative to include a structural linkage between summer bottom temperature and catchability.

Some previous studies have combined survey and fishery CPUE, accounted for seasonality, and improved the estimation of the spatial distribution and abundance index of marine species (Bourdaud et al., 2017; Pinto et al., 2019; Thorson, 2019b). More recently, integrated population models have been developed to account for seasons explicitly (Thorson et al., 2020) and have combined both fishery and survey data to account for preferential sampling in fishery CPUE data (Rufener et al., 2021). Future work should focus on integrating all those data (seasonal, fishery and survey CPUE, and environmental variables) within spatio-temporal models on a sub-seasonal interval to capture seasonal movement. Such models will estimate the spatial distribution of each species in relation to temperatures year-round, and will form the basis for a spatio-temporal modeling approach to standardize the survey biomass data for each assessment. Those models might also inform forecasts of future stock distribution and habitat usage under various future climate and fishing pathways. In addition, the spatio-temporal modeling approach developed for this project could be applied to other economically important species to inform future prediction of habitat usage and distribution. In terms of management implications, this could have major impacts on fishing operations and could improve our ability to estimate accurate reference points in assessments.

Conclusion

Our study incorporates the effects of species distribution shifts into climate-ready ecosystem-based fisheries management. Fishery management under global change is challenging because if environmental variability ignored this could lead to overharvesting or missed harvesting opportunities, changes in stock productivity, changes in life history and reductions of spawning success. Our study provides a framework that could be used in climate monitoring and impact analysis on fisheries. Species distribution models with spatially varying coefficients linking

density and environmental covariates have to be promoted to represent the response of fish to environmental changes with a spatial structure (Bartolino et al., 2012, 2011; Porter and Ciannelli, 2018; Thorson, 2019c). Future research should be done to apply our framework to other highly mobile species like flathead sole (*Hippoglossoides elassodon),* crab species in the EBS, Atlantic bluefin tuna (*Thunnus thynnus)*, Mediterranean albacore (*T. alalunga)*, and bullet tuna (*Auxis rochei.)* (Reglero et al., 2012; Zacher et al., 2018) to infer changes in movement phenology and account for changes in availability within stock assessment to provide management approaches that reduce climate-induced variability.

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Maxime Olmos: Conceptualization (evolution of overarching research goals and aims), Formal analysis, Investigation, Data curation, Methodology, Visualization, Writing – original draft.

James Ianelli: Writing, Data provision, Assessment application, Resources, Mentorship.

Lorenzo Ciannelli: Writing, Funding acquisition, Project administration, Mentorship.

Ingrid Spies: Writing, assessment application

Carey R. McGilliard: Conceptualization (Ideas), Funding acquisition, Writing, Project administration, Mentorship.

James T. Thorson: Conceptualization (Ideas), Methodology, Software, Funding acquisition, Writing, Project administration, Mentorship.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY STATEMENT

Fisheries CPUE data are confidential data and they are available on specific request to jim.ianelli@noaa.gov.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

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Table 1: Summary of the hypotheses tested, the associated model configurations and AIC values attributed to each model. ΔAIC is the difference in AIC score between the best model and the model being compared

Models	**Spatiotemporal variations in CPUE are explained by**	**Ecological hypothesis**	**Equations**	**ΔAIC**
M0	Year effect, Spatial main effect, and year spatial effect	Does not account for seasonality and interannual temperature changes	$log\ [b(s_i,t_i)] = \beta(t_i) + \omega(s_i) + \varepsilon(s_i,t_i)$	658
M1	M0 + spatial effect of seasons *u*, on CPUE	Account for seasonality, (i.e changes in movement phenology) but not interannual temperature changes	$log\ [b(s_i,t_i)] = \beta(t_i) + \sum\big((\lambda(k_u) + \varphi(s_i,k_u))q(i,k_u)\big) + \omega(s_i) + \varepsilon(s_i,t_i)$ With *u =c(Early, Intermediate, Late)*	654
M2	M0 + spatial effect of interannual temperature changes *v*	Account for impact of interannual temperature changes, but not for seasonality	$log\ [b(s_i,t_i)] = \beta(t_i) + \sum\Big((\lambda\big(k_{v(t)}\big) + \varphi\big(s_i,k_{v(t)}\big))q\big(i,k_{v(t)}\big)\Big) + \omega(s_i) + \varepsilon(s_i,t_i)$ With *v = c(Cold, Warm)*	170
M3	M0 + spatial effect of the interaction of seasons *u* and interannual temperature changes *v*	Account for changes in movement phenology in response to interannual temperature changes	$log\ [b(s_i,t_i)] = \beta(t_i) + \sum\Big((\lambda\big(k_{u,v(t)}\big) + \varphi\big(s_i,k_{u,v(t)}\big))q\big(i,k_{u,v(t)}\big)\Big) + \omega(s_i) + \varepsilon(s_i,t_i)$ With *v = c(Cold, Warm) and u =c(Early, Intermediate, Late)*	0

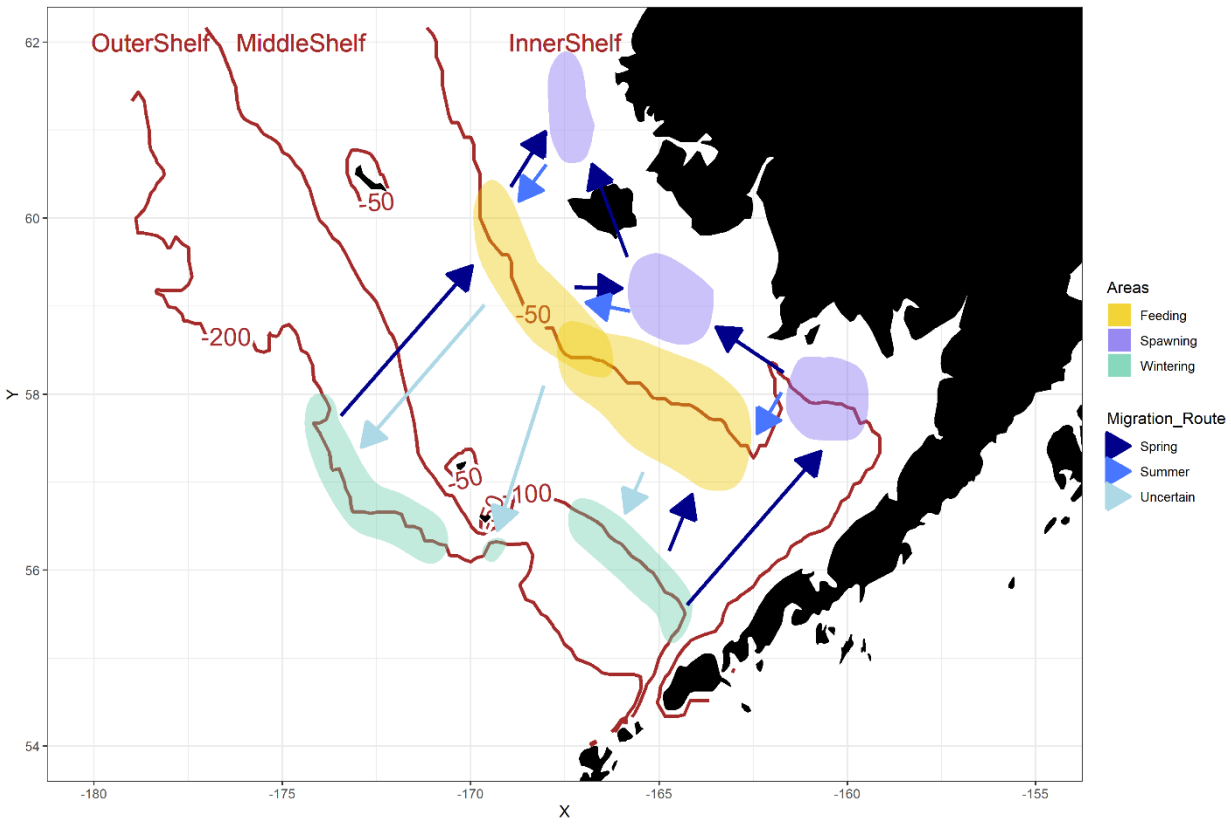


Figure 1: Distribution of wintering, spawning, and feeding areas for yellowfin sole in the Bering Sea, and observed regional grouping. Migration routes from wintering to feeding take place in spring, and the dates that Yellowfin Sole return to their wintering areas are unknown. Outer, middle, and inner shelf are defined for bathymetry between 200-100 meters, 100-50 meters and <50 meters respectively. (Adapted from Wakabayashi (1989) and Spies et al. (2019))

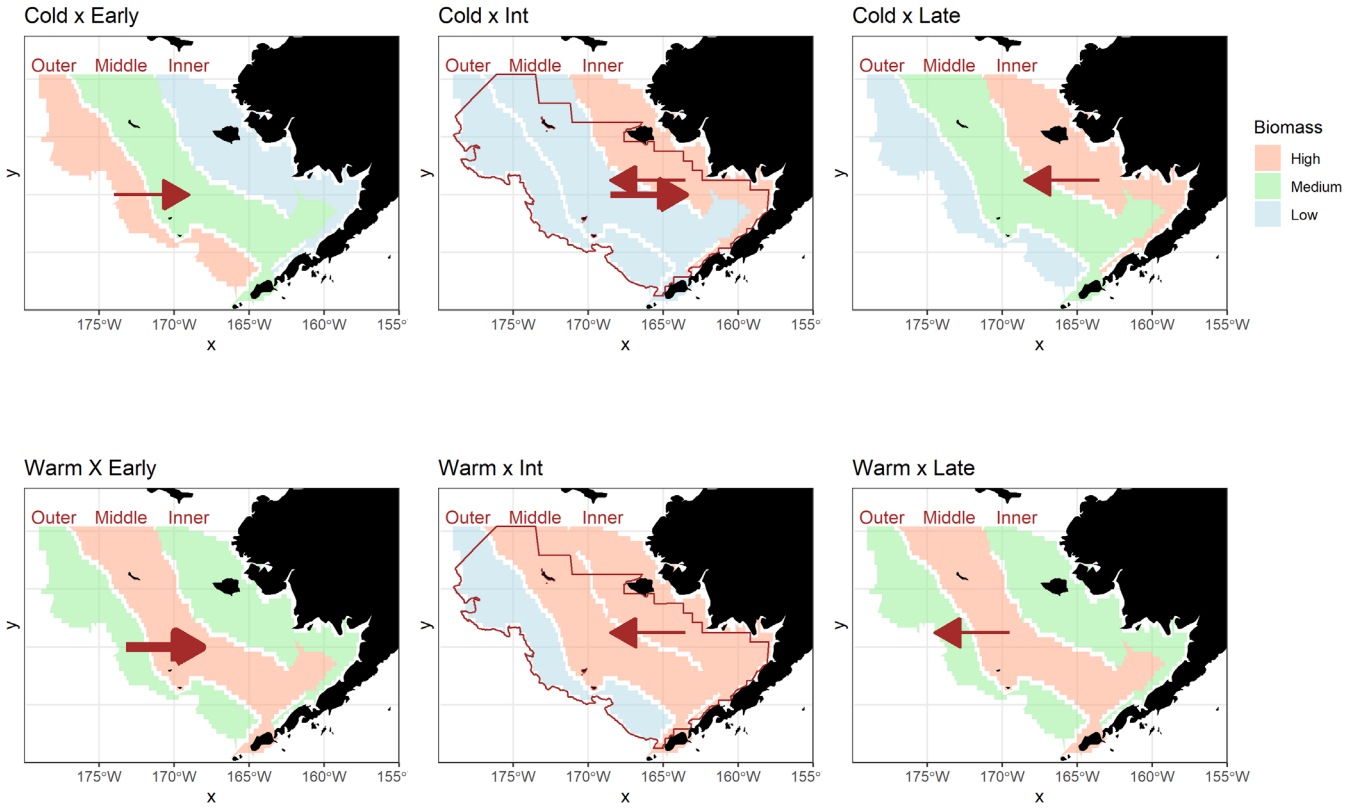


Figure 2: Conceptual expectation about how temperature changes (warm or cold years) and seasons (Early, Intermediate, Late) may affect the spatial distribution of biomass. Survey area (brown lines) is represented when survey occurs during the intermediate season. Brown arrows represent the hypothesized ontogenetic migrations (the thickness represents the intensity of the migration in term of biomass).

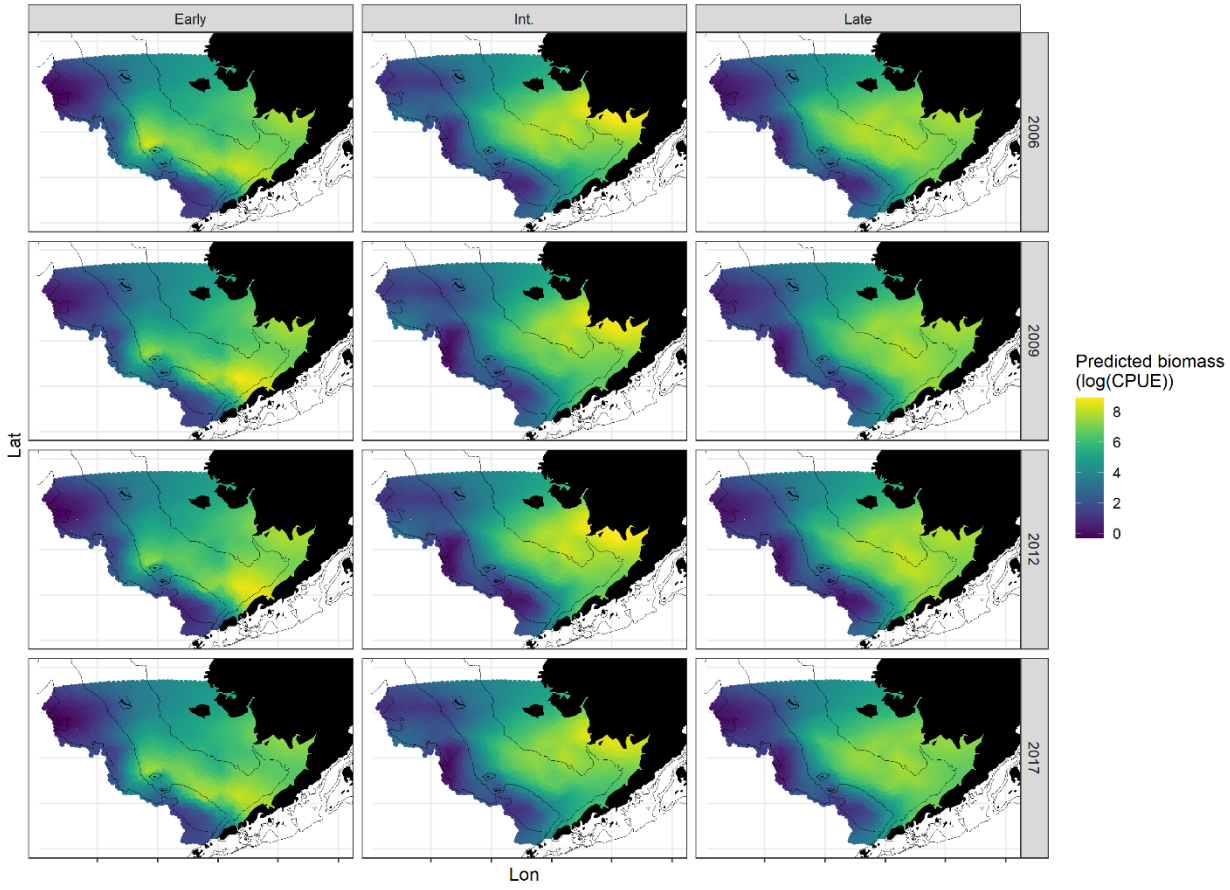


Figure 3: Seasonal spatiotemporal distribution of CPUE. Seasons are defined as Early, Intermediate (Int.) and Late) (Years 2006, 2009, 2012, 2017 (cold years) are chosen as example because seasonality changes are more pronounced for cold years). Full panels are in Suppl. Mat. Fig. S12.

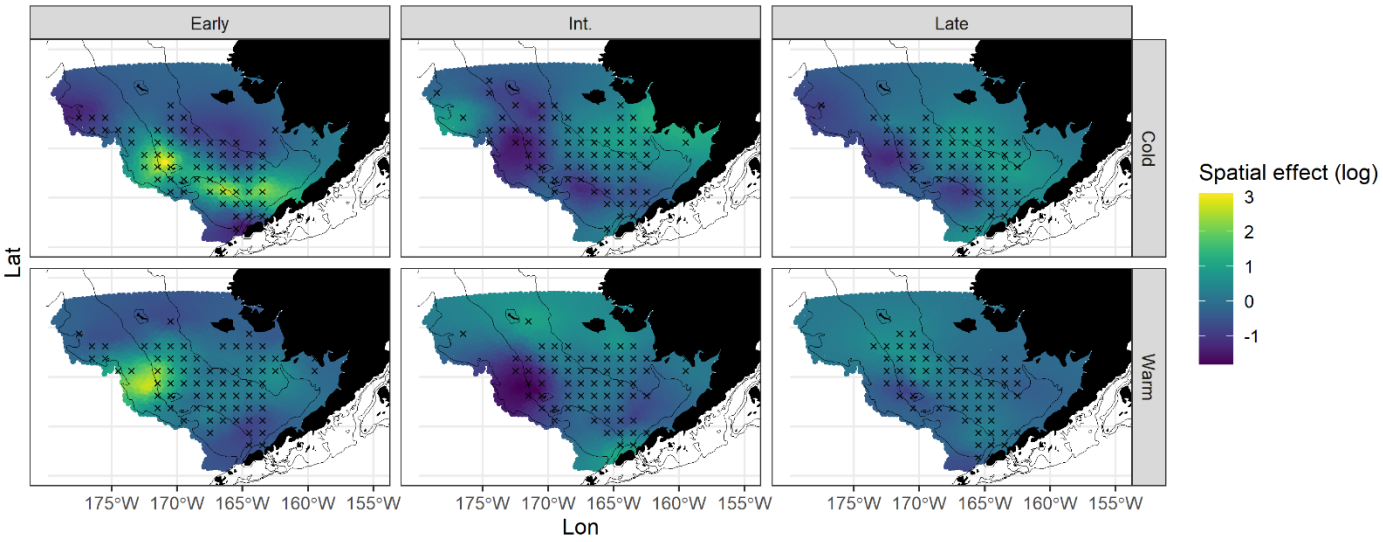


Figure 4: Spatial variation covariate effects φ on fisheries CPUE. Covariates represent the combined effect of *season* and *temperature* (ColdEarly, ColdIntermediate, ColdLate, WarmEarly, WarmIntermediate, WarmLate). Black crosses represent the spatial distribution of the data for each combination of *season* and *temperature* when aggregating across years. The model uses a log-link such that a location with value 0.1 is expected to have a exp(0.1) ≈10% higher expected CPUE than a location with value 0.

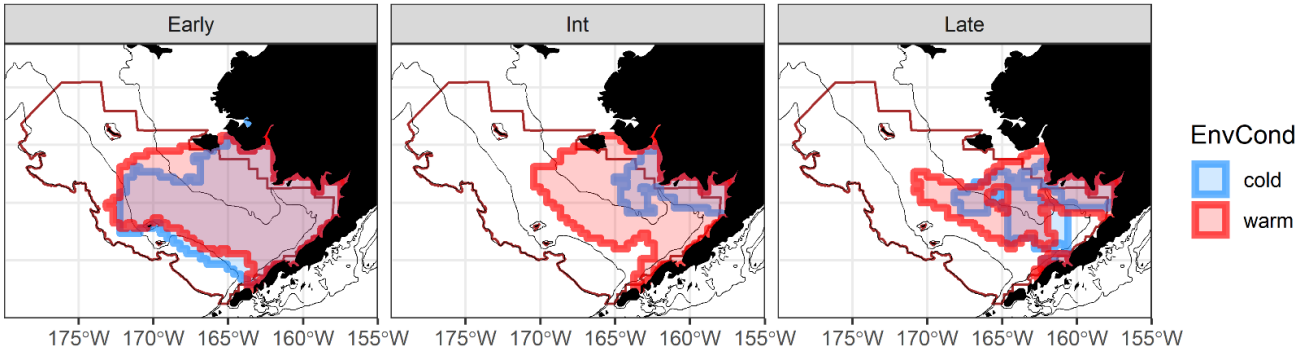


Figure 5: Seasonal spatial biomass distribution of yellowfin sole averaged for warm years (red) and cold years (blue). Red and blue polygons represent the cumulative biomass including 95% of the total biomass ($b(s,u,v^*)$ Eq. 5) across the entire spatial area for warm and cold years respectively and for each season. Brown polygon represents the survey area.

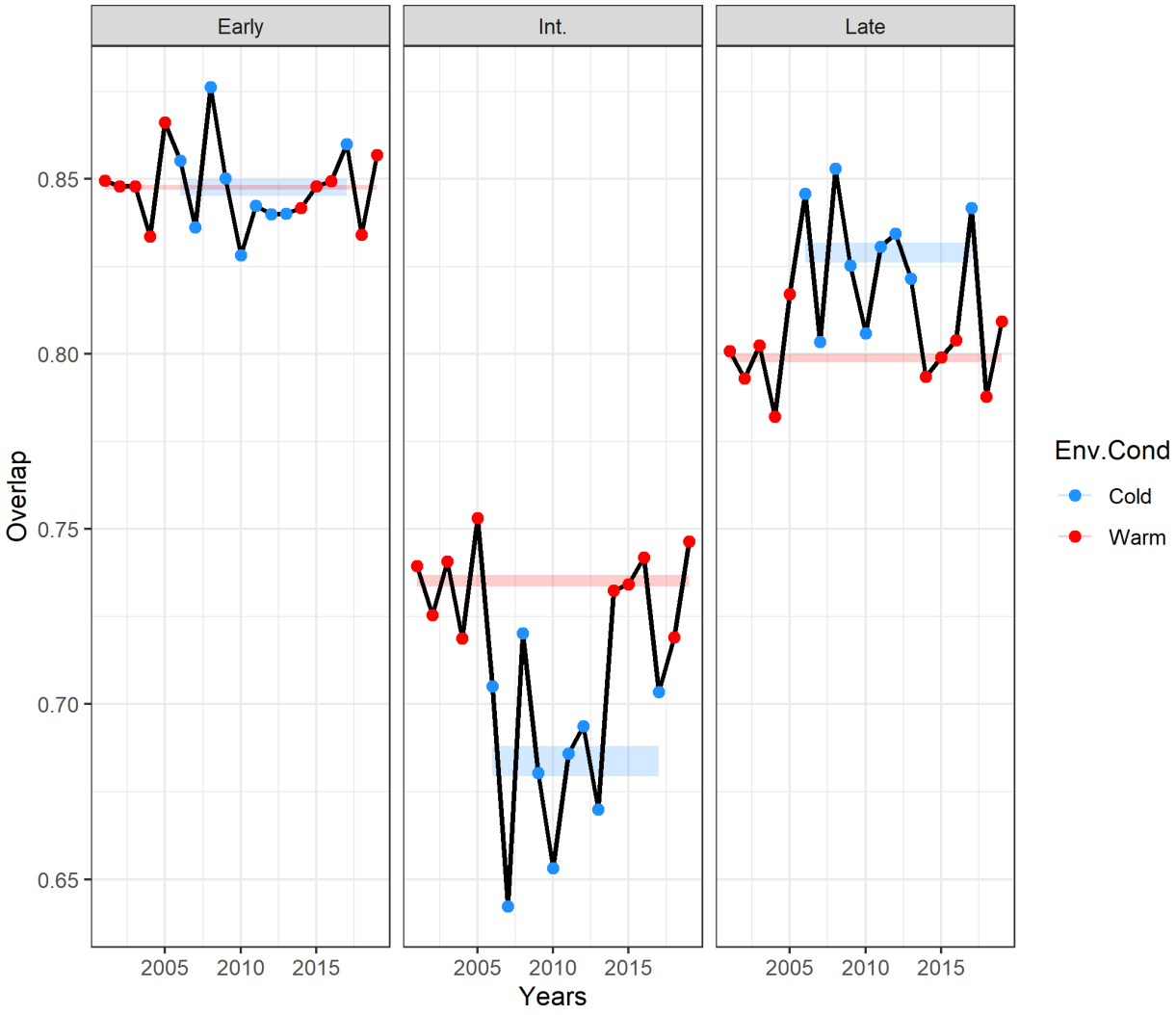


Figure 6: Time series of the overlap between spatial distribution of fishery CPUE biomass and survey spatial footprint during the different seasons (columns) Thick lines represent the averaged overlap across years (thickness of the line represents the standard deviation).

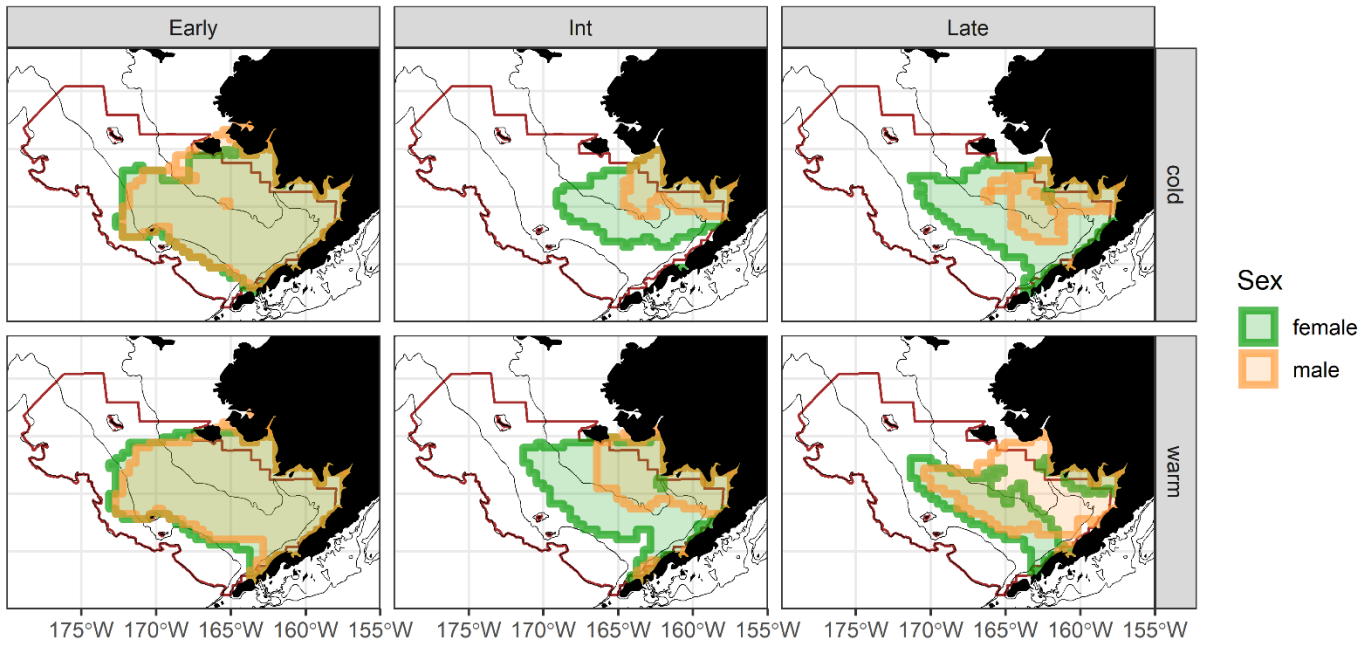


Figure 7: Mean seasonal spatial biomass distribution of yellowfin sole for cold years (1st row) and warm years (second row) for females and males. Green and orange polygons represent the cumulative biomass including the 95% of the total biomass across the entire spatial area for females and males respectively and for each season. Brown polygon represents the survey area.

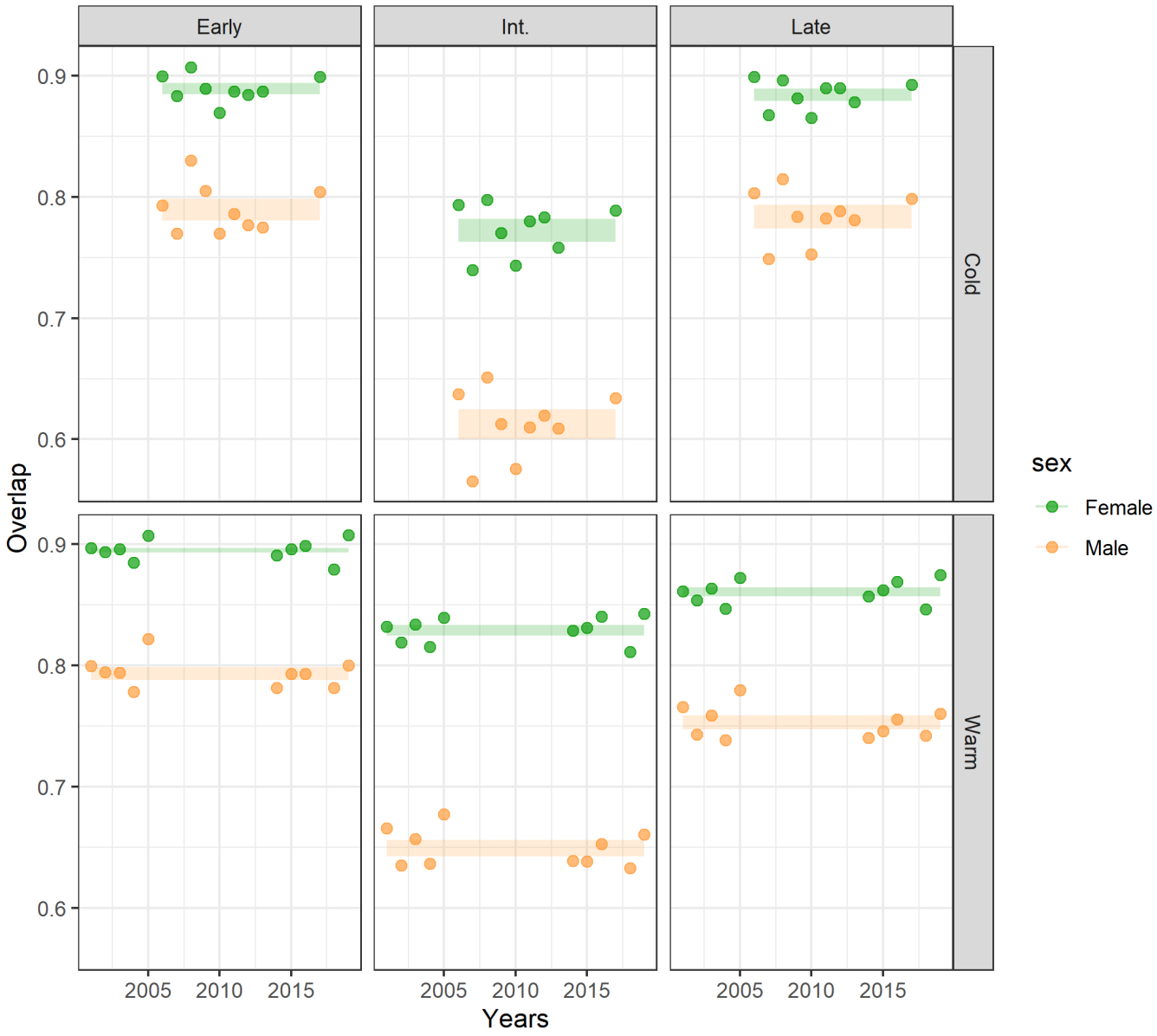
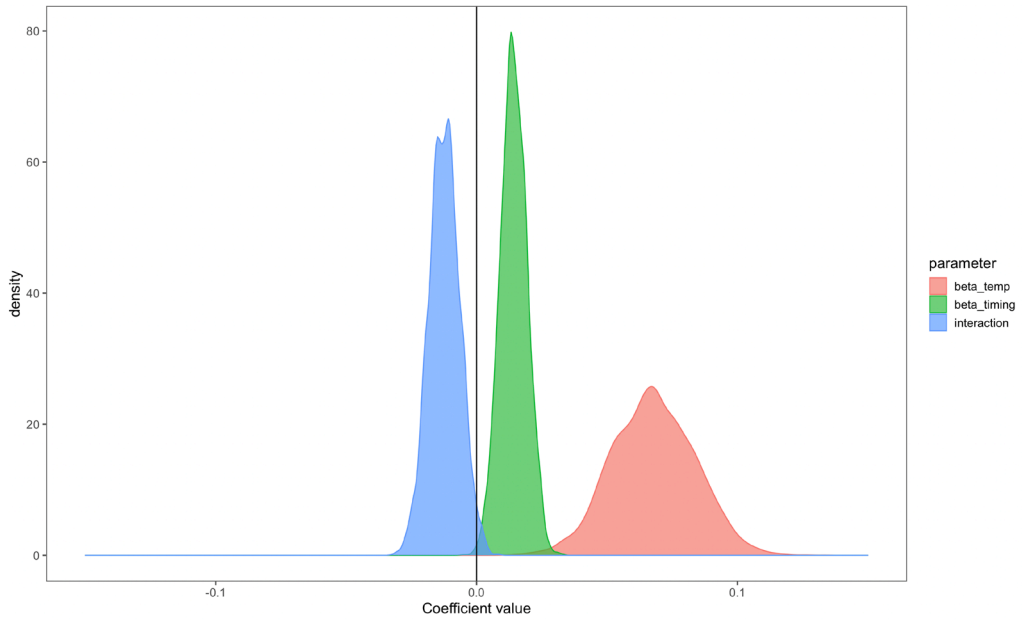


Figure 8: Time series between spatial distribution of fishery CPUE biomass and survey spatial footprint for females (orange) and males (green) during the different seasons (columns) and in cold and warm years (rows). Thick lines represent the average overlap across years (thickness of the line represent the standard deviation).

a)



b)

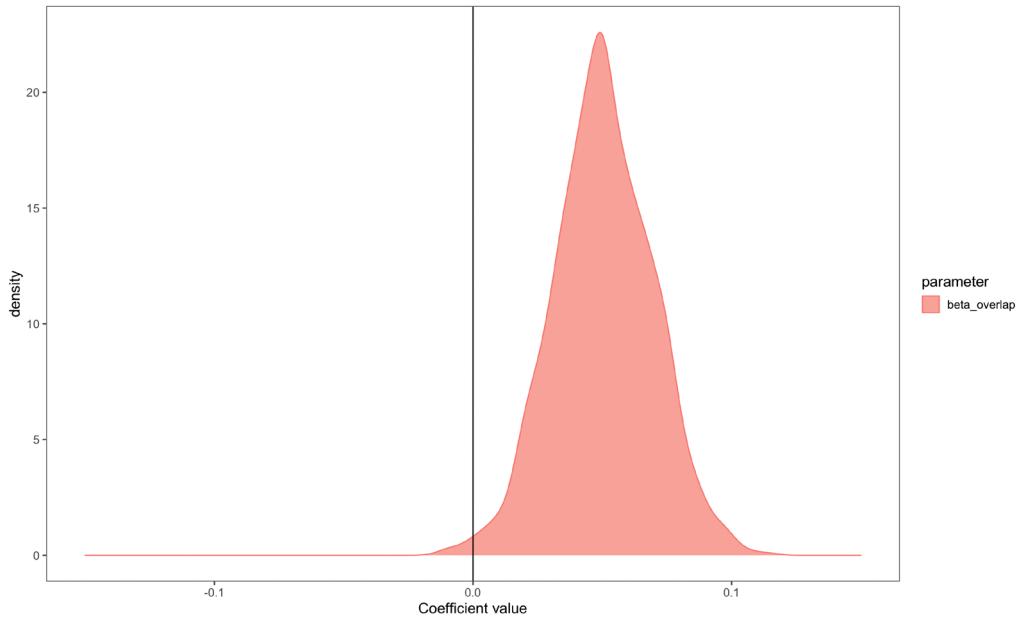


Figure 9: Posterior densities of coefficients as estimated from the stock assessment model (Spies et al. 2021) for model SAM.1 (panel a), and for the new overlap index, SAM.2, "beta_overlap" (panel b). These coefficients affect survey catchability (availability) applied to zero-centered anomalies.

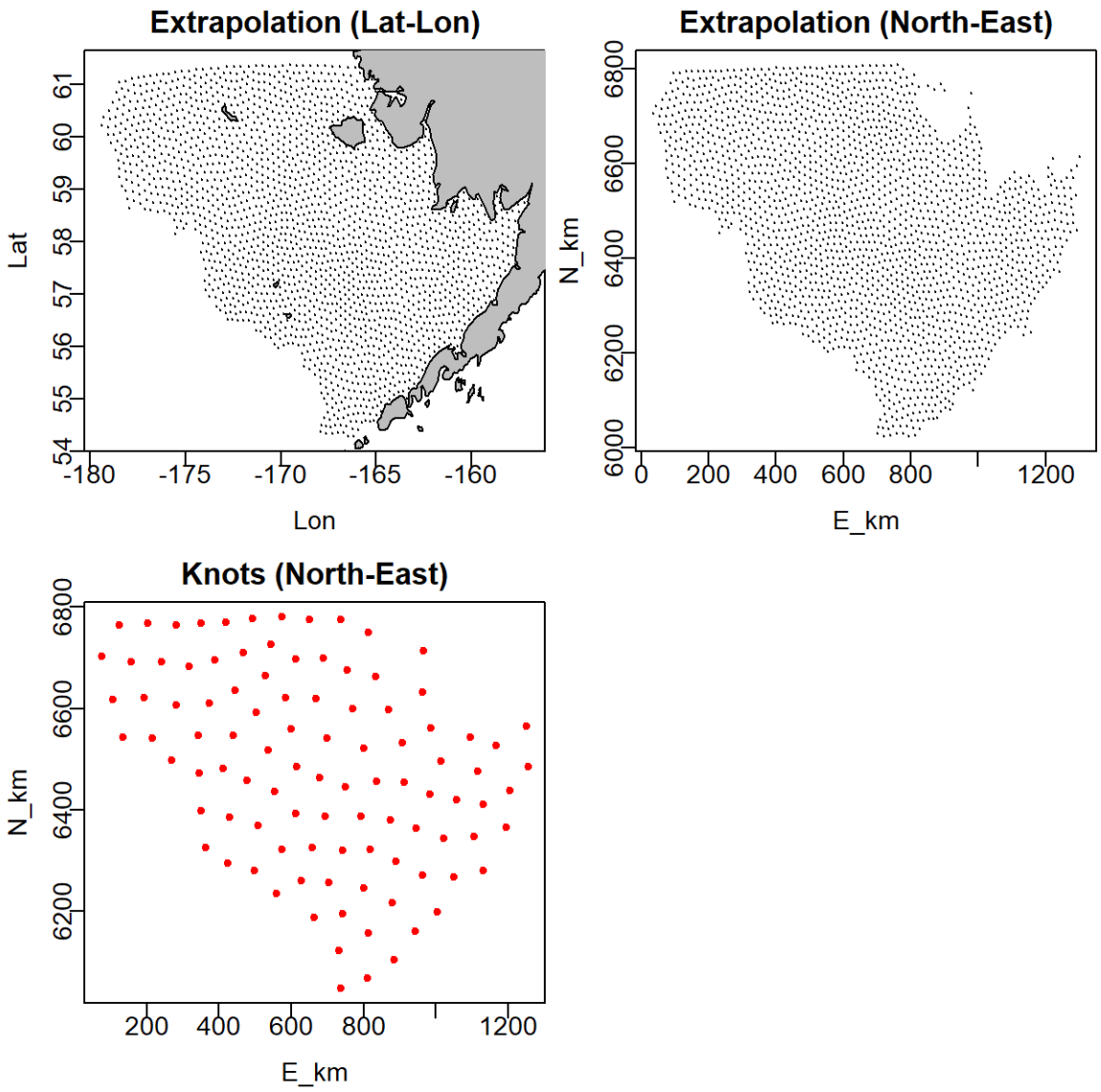


Figure S1: Spatial resolution of the study. Extrapolation grid and spatial distribution of the knots.

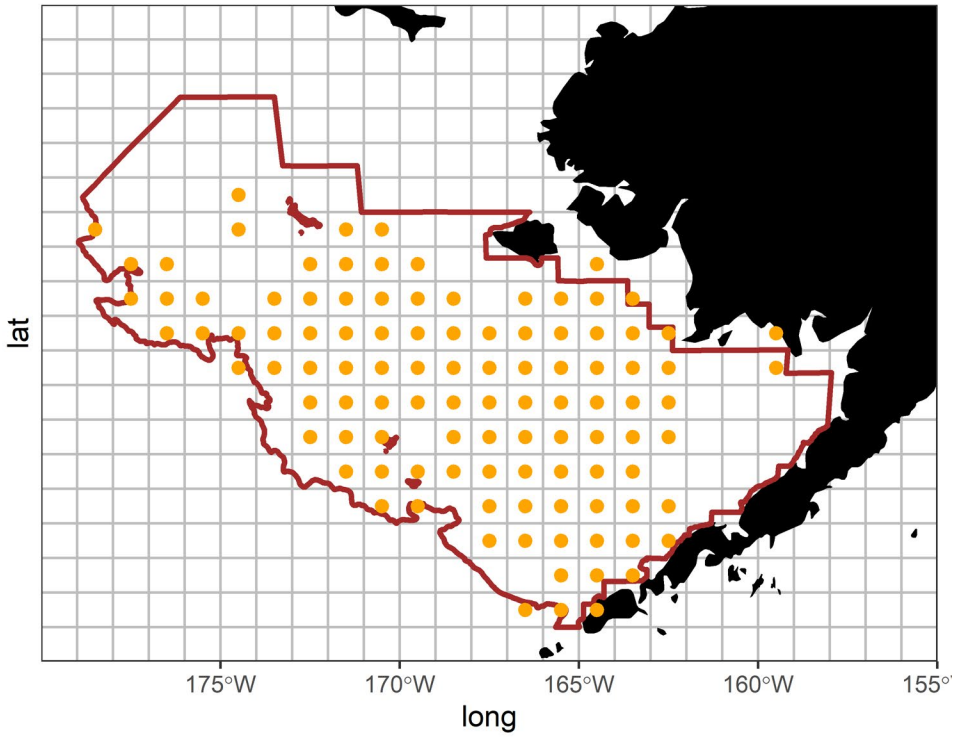
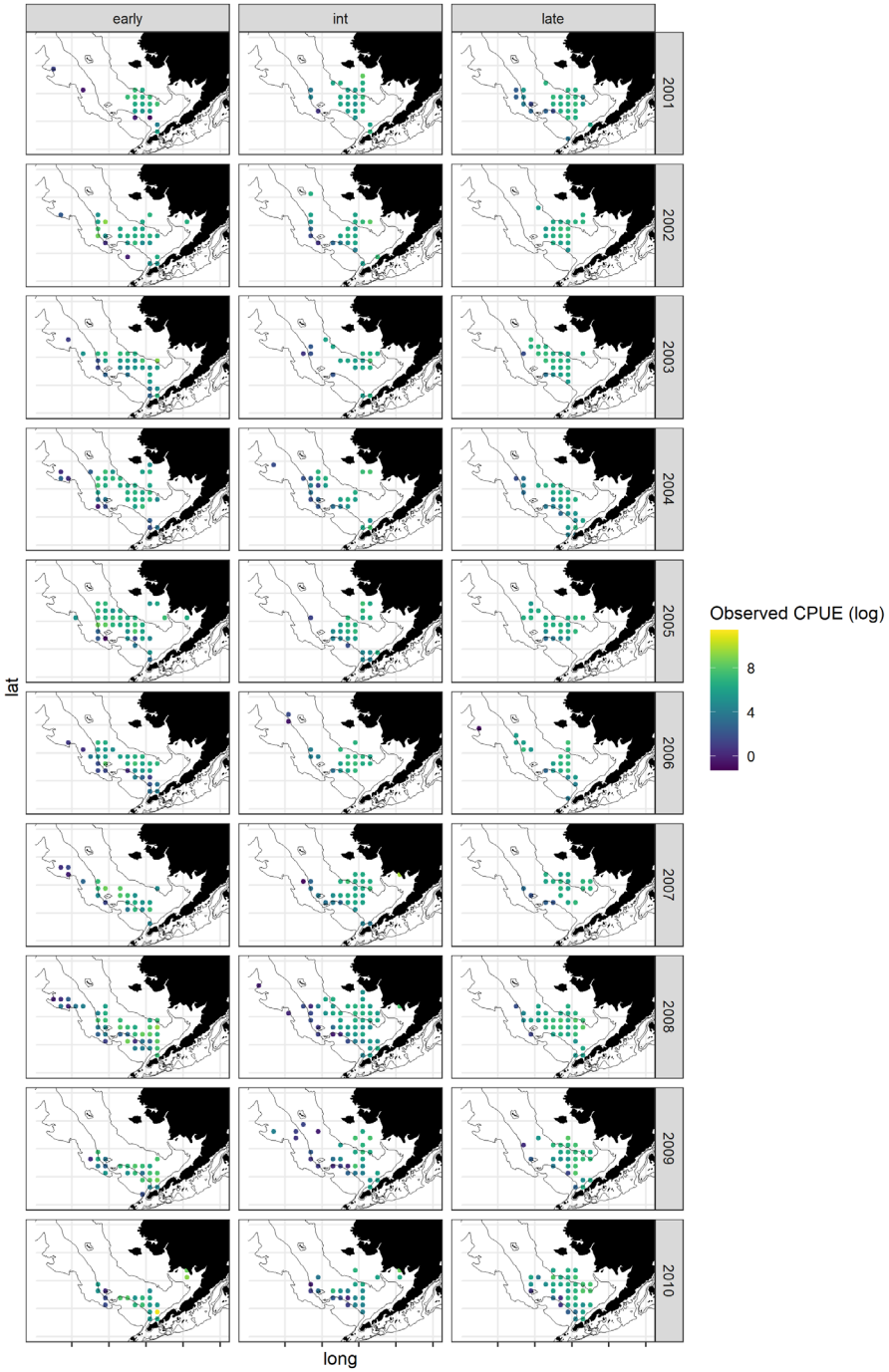


Figure S2: Spatial resolution of data. Grid represents the ADFG cells. Brown polygon is the survey area. And orange dots are the location of fisheries CPUE (2001-2019)


early
int
late
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
lat
long
Observed CPUE (log)
8
4
0

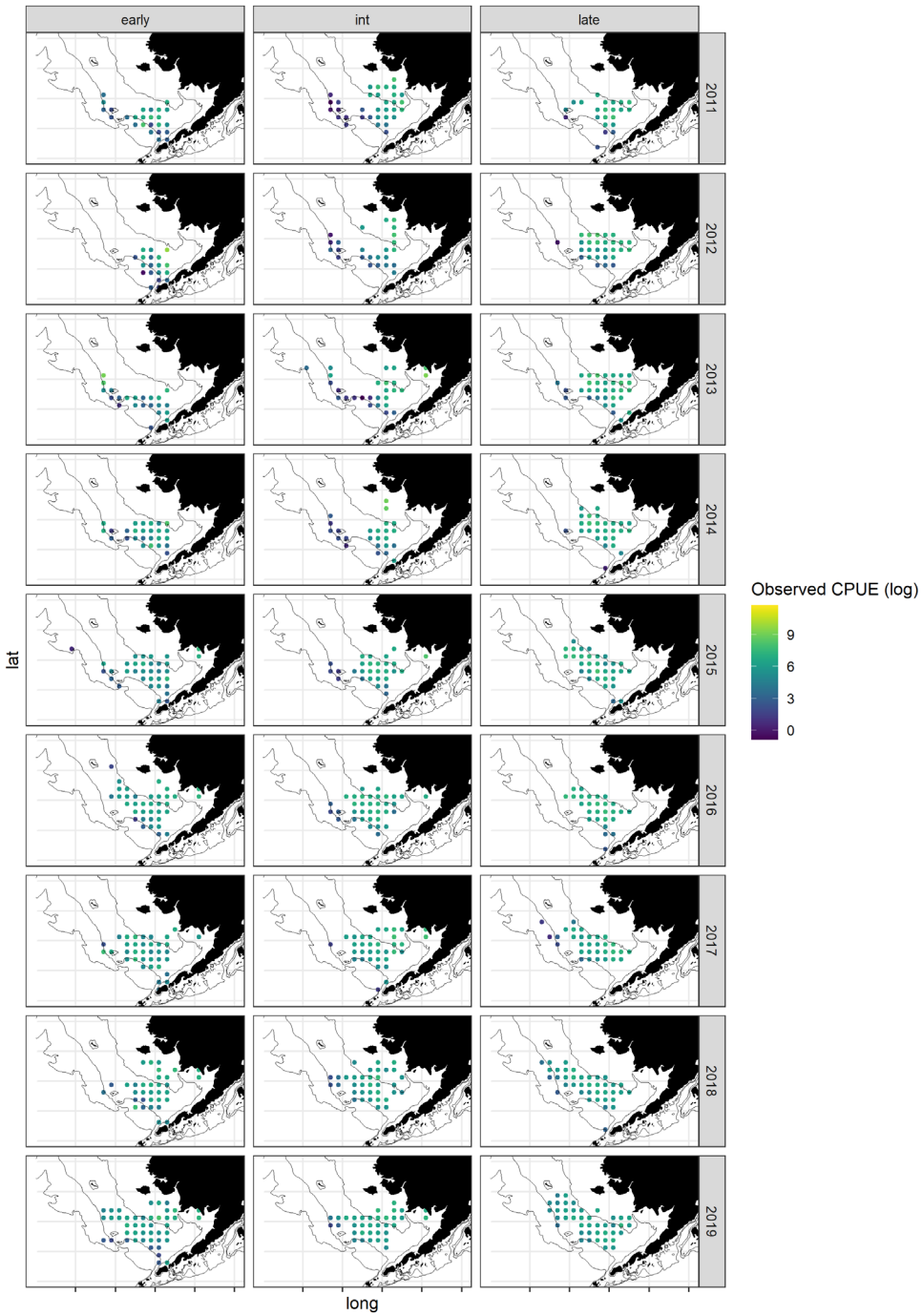


Figure S3: Spatiotemporal distributions of observed CPUE fisheries data

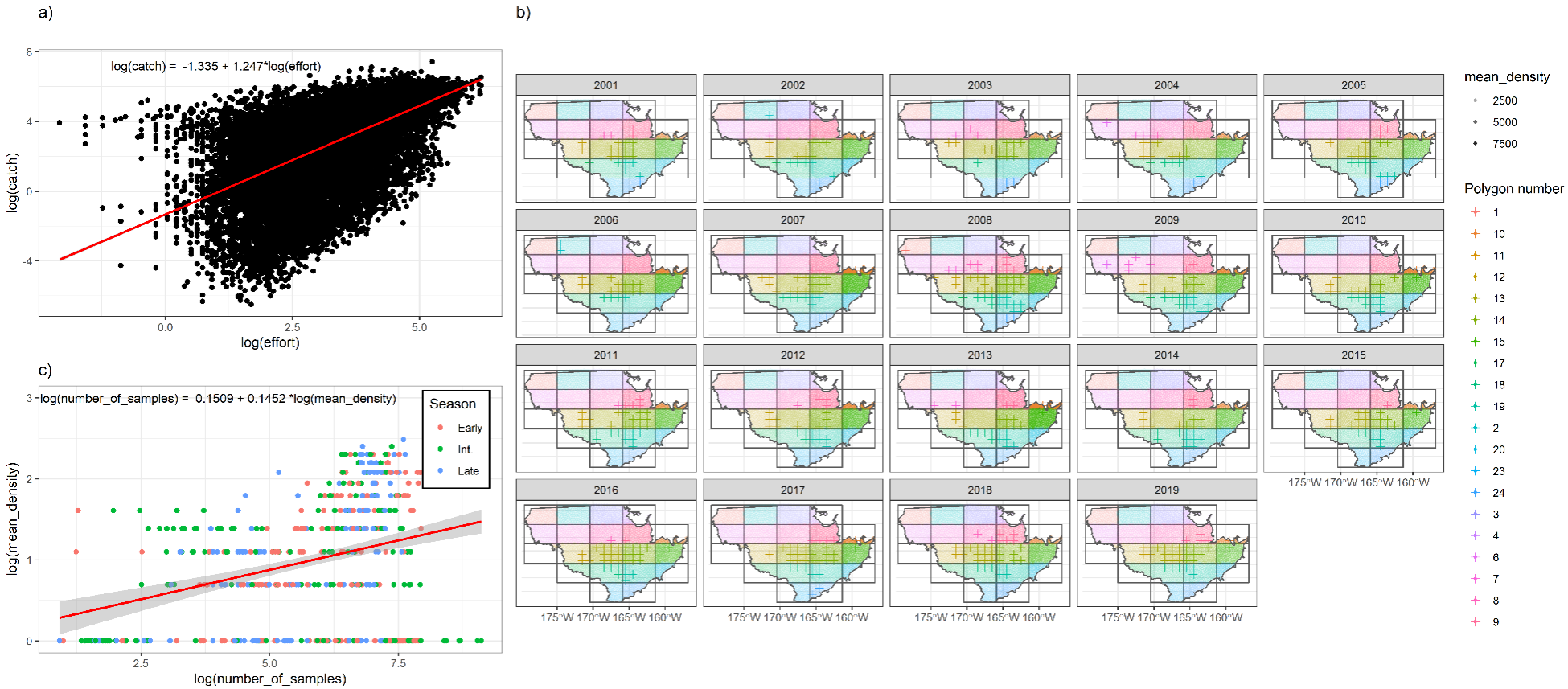


Figure S4: Diagnosis of any potential strong preferential sampling. a) Log-log plot between observed effort (sampling intensity) and observed catches. b) and c) aim at investigating any potential strong preferential sampling using predicted quantities by the model. b) For each season (here only intermediate season is represented), we divided the study area into a reduced number of 24 polygons (each polygon is associated with a specific color). Then for each season and year, we calculated the number of samples (represented by crosses) within each polygon and also we calculated the average predicted biomass within each polygon (low biomass are transparent and high biomass are plain colors). c) Log-log plot between number of samples and average biomass in each polygon for each season. A slope of 0.145 suggests a low sampling preference (based on Alglave et al. (2022)

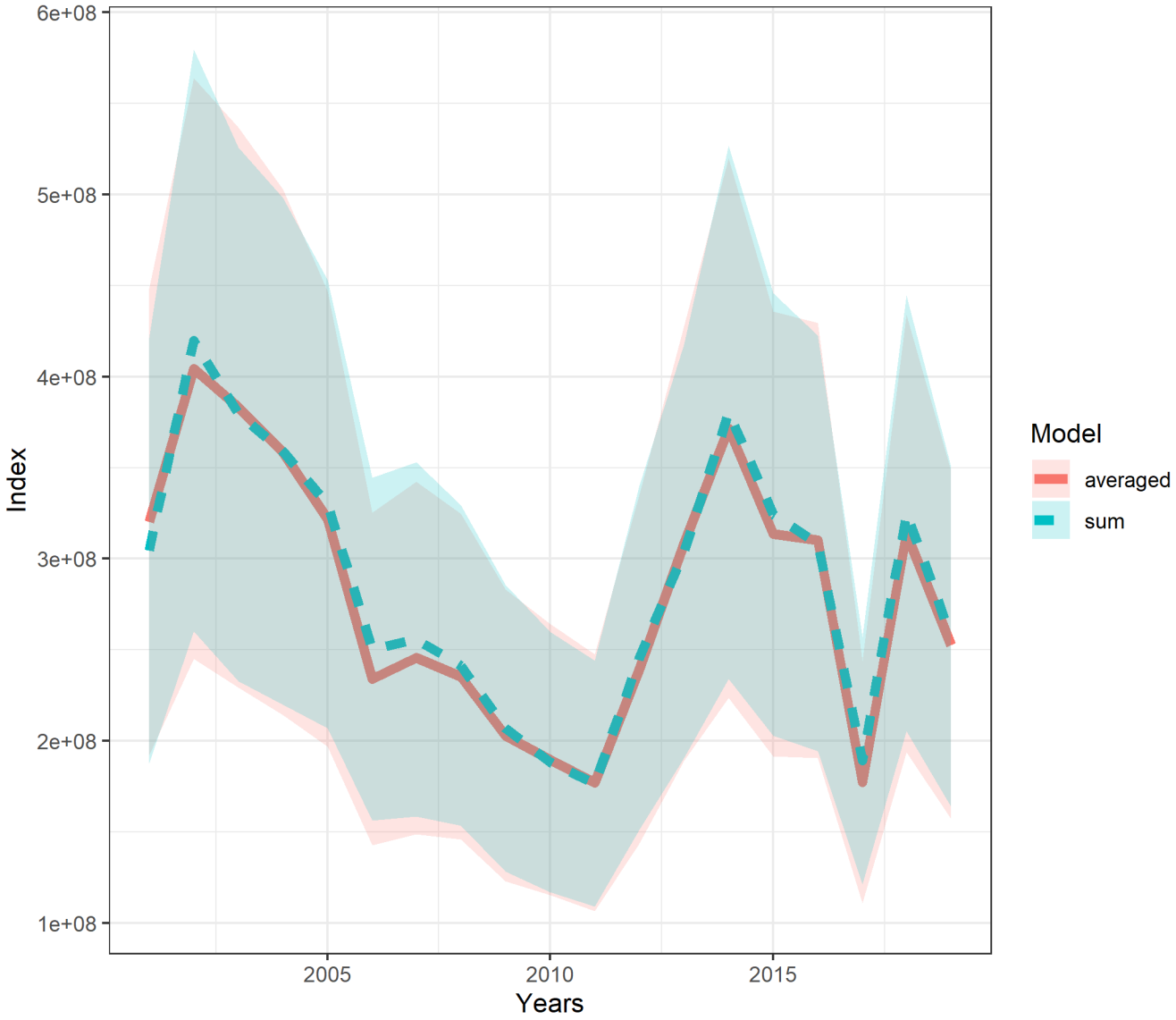


Figure S5: Comparison of index of biomass between models calculating CPUE as the ratio of the total catch in kg and the total effort within a ADFG cell (Model = sum) and as the ratio of catches in kg and effort averaged across ADFG (Model = averaged).

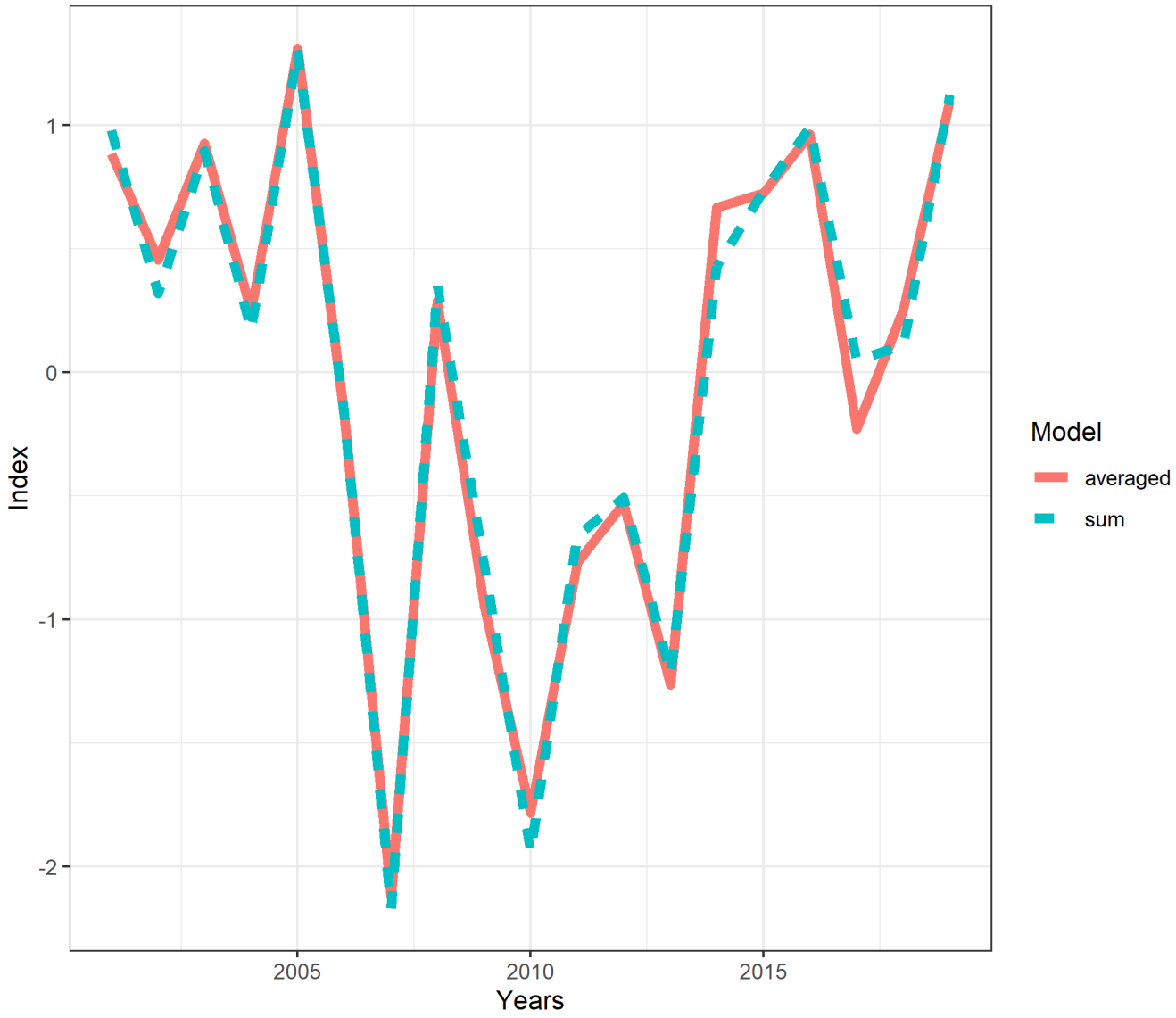


Figure S6: Comparison of overlap index of biomass between models calculating CPUE as the ratio of the total catch in kg and the total effort within a ADFG cell (Model = sum) and as the ratio of catches in kg and effort averaged across ADFG (Model = averaged).

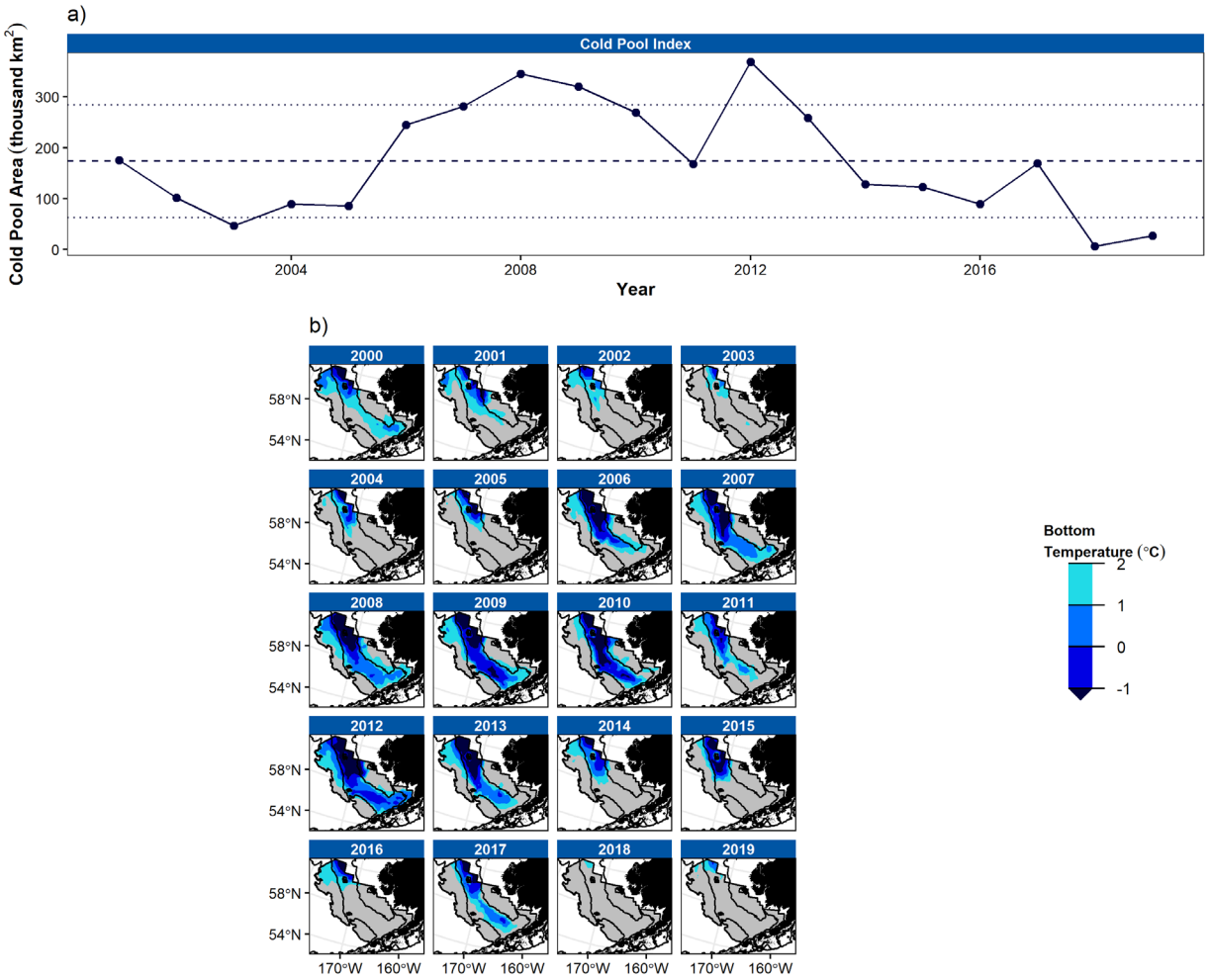
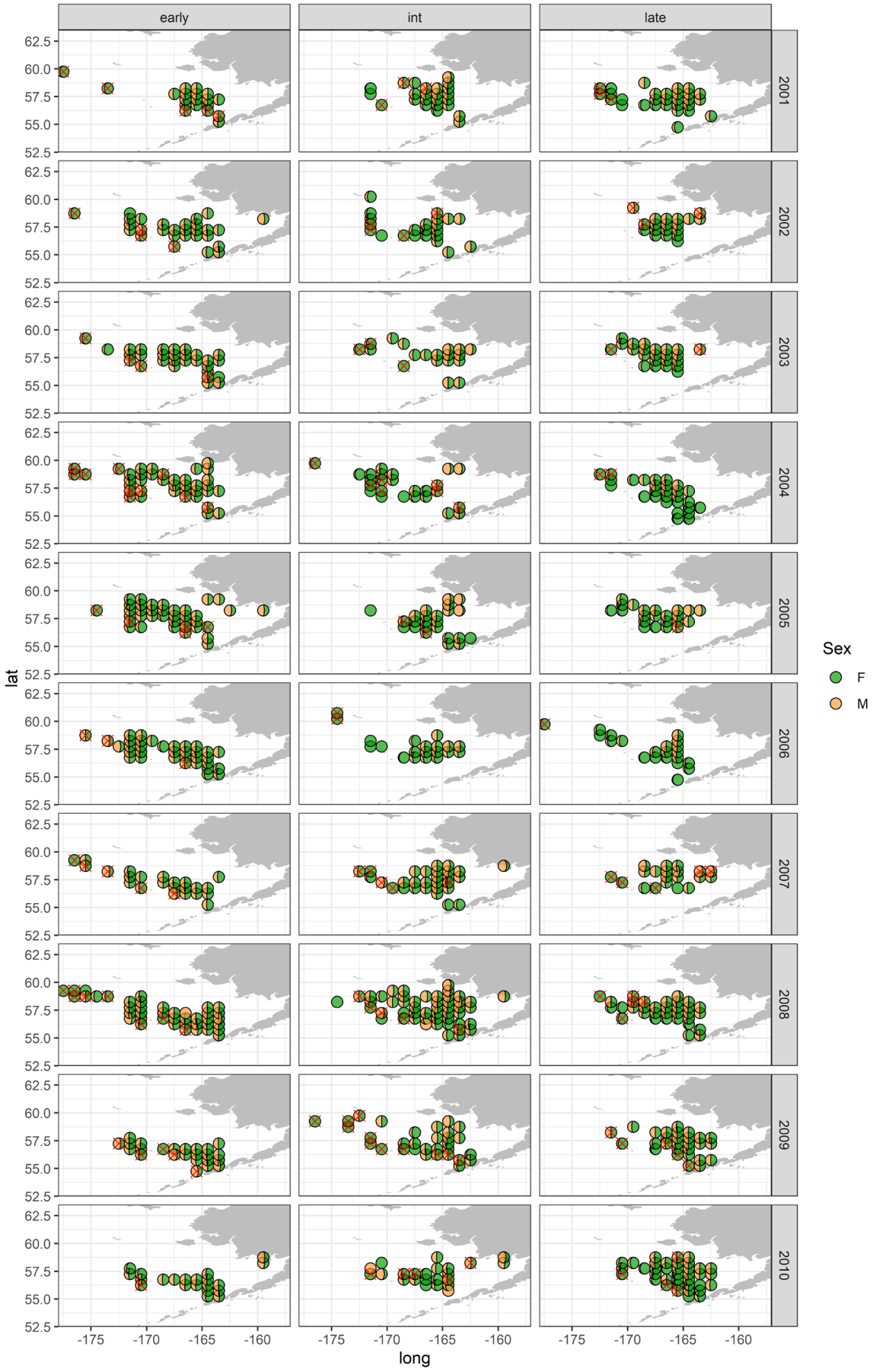


Figure S7: a) Standardized time series of cold pool extent (2001-2019). b) Spatial distribution of the cold pool (adapted from *akgfmaps* package (https://github.com/afsc-gap-products). According to Nichol et al., (2019) warm years are 2002,2003,2004,2005,2014,2015,2016 and cold years are 2006,2007,2008,2009,2010,2012,2013,2017. Years 2001, 2011 and 2017 are not particularly warm or cold (2018 and 2019 were not included in Nichol's study but can be defined as warm years). Because we did not want to define a supplementary level "Temperate" for the covariate *environmental conditions* (not enough data to have a balanced sampling with 3 levels for the covariate *environmental conditions*), we decided to define 2001 as a warm year and 2011 and 2017 as cold years. Indeed, yellowfin sole being a bottom fish, we considered that 2001 warmer than 2011 and 2017 because based on panel b) the extend of cold water (<1 C) is smaller for 2001 than for 2011 and 2017.


early
int
late
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
lat
long
62.5
60.0
57.5
55.0
52.5
-175
-170
-165
-160
Sex
F
M

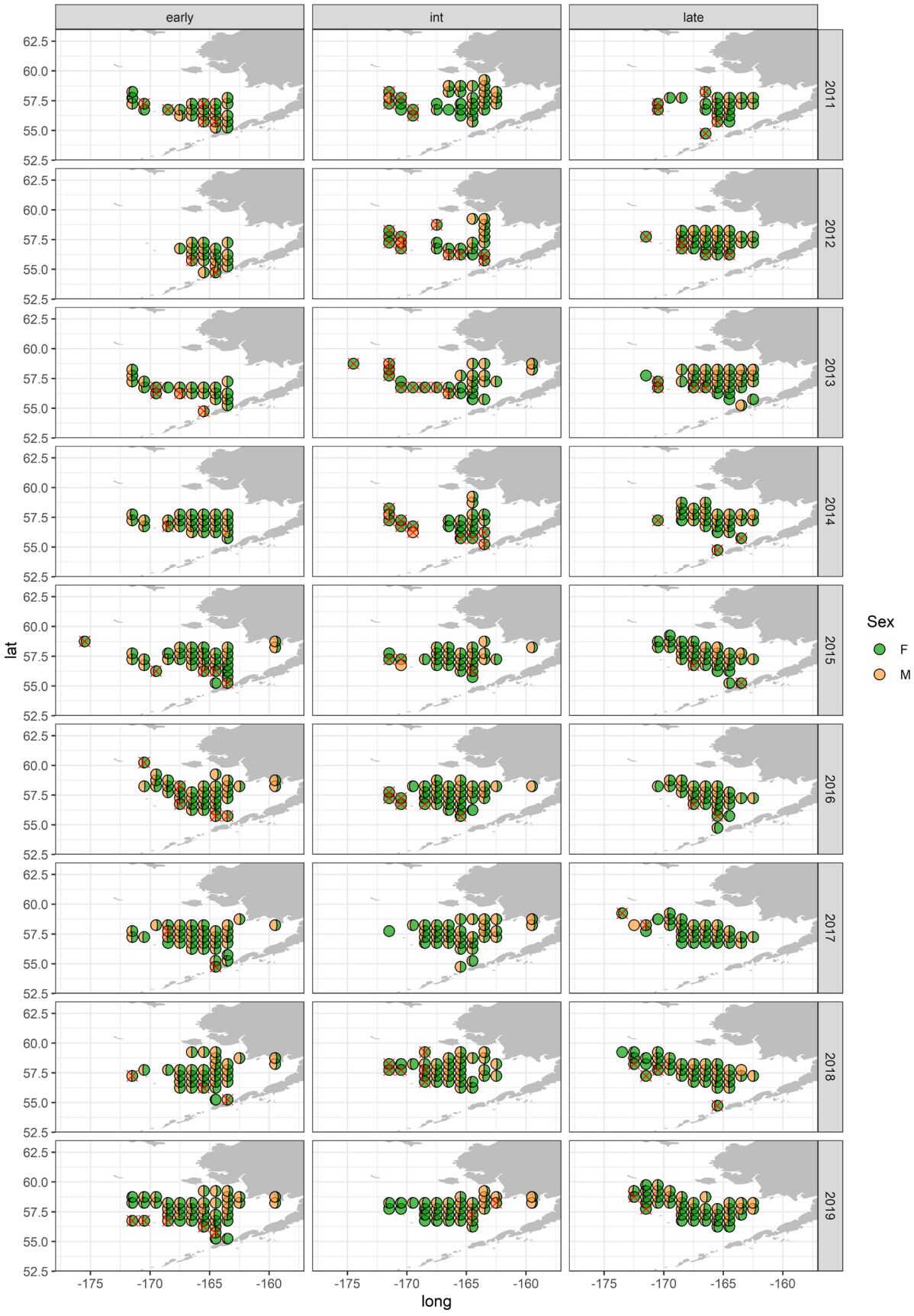


Figure S8: Spatiotemporal distribution of proportion of male and female CPUE (green=Female, orange=Male). Red cross represents locations were not data were available. We attributed to these locations the value of the closet neighbor for a given year and a given combination of covariates (i.e all combinations of levels constituting seasons and environmental covariates)

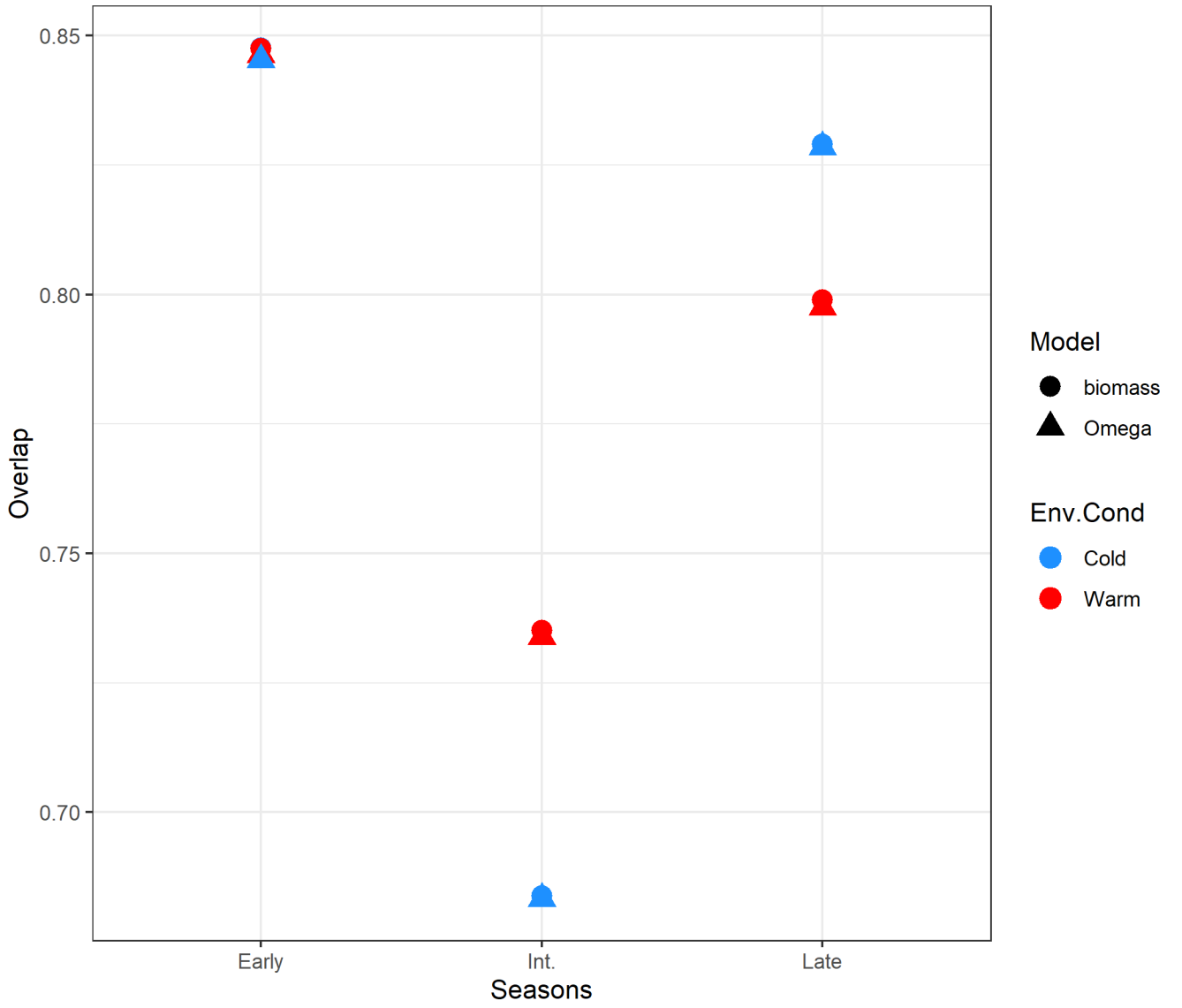


Figure S9: Comparison of averaged overlap among seasons and environmental conditions. Overlap was calculated from the predicted biomass (Model=biomass) or from the expected spatial main effect (model= Omega)

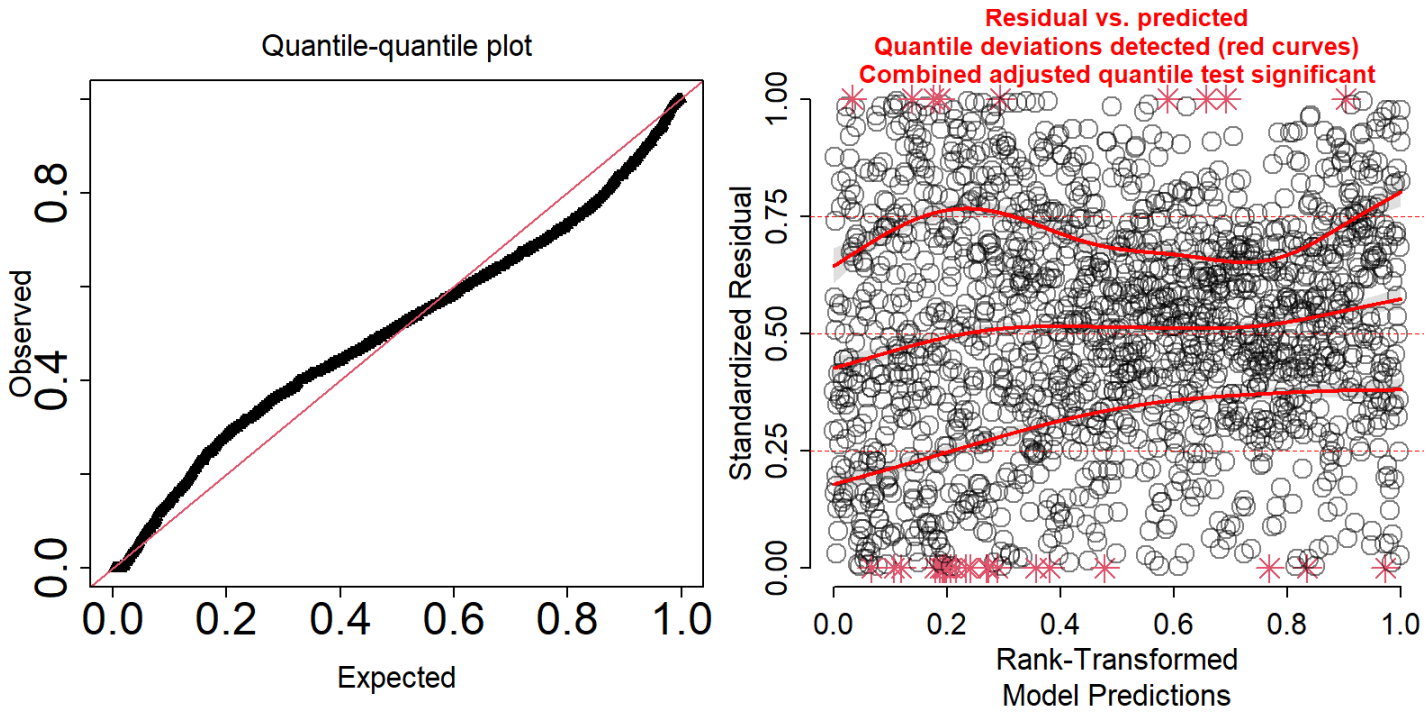


Figure S10 : Model diagnostics output showing the Q-Q plot residuals and how residuals vary with magnitude of the predications.

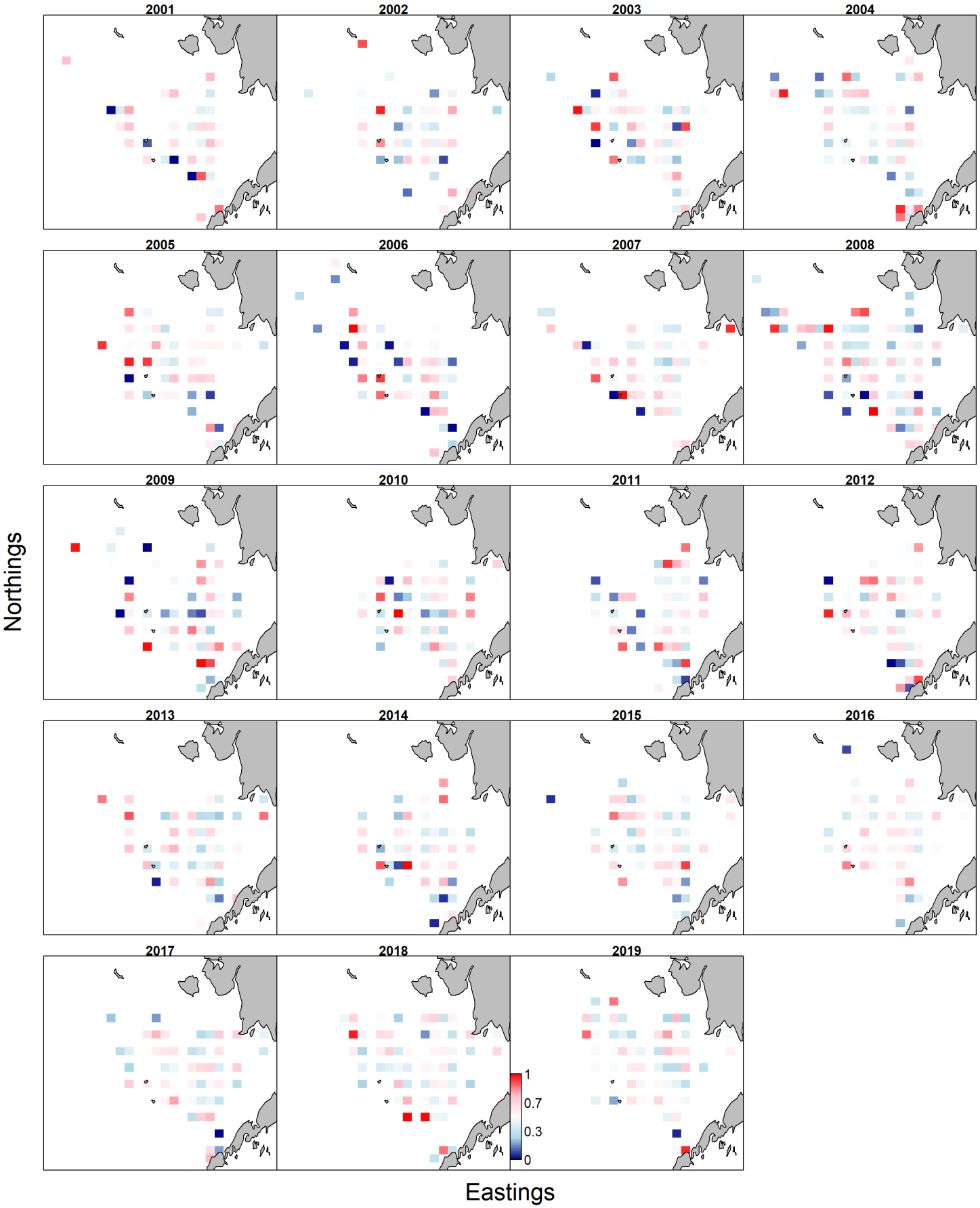
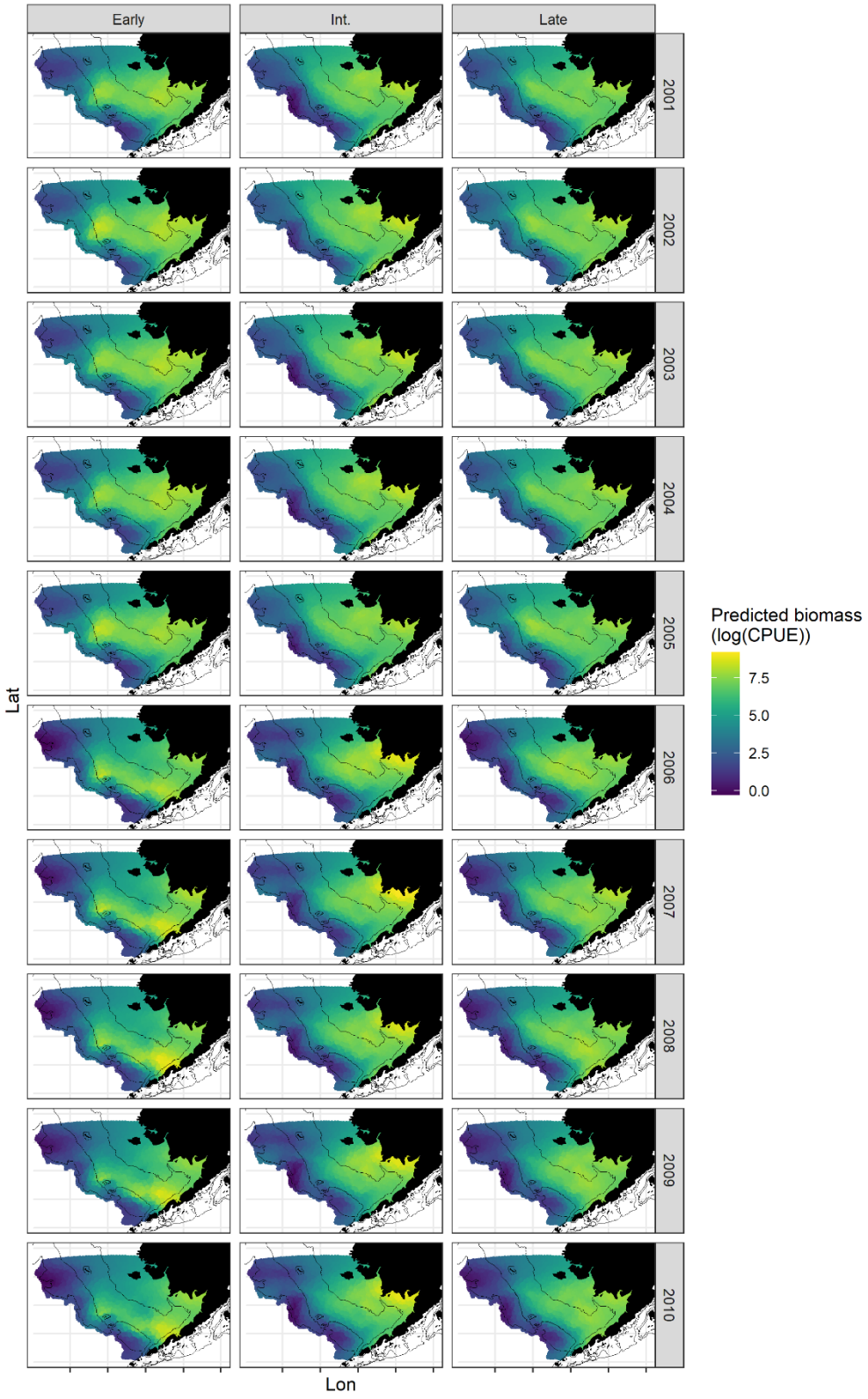


Figure S11 : Models diagnostics outputs showing spatial map of quantile residuals


Early
Int.
Late
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
Lat
Lon
Predicted biomass
(log(CPUE))
7.5
5.0
2.5
0.0

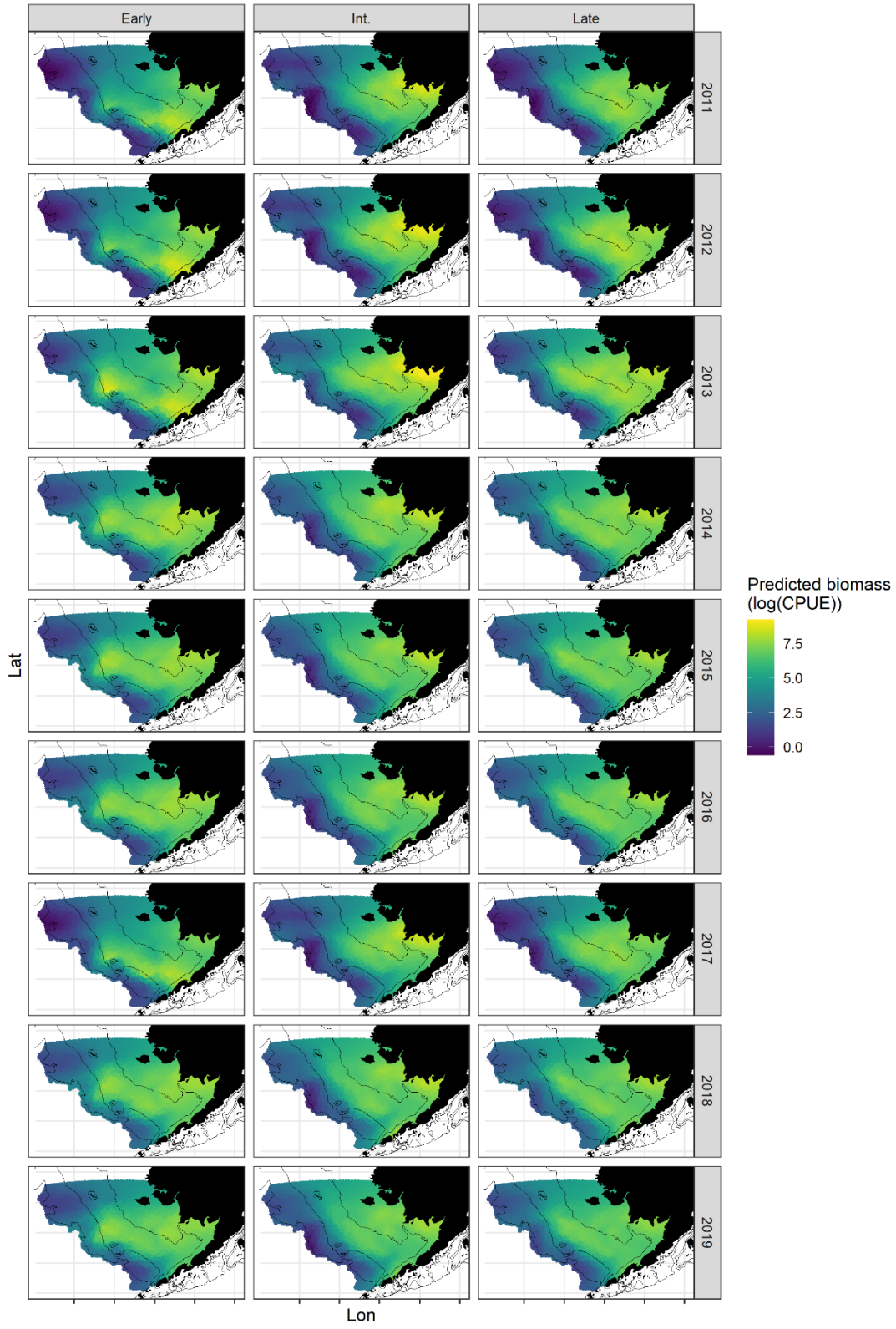


Figure S12: Seasonal spatiotemporal distribution of CPUE. Seasons are defined as Early, Intermediate (Int.) and late seasons).

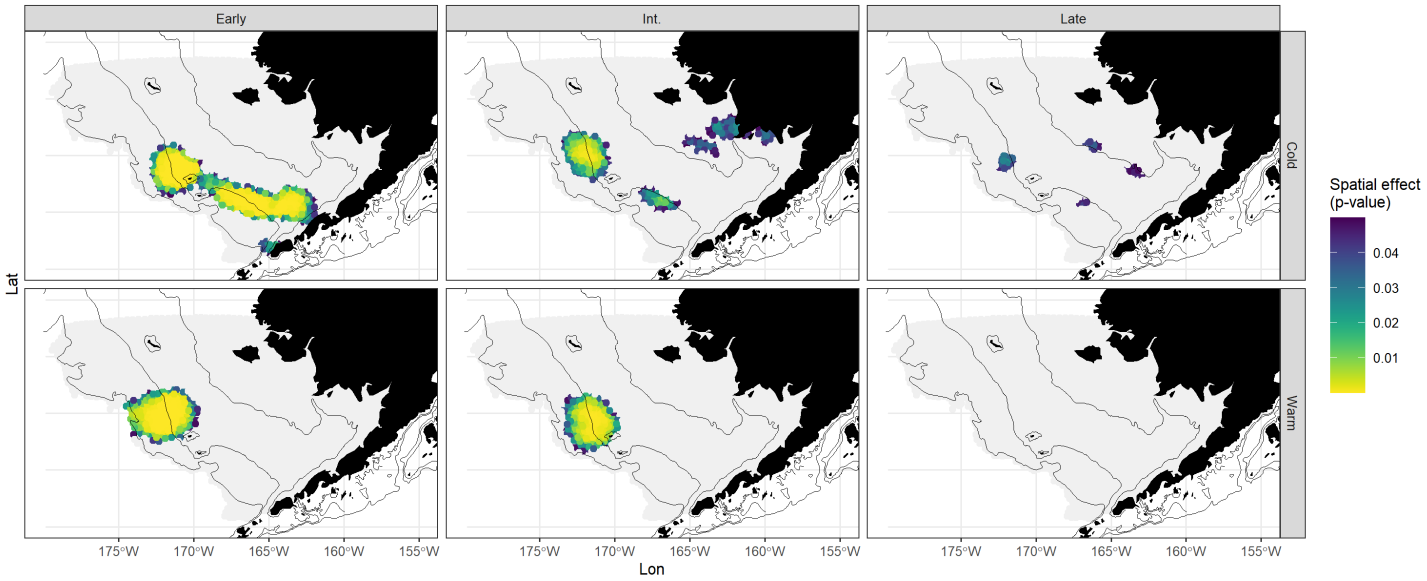


Figure S13: Significant effects of spatial variation covariate effects φ on fisheries CPUE

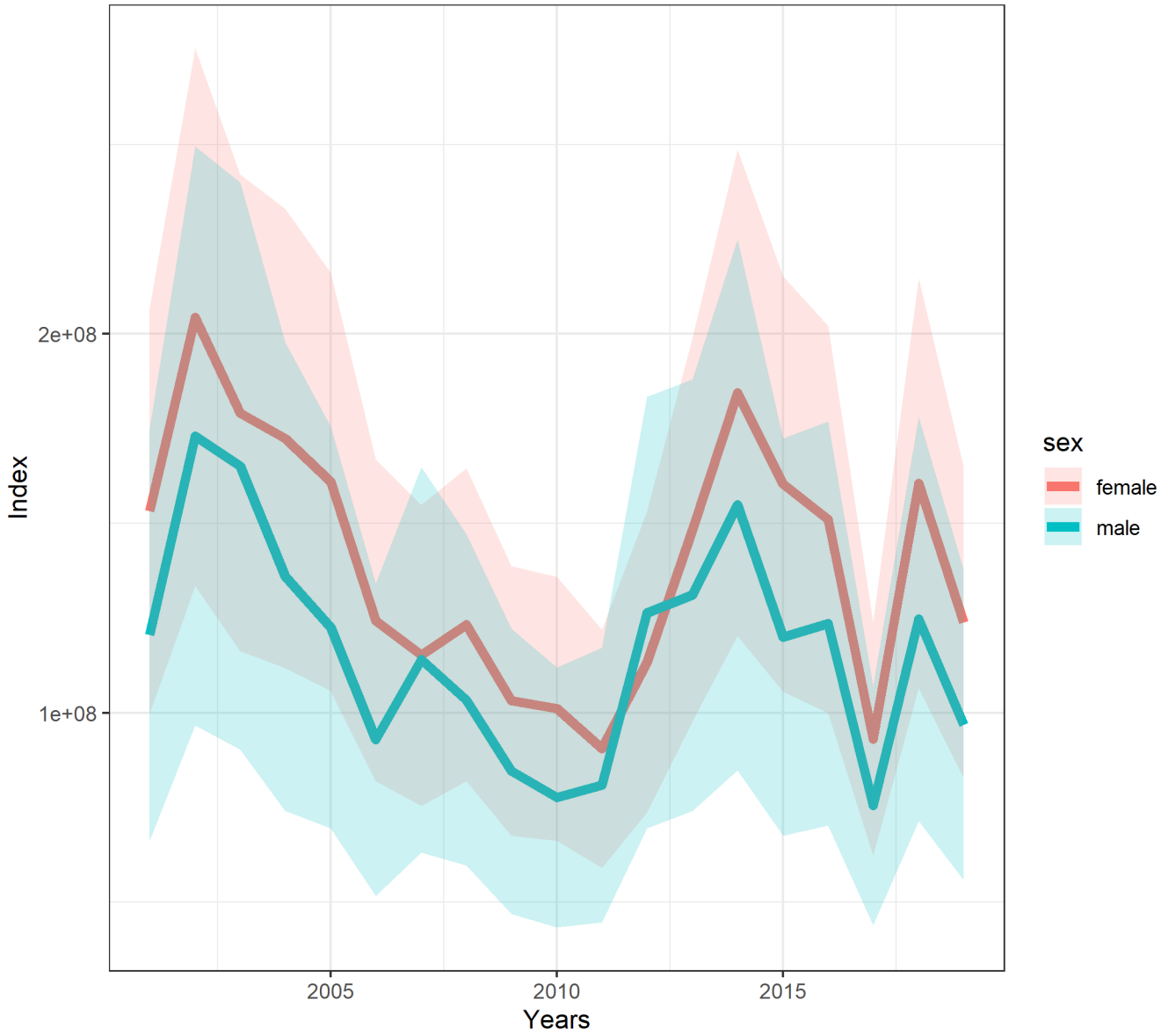


Figure S14: Time series of index of biomass for female and male yellowfin soles

S15: Comparing results using fishery dependent data to results from independent data

To justify that the ecological processes we are studying in this paper can be only inferred with fishery-dependent data and no fishery independent data, we also ran our analysis with fishery independent data as a sensitivity analysis.

Method

To this goal, we extended our approach by applying our model (Eq1.) to survey data for years 2001 to 2019. In particular, we represented the relationship among observed biomass (ratio of biomass and area swept) at time t_i at location s_i and the predicted positive local biomass (ratio of biomass and area swept) and the encounter probability using the widely used "Poisson-link" delta model (Thorson, 2018; Thorson & Barnett, 2017). We accounted for temperature effect only on the encounter probability because the goal of this study is to investigate how temperature affects movement phenology, i.e the presence of fish in a given area at a specific moment.

To sum up, in this new model:

- There is only one season (Intermediate Season, because no fishery independent data are available for the early and late seasons)
- We accounted for the effect of temperature (cold year vs warm years on survey CPUE) on biomass
- We used the same extrapolation grid (Fig.S1) that the one we used for the model with fishery dependent data. Using this extrapolation grid (that includes the fishery independent footprint and the area not available to the survey) we are able to show if the model with fishery independent data is able to infer the processes occurring outside the survey area.
- We finally re-generated Fig.5, Fig.6, and Fig.S13 to figure out if we can answer the questions addressed in this study.

Results

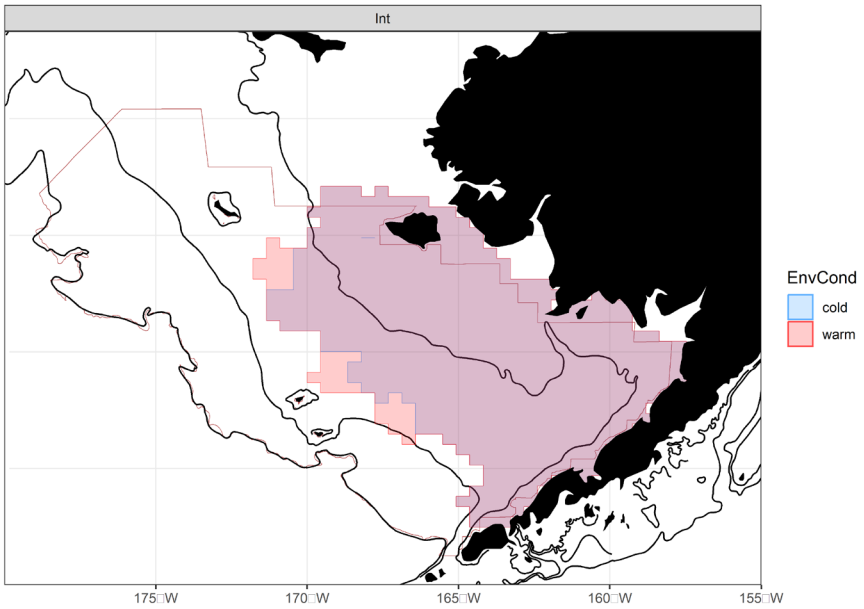


Figure S15.1: Spatial biomass distribution of yellowfin sole averaged for warm years (red) and cold years (blue). Red and blue polygons represent the cumulative biomass including 95% of the total biomass across the entire spatial area for warm and cold years respectively and for the Intermediate season (survey season). Brown polygon represents the survey area.

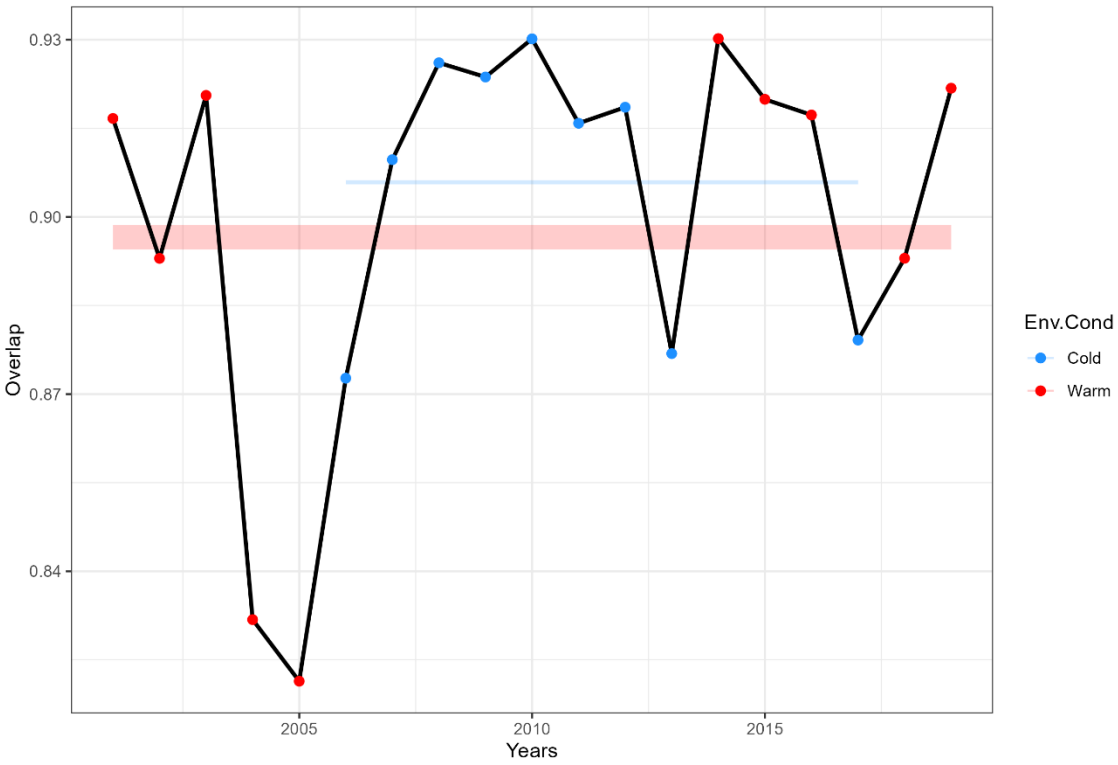


Figure S15.2 Time series of the overlap between spatial distribution of fishery CPUE biomass and survey spatial footprint during the intermediate season (survey season). Thick lines represent the averaged overlap across years (thickness of the line represent the standard deviation)

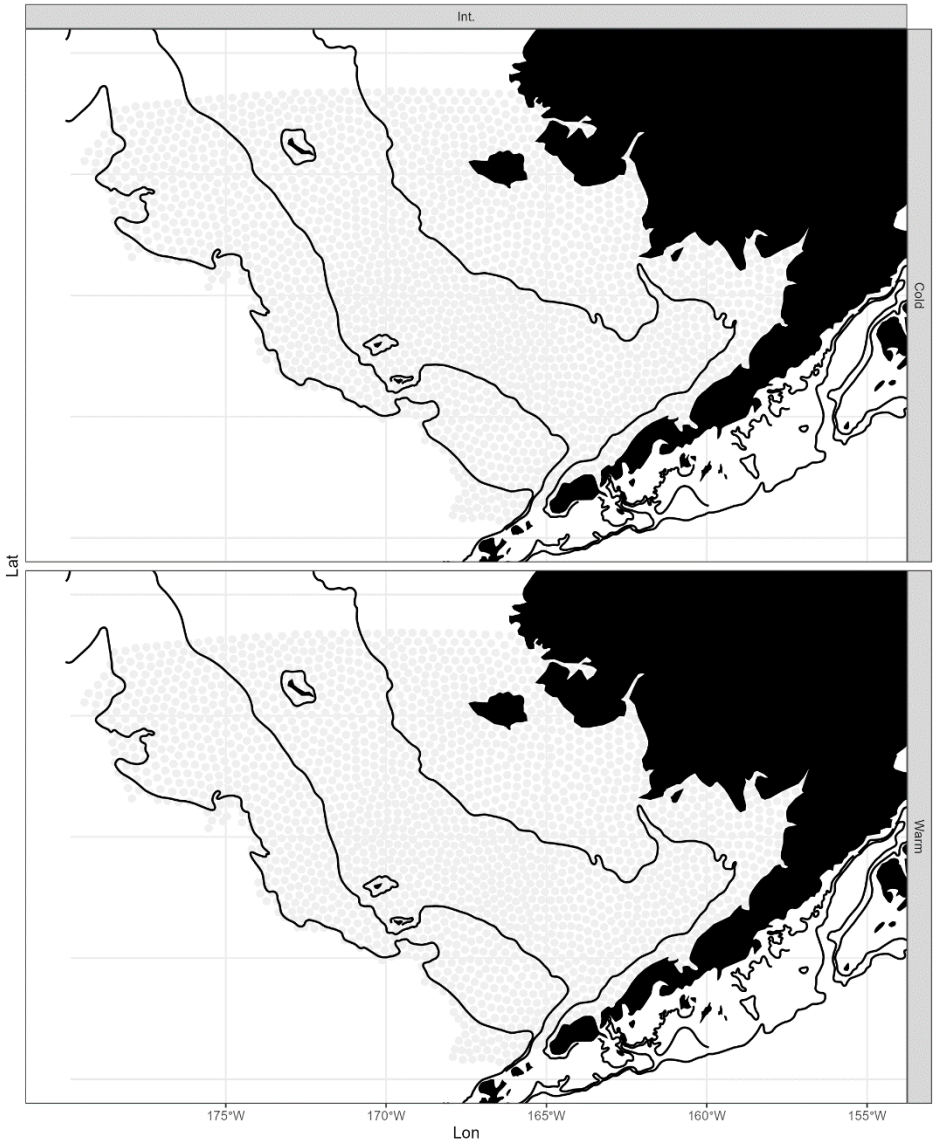


Figure S165.3: Significant effects of spatial variation covariate effects φ on survey data. Grey dots represent a non-significant effect.

First because survey data are only available during the intermediate season and are not defined across the all study area it is very difficult to infer changes in movement phenology based on those data. Then, this present sensitivity analysis justifies that the ecological processes we are investigating in this study can be only inferred with fishery-dependent data and no fishery independent data, and this because of three main reasons:

1. When using survey data, there is small differences in distributions of survey data between cold and warm years. In warm years the distributions of survey data are more spread out over the middle shelf (Fig S15.1). However, the model cannot predict any differences on the inner shelf (Fig S15.1), unlike the model using fishery data (Fig. 5).
2. Additionally, the model using survey data cannot infer any significative effect between temperature changes and survey biomass (Figure S15.3).
3. Predicting the survey biomass outside the survey area using VAST (i.e, autocorrelated function) did not provide any insight about the presence of fish outside the survey area (Fig. S15.2) because of the higher predictive uncertainty when predicting density in areas with zero observed data (Fig. S15.2).