Spatio-temporal dynamics of bluefin tuna (*Thunnus thynnus*) in US waters of the northwest Atlantic

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Abstract

Atlantic bluefin tuna (*Thunnus thynnus*) are large, highly migratory fish that support important fisheries. Oceanic conditions influence Atlantic bluefin tuna distribution and it has been hypothesized that stock distributions have shifted in recent years. Distributional shifts can affect regional availability and fleet catchability, introducing a potential bias in fisheries dependent data used for indexing population trends. We developed a vector auto-regressive spatio-temporal model (VAST) to estimate changes in bluefin tuna spatial distribution in US waters and created standardized indices of abundance for large (> 177 cm) and small size classes (≤ 177 cm) of fish. Local-scale environmental factors (sea surface temperature (SST), ocean depth) and regional-scale drivers (e.g., Atlantic Multidecadal Oscillation (AMO) and prey biomass) of spatial distribution were explored. Results indicated that from 1993 to 2020, spatial distribution of the larger size class was highly variable, but on average, the total estimated area occupied increased by 96 km^2/year and the center of gravity shifted 2 km/year north and 3 km/year east. Results were similar for the smaller size class fish with an average increase in area occupied of 71 km^2/year. The center of gravity shifted an average of 1 km/year north and 2 km/year east. The primary factor driving the spatial shifts for both large and small fish was local-scale SST. Standardized indices of abundance were produced and incorporated SST as a covariate of local density. In comparison to prior standardization results, spatio-temporal indices demonstrated less inter-annual variability and produced similar overall trends. This study advanced our understanding of bluefin tuna spatial distributions and generated indices of relative abundance in US waters of the Northwest Atlantic that are more robust to spatio-temporal changes in tuna distributions for consideration in future stock assessments.

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) are highly migratory fish with complex spatial and temporal distribution patterns. Their fisheries are assessed and managed as two distinct stocks (eastern and western) by the International Commission for the Conservation of Atlantic Tunas (ICCAT) with the management boundary at the 45º west meridian (ICCAT 2017, 2020; Kerr et al. 2020). For the western stock, conventional and electronic tagging data showed wide-ranging movements of bluefin tuna between feeding and spawning areas, with seasonal migrations observed between the northern U.S. and Canada to the Gulf of Mexico and back (Galuardi et al. 2010). In addition, extensive mixing of fish across the management boundary was documented (Block et al. 2005, Boustany et al. 2008), supported by evidence of catches in the West Atlantic fisheries containing large proportions of eastern Atlantic origin fish (Kerr et al. 2020). Further, ocean climate is known to be an important determinant of the distribution and dynamics of bluefin tuna (Humston et al. 2000, Schick et al. 2004, Golet et al. 2013, Druon et al. 2016) with substantial shifts in the spatial distribution of bluefin tuna being documented in response to changing ocean conditions (e.g., Golet et al. 2013, Fromentin et al. 2014, MacKenzie et al. 2014, Druon et al. 2016).

U.S. fisheries for Atlantic bluefin tuna operate in the northwest Atlantic, a productive foraging region for bluefin tuna. Substantial changes in oceanographic conditions have occurred in the region over the last two decades, including an increase in sea surface temperature at a rate that faster than most regions of the world's ocean (SST; Pershing et al., 2018). Coincident with these changes in fish habitat, are well documented poleward shifts in marine taxa distributions (Nye et al., 2009; Pinsky et al., 2013). It is hypothesized that similar spatial distribution shifts have occurred for bluefin tuna; however, the exact extent and drivers of bluefin tuna spatial distribution remain unknown (Walter, 2018). For other species, distribution shifts in the region have been attributed to local environmental variables (SST and depth); regional drivers (e.g., length of summer; Henderson et al. 2017); basin wide climate indices (e.g., AMO; Nye et al., 2009); prey distribution (Golet et al., 2013) and fishing effects (Adams et al., 2018). To identify the primary causes of distributional change, it is important that potential drivers are evaluated using a consistent framework, so that estimation models can accurately quantify the effect and variation attributed to the various factors (Thorson et al., 2017; Perretti and Thorson, 2019).

In the West Atlantic region, the recent stock assessments of bluefin tuna relied on two analytical models (i.e., Virtual Population Analysis and Stock Synthesis) that were fit to fishery dependent indices of abundance in the form of flag and fleet-specific catch-per-unit-effort (CPUE) time series (ICCAT, 2020).

The assessments were challenged by the need to resolve conflicting trends between U.S. and Canadian CPUE indices (ICCAT, 2017). Researchers hypothesized that conflicting trends resulted from bluefin tuna shifting northward away from U.S. fishing areas toward Canadian waters as a result of changing ocean conditions (Walter, 2018). Shifting spatial distributions can complicate the interpretation of data used in the stock assessment due to systematic change in fish availability to regional fishing fleets (i.e., time-varying catchability). The change in availability could be misinterpreted as a stock decline in regions where the fish have migrated away from, or stock abundance increase in the regions with increased fish availability or density (Wilberg et al. 2010, Link et al 2011). Stock assessment analysts explored several approaches to reconcile conflicting trends, and ultimately decided to incorporate the influence of an environmental covariate (i.e., Atlantic Multidecadal Oscillation) on catchability for U.S. and Canadian handline indices using Stock Synthesis. In contrast, the assessment team removed the U.S. and Canadian commercial handline indices from the Virtual Population Analysis, as divergent trends in the commercial fisheries could not be reconciled within the model (ICCAT 2020).

Currently, two standardized indices are produced from the U.S. handline (i.e., rod and reel) fisheries; one indexing smaller tuna (66-144 cm) caught by the recreational fishery and a second index of commercially-sold, large-sized fish (>177 cm). Standardization models applied to the fishery dependent data did not explicitly account for spatio-temporal changes, but attempted to account for spatial changes associated with thermal habitat characteristics by modeling SST as a covariate of fleet catchability (Hansell et al., 2021a; Lauretta et al., 2021). A potential problem with the approach is that SST may affect localized fish density or abundance, and if so, the approach may mask a trend in abundance and attribute the change in CPUE as a catchability effect.

Here, we applied a vector auto-regressive spatio-temporal model (VAST) to produce indices of Atlantic bluefin tuna relative abundance in U.S. waters for two size classes, large commercially-sized (> 177cm) and small tuna caught by the recreational fishing fleet (≤ 177 cm). We evaluated the extent to which spatial shifts in bluefin tuna distribution occurred, and whether these shifts can be attributed to local or regional oceanographic factors, or prey abundance. The influence of different environmental covariates was assessed to determine the effects of changes in fleet catchability versus local density. The results provided new insight into bluefin tuna spatial distribution in U.S. fishing areas and produced two indices of relative abundance that are expected to be more robust to spatio-temporal drivers of both fish availability and fleet catchability. We recommend that future stock assessments take into account these data improvements, as the CPUE series provide essential data on fishery and stock trends.

Methods

Fishery Data

The U.S. Large Pelagics Survey is a dockside survey of private vessel and charter boat captains who have just completed fishing trips directed at large pelagic species (Foster et al. 2008). The survey is conducted at public fishing access sites that are likely to be used by offshore anglers, and was primarily designed to collect detailed catch and effort data. For this study, analyses focused on trips that targeted bluefin with rod and reel from June to October and spent less than 24 hours fishing because this is when the majority of fishing occurs (Figure 1). Information collected by the survey included: date, fishing location (lat/lon), number of fishing lines in the water, hours fished, and catch by size category (Lauretta et al 2020; Table 1). Past CPUE standardizations did not incorporate young school (< 66 cm SFL) and small medium size classes (145-177 cm SFL). However, in this study all sizes of bluefin tuna were included in model development. For all model runs, bluefin tuna were aggregated into two size categories: 1) small (≤ 177 cm) and 2) large (> 177 cm).

Spatio-temporal model

VAST is a delta-model that separates catch into two components: 1) the probability of a positive catch, and 2) the positive catch rate. The probability of a positive catch observation was estimated using a logit-linked linear predictor. Several alternative probability distributions were explored for the second component that modeled the catch rate on positive (at least one bluefin tuna was caught) fishing trips, including Poisson, negative binomial, gamma, log-normal models.

Probability of a bluefin tuna observation:

$$logit^{-1}\left(P_{1,i}\right) = \beta_1(t_i, c_i) + \omega_1(s_i, c_i) + \varepsilon_1\left(s_{i,}, c_i, t_i\right) + \sum_{j=1}^{n_j} \lambda_1(j, c_i) x(j, s_i, t_i) Q(i, k_1)$$

Bluefin tuna catch rate on positive trips:

$$log\left(P_{2,i}\right) = \beta_2(t_i, c_i) + \omega_2(s_i, c_i) + \varepsilon_2\left(s_{i,}, c_i, t_i\right) + \sum_{j=1}^{n_j} \lambda_2(j, c_i) x(j, s_i, t_i) Q(i, k_2)$$

Where P_1 is the probability of positive catch, P_2 is the probability of the catch given the catch is positive,

$\beta(t_i)$ is the intercept for each year *t* and length-group *c* and is modeled as a random walk, $\omega(s_i)$ is a time-invariant spatial autocorrelated variation for knot *s* and length-group *c*, $\varepsilon(s_{i,}c_{i,}t_i)$ is a time-varying spatial-temporal autocorrelated variation for knot *s* and length-group *c* in year *t*, $\lambda(j, c_i)$ is the effect of covariate *j* on length group *c* , n_j is the number of covariates and $x(j, s_i, t_i)$ is the value of covariate *j* in knot *s* in year *t*, $Q(i, k)$ is the fixed effect estimates for catchability, and the integer subscripts denote the model component (1: presence/absence, 2: non-zero density) for observation *i*.

The spatial processes ($\omega_1(s_i, c_i)$; $\omega_2(s_i, c_i)$) were modeled as Gaussian Markov random fields with correlation over two spatial dimensions and among fish size (e.g., ≤ 177 or > 177 cm).

$$vec(\Omega_p) \sim GRF(0, R_p \otimes V_{wp})$$

Where Ω_p is a matrix composed of $\omega_2(s_i, c_i)$ at every knot *s* and length bin *c*, R_p is correlation between knots, and V_{wp} is correlation between length bins.

$$V_{wp} = L_{wp} L_{wp}^T$$

Where L_{wp} is a matrix representing covariance among length bins. The spatial covariance between knots *s* and s^* was modeled as a Matern process.

$$R_p(s, s^*) = \frac{1}{2^{v-1} T(v)} (K_p H |\, s - s^*|)^v K_v (K_p H |\, s - s^*|)$$

Where *v* is a smoothness parameter that is fixed at 1, K_p controls the distance correlation and reduces to zero, K_v is a Bessel function and ***H*** is a two dimensional anisotropic distance function. The spatio-temporal processes ($\varepsilon_{1,2}(s_{i,}, c_i, t_i)$) were fit independently for each year, and were modeled with Gaussian Markov random fields assuming a Matern covariance.

In addition to catchability covariate effects, estimated values of the fixed and random effects predicted local density (*d*(*s*, *t*)) for knot *s* and length-group *c* in year *t*.

$$d(s, t) = logit^{-1}\left(\beta_1(t_i, c_i) + \omega_1(s_i, c_i) + \varepsilon_1(s_{i,}, c_i, t_i)\right) \times\ exp\left(\beta_2(t_i, c_i) + \omega_2(s_i, c_i) + \varepsilon_2(s_{i,}, c_i, t_i)\right)$$

The index of abundance (*B*(*t*)) is calculated as the sum of the density of each knot using an area weighted approach:

$$B(t) = \sum_{s=1}^{n_s} (a(s) \times d(s,t))$$

Where $B(t)$ is the area weighted density for each knot in year t throughout the specific domain, which in this study is Virginia to Maine and $a(s)$ is the area of knot s. A mesh approach (200 knots) which allows for anisotropy was used to fit the model. Parameter estimation used Template Model Builder (Kristensen et al. 2016) and the R program (R Core Team 2020). Model convergence was examined by ensuring the maximum gradient of the likelihood estimation was less than 0.0001 for all parameters and the Hessian matrix was positive definite.

Explanatory covariates

We explored local and regional covariates as drivers of catchability and density. Local covariates varied across space, while regional covariates were univariate and represented temporal changes affecting the stock. Number of fishing lines were explored as an influence on catchability, while local covariates, month, SST and depth were explored as drivers of catchability or density (Figure 2). Bathymetry data acquired from the marmap package in R (Pante and Simon-Bouchet, 2013) was used to estimate depth at each fishing location, while satellite-derived estimates of weekly mean SST were matched to each fishing event on a one-degree latitude by one-degree longitude scale (NOAA 2021a). All local covariates were fit with polynomial splines to allow for non-linear relationships, which are common in ecological data. The optimal number of knots used to fit each polynomial spline was determined automatically by the *Splines2* package in R, which accounts for degrees of freedom and the quantiles of the explanatory covariates (Wang 2021). Regional covariates were estimated as annual time series and included annual deviations in SST and prey abundance (Figure 3). Deviations in SST were estimated as the AMO index, matching the time series used in the last western bluefin tuna stock assessment, applied to large fish index analysis (ICCAT, 2020; Hansell et al. 2020). In characterizing prey abundance, we focused on a key prey of bluefin tuna, Atlantic herring. Atlantic herring biomass and estimates were obtained from the 2020 Atlantic herring stock assessment (Golet et al. 2013; NOAA, 2021b).

In VAST, estimated spatial random fields were expected to account for the changes in distribution over the time series and capture residual patterns that cannot be attributed to fixed effects (explanatory covariates). Thus, we used the approach to determine the importance of each variable in potential distribution shifts by setting the spatial effects of the model to zero and generating a time series of center-of-gravity estimates. The center-of-gravity estimates from the model without the random fields were then compared to the model with random fields to determine the amount of variation caused by each covariate; this process is referred to as counterfactual analysis (Pearl, 2009; Perretti and Thorson, 2019). Collinearity of covariates was examined using generalized variance-inflation factor (GVIF) scores. Any covariate with a score greater than three was removed, and the GVIFs were recalculated (Zuur, et al. 2012). For CPUE standardization, Akaike Information Criterion (AIC) scores were used to determine the best-fitting model. If AIC scores were within two units of one another, the most parsimonious model was selected (Burnham and Anderson, 2004). AIC was used to determine if a covariate improved model information content as an index for catchability versus density.

Results

CPUE was measured as the number of fish caught per hour (catch/hour; Table S1). A gamma probability function was selected to model the distribution of positive catch rates. All models using CPUE and gamma distributions converged and diagnostics suggested no major issues with model performance occurred. SST and month were collinear; therefore, month was excluded from model runs (Figure S1 – S4; Table S2 & S3).

A model fit with all local and regional environmental covariates suggested that from 1993 to 2020, large fish spatial distributions varied notably; however, on average, the area of occupancy increased by 96.4 km^2/year, and the center of gravity shifted north and east at an average rate of 2.3 km/year and 3 km/year (Figure 4;6-7). We observed similar patterns for small fish distributions with the area of occupancy increasing on average 70.6 km^2/year, and the center of gravity shifting north and east at an average rate of 1.1 km/year and 1.7 km/year (Figure 5-7). Counterfactual analysis suggested that the covariates in the model accounted for the majority of observed spatial distribution deviations (Figure 8). Sensitivity runs suggested that SST was the primary driver of observed spatial distribution shifts, with depth, AMO, and herring abundance having considerably less influence (Figure 9).

The best-fit model, as determined by AIC, included SST as a covariate for density (Table 2). Estimated indices of bluefin tuna abundance, from the best fit model, showed variability throughout the time series for both large and small size classes; however, an increased trend in the large fish index was clear after 2013 (Figure 10). Compared to the conventional index, the large fish index from VAST produced a lower abundance estimate in the 1990’s and early 2000’s while producing higher estimates from 2004 to 2010. The small fish index from VAST produced lower abundance estimates at the beginning and end of the time series (Figure 10).

Discussion:

The VAST model provided a single integrated spatio-temporal framework to examine the spatial distribution changes of bluefin tuna and estimate indices of relative abundance by size. VAST estimated that the area of occupancy increased over the entire time period and the center of gravity shifted northeast for both large and small bluefin. These results confirm previous hypotheses that the population of bluefin tuna has shifted northward away from U.S. fishing areas towards Canadian waters (Walter et al. 2018; Hansell et al. 2020).

Understanding the underlying mechanisms of tuna spatial distributions is essential to account for changes in fish availability, particularly in terms of fisheries management and fleet catch allocations (Link et al. 2011). In this study, the primary driver of bluefin tuna distribution was local SST, which may have multiple influences on Atlantic bluefin tuna and their prey (Table 2; Figure 9). Previous work has demonstrated the importance SST plays in bluefin tuna habitat/distribution. Thus, it was not surprising our analyses estimated SST as an important driver of bluefin tuna spatial distribution (Teo et al. 2007; Schick et al. 2004; Golet et al 2013). Additionally, the North Atlantic has experienced substantial increases in SST in recent years and these increases have been linked to the northward shift of many taxa in the region (Nye et al. 2009; Pinsky et al. 2013). Our results corroborate those observed patterns for Atlantic bluefin tuna.

We expected herring abundance or the AMO index to have more of an effect on bluefin tuna distribution estimates, given previous work showing that both of these covariates are important in bluefin tuna distribution (Golet et al. 2013; Faillettaz et al. 2019). For herring, differences in this study could be the result of scale, because past studies have examined fine scale data while this study examined data at an annual time step (Golet et al. 2013). The lack of influence of the AMO in this study could be due to the short time series of data (1993-2020) evaluated. During this time period, the AMO was in a consistent warm phase (Figure 3). Additionally, in fitting the AMO as a climate indicator in the stock assessment, it was estimated to have a stronger relationship with Canadian indices then US indices. The differential effect on northern areas may be a factor contributing to a lack of estimated effect in the U.S. fishing areas (Hansell et al., 2020). Despite identifying the primary driver of spatial distribution change (SST) it is possible other environmental drivers (e.g., Atlantic Meridional Overturning Circulation), or prey species could be influencing bluefin distribution. Especially since bluefin tuna have complex migration patterns, are top predators with a diverse diet and the data in this study only focuses on a short seasonal window (June – October) when the fish are available to the fishery.

In the U.S., a reliable fisheries independent survey is not available for bluefin tuna and thus, this study relied on fisheries dependent data. In the absence of surveys, fisheries data is commonly used as an input to stock assessment; however, fishing locations are not chosen at random (Maunder and Punt, 2004). Thus, it was difficult to determine if spatial distribution shifts were related to changes in fish distribution or changes in fishing behavior.

Our results suggest that abundance of small fish in the area was highly variable from one year to the next, but abundance of large fish increased in recent years. These findings are consistent with previously developed indices of abundance for bluefin tuna (Figure 10). Results also supported previous hypotheses that spatial distribution changes have occurred in both the population and the fishery (Walter, 2018; Figures 4-7), validating the use of a spatio-temporal model for CPUE standardization. The use of spatio-temporal approach is further validated due to low captures (< 100 fish), in the Large Pelgics Survey, in certain years (Table S1). VAST can handle low sample sizes and provide estimates for missing covariates (Thorson, 2019); however, despite this ability model results for these years (2003, 2006, 2008, 2014) are probably more uncertain and should be viewed with caution.

The VAST model presented here improved upon previous conventional CPUE standardization approaches that modeled size classes separately and accounted for spatial changes by incorporating SST (Hansell et al., 2021; Lauretta et al., 2021). The time series of abundance produced from VAST were similar to previous methods; however, there were some differences in the large fish index in the early 2000 and the small fish index near the end of the time series (Figure 10). Potential differences in relative abundance were not necessarily the result of model structure but could be the result of data decisions. For example, past indices of abundance used captures as the explanatory variable and effort as an offset, while the VAST model used CPUE (catch/hours). Typically, it is not appropriate to use hours in the denominator of CPUE because it assumes each hour of fishing has the same probability of catching a fish (Peterson et al., 2017). However, we believe this is not a substantial problem here because all fishing trips used were relatively short (< 24 hours). The index applies to the rod and reel fishery where bait was constantly checked, and fishermen chum to attract fish. Another difference between the VAST model and past standardizations was that two additional size classes are included in the model for small fish (<

66 cm and 145-177 cm; Table 1). Lastly, the large fish index used all trips from Virginia to Maine, while the previous model focused solely on trips in the Gulf of Maine (Hansell et al., 2020).

We recommend that future assessments should explore incorporating the indices produced here into the stock assessment because geo-statistical approaches like VAST are expected to yield more accurate indices of abundance (Shelton et al. 2014). Additionally, using these models in assessments may lead to lower retrospective bias (a notable problem identified during the last stock assessment, particularly the VPA), and potentially provide more accurate biomass estimates compared to design based index-driven models (Cao et al. 2017). Further, VAST supported the use of local SST as being an important driver of density and distribution changes; however, current standardization models incorporate SST as a covariate of catchability. Thus, current approaches may be detrending the effect of SST, which could alter year effect estimates. We anticipate this approach will continue to be useful as sea temperatures in the Northeast U.S. are projected to continue to increase at three times the global rate of change (Saba et al. 2016).

Future work should also explore combining the results presented here with commercial fisheries data in Canada. Combining data into a joint index would create a single time series that could resolve residual patterns between the two fleets (Hansell et al., 2020). A similar approach of a combined index was applied to U.S. and Mexican longline fisheries that target bluefin tuna in the Gulf of Mexico (Lauretta et al., 2021). Previously, a joint index between U.S. and Canadian fisheries was explored by the ICCAT Index Working Group; however, it was not recommended due to differences in catch distribution between the countries (Hansell et al., 2021). VAST can potentially reconcile this issue because it has the ability to combine multiple data types into an integrated modeling framework (Gruss et al., 2019). Additionally, adding the Canadian data into VAST could allow for the exploration of larger-scale distribution shifts and potential drivers of bluefin tuna habitat that are more reflective of the population as a whole.

In conclusion, the VAST model provided a single framework to estimate distribution changes and indices of bluefin tuna relative abundance in US waters. The model estimated that for both large and small fish, the area occupied increased, and the center of gravity shifted northeast. Our results highlighted local SST as a primary driver of the estimated spatial shifts. Compared to conventional standardization models, spatio-temporal indices showed less inter-annual variability between year effects, but produced similar overall trends. Results are expected to increase the understanding of bluefin tuna spatial distribution in U.S. waters and produce indices that are more robust to spatio-temporal changes. The findings have implications for the management of bluefin tuna in terms of stock status determinations and sustainable catch forecasts, and we recommend that the indices produced be directly incorporated into future stock assessments.

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Table 1. Size categories for Atlantic Bluefin tuna defined in the Large Pelagics Survey.

Size Categories	Size
Young school	< 26 in (66cm) SFL
School	26-44 in (66-114 cm) SFL
Large school	45-56 in (115-144 cm) SFL
Small medium	57-69 in (145-177 cm) SFL
Large medium	70-76 n (178-195 cm) SFL
Giant	> 76 in (195 cm) SFL

Table 2. AIC step-wise model selection for VAST catch per unit effort (CPUE) standardization. The table shows the influence of each covariate on model selection. The null model does not include any covariates and delta AIC represents the change each covariate has on overall AIC.

Covariate	Density		Catchability	
	AIC	Δ AIC	AIC	ΔAIC
Null	16489.75			
Number of Lines	-		15977.04	-512.71
SST	15931.1	-558.65	15969.25	-520.5
Depth	16091.89	-397.86	16184.37	-305.38
AMO	16091.89	-397.86	16271.19	-218.56
Herring	16111.23	-378.52	16277.14	-212.61

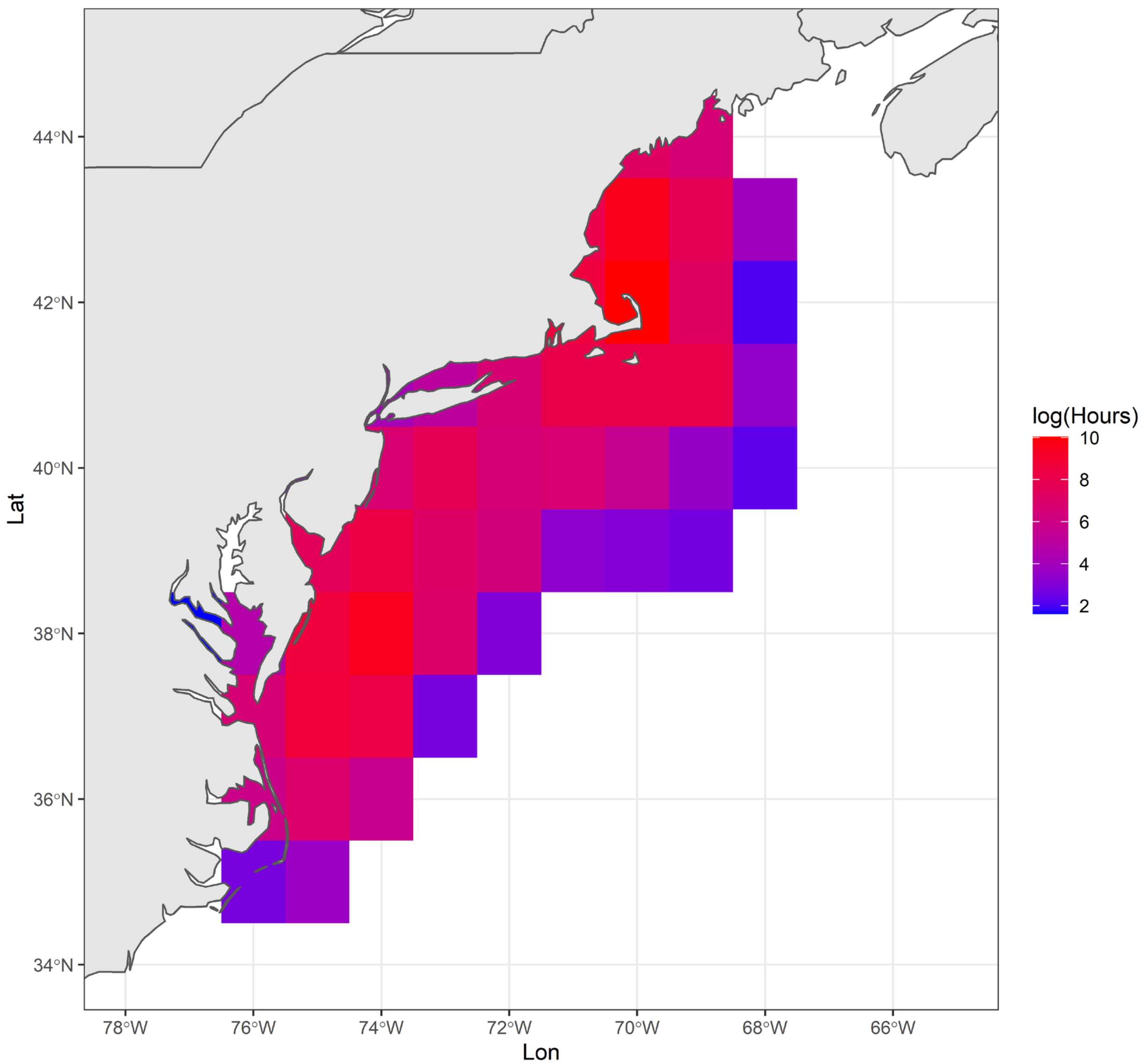

Figure 1. Spatial footprint and number of hours targeting Atlantic bluefin tuna.

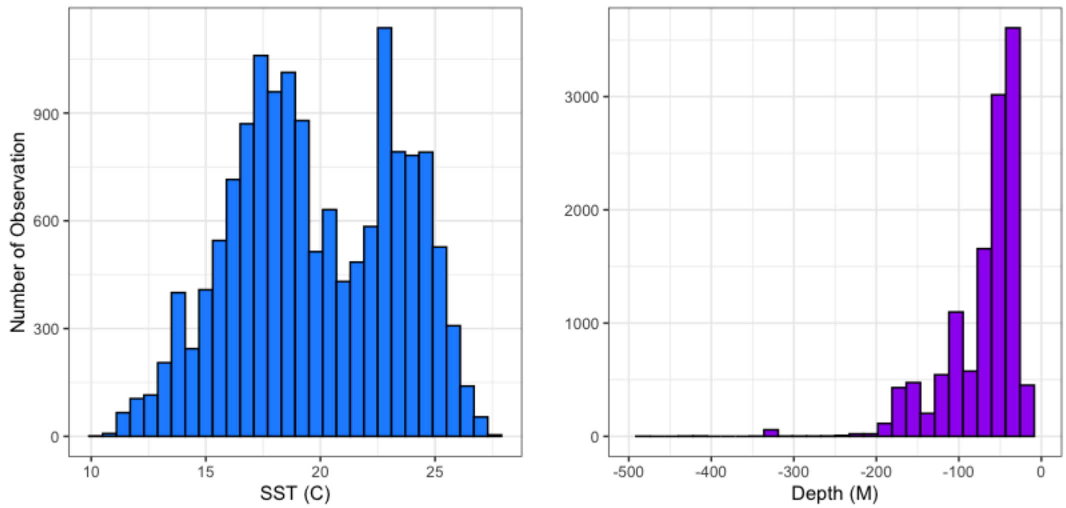

Figure 2. Distribution of local covariates, sea surface temperature (SST) and depth, explored in VAST models examining the spatio-temporal dynamics of Atlantic bluefin tuna.

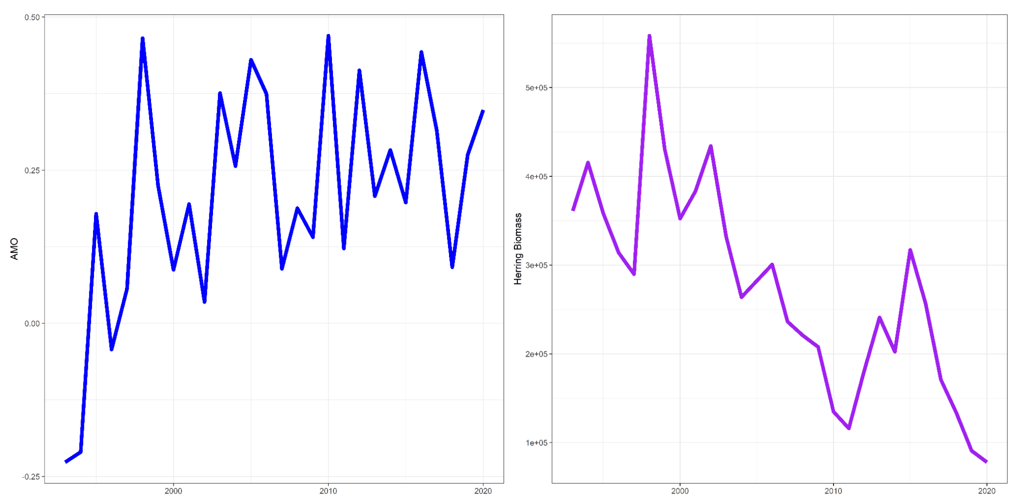

Figure 3. Regional time series explored in VAST models examining the spatio-temporal dynamics of Atlantic bluefin tuna.

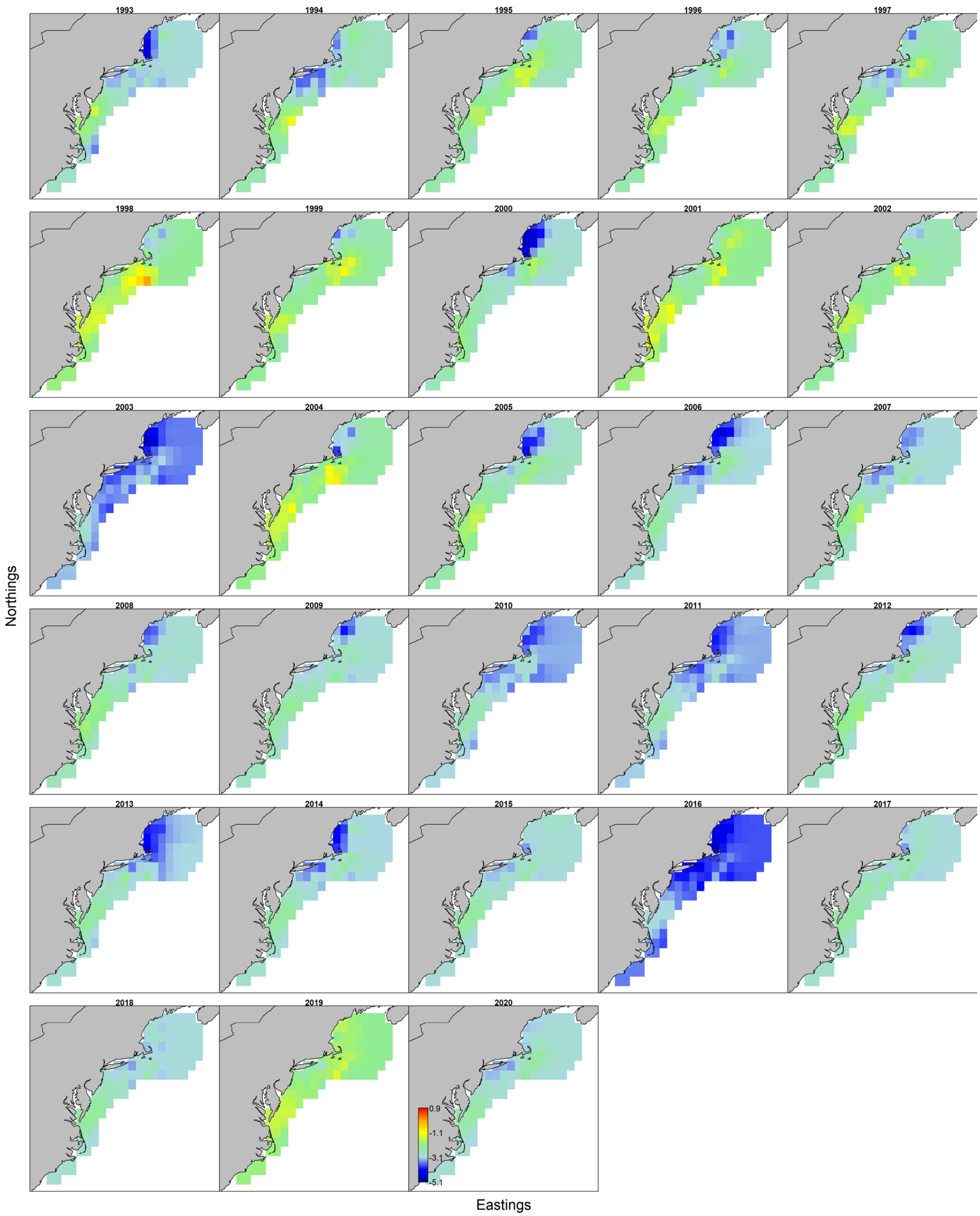

Figure 4: For large Atlantic Bluefin tuna, log density estimates from VAST model fit with all covariates (SST, AMO, herring abundance).

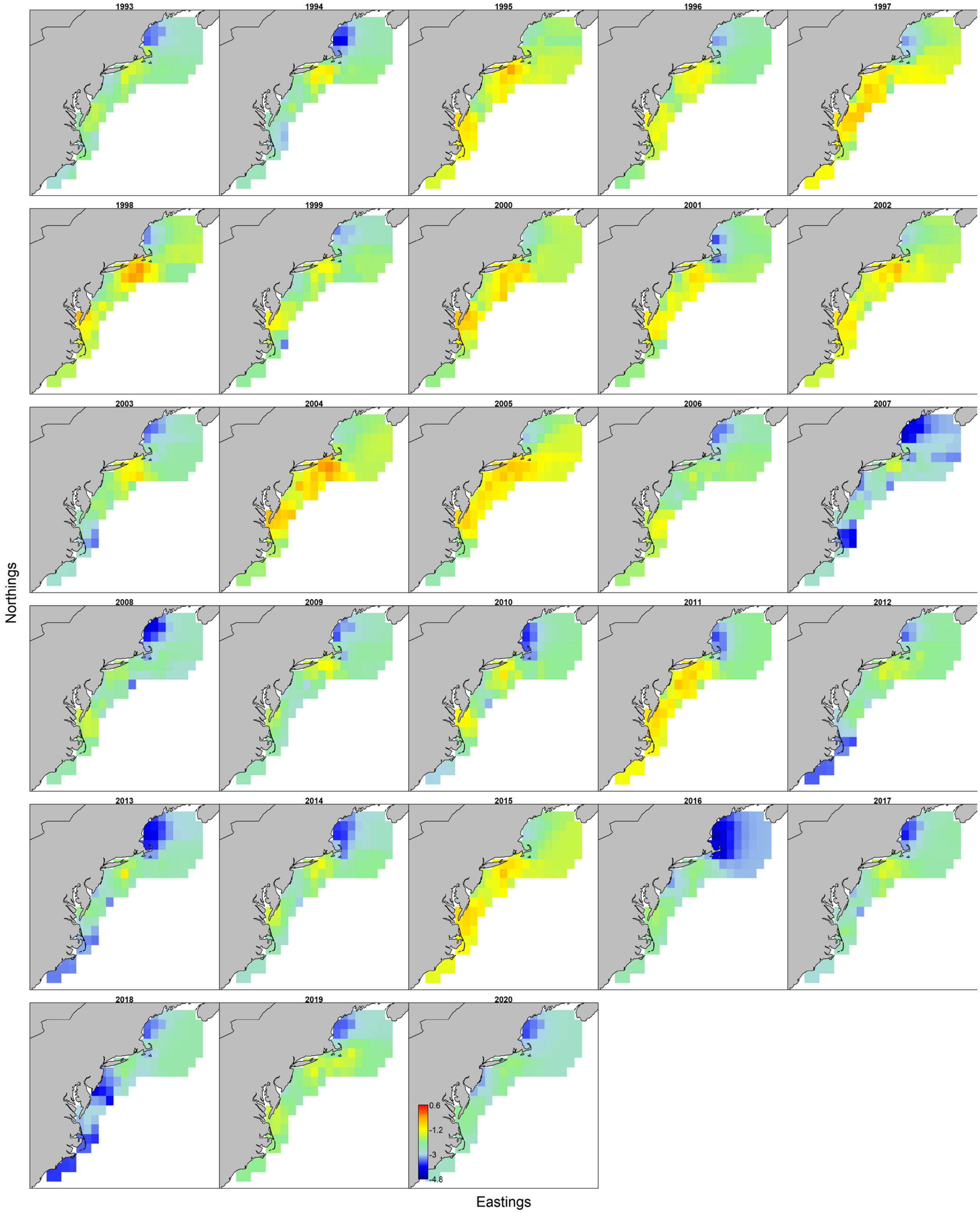

Figure 5: For small Atlantic Bluefin tuna, log density estimates from VAST model fit Gaussian Markov random fields and all covariates (SST, AMO, herring abundance).

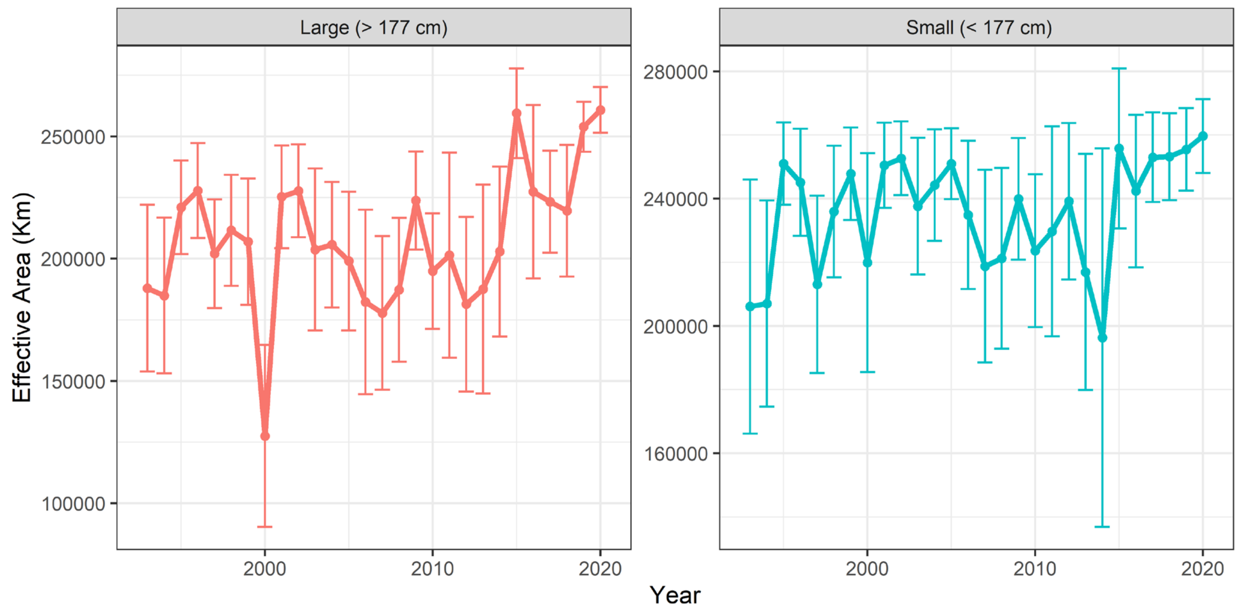

Figure 6. VAST effective area occupied estimates for large and small Atlantic Bluefin tuna. The model is fit with Gaussian Markov random fields and all covariates (SST, AMO, herring abundance).

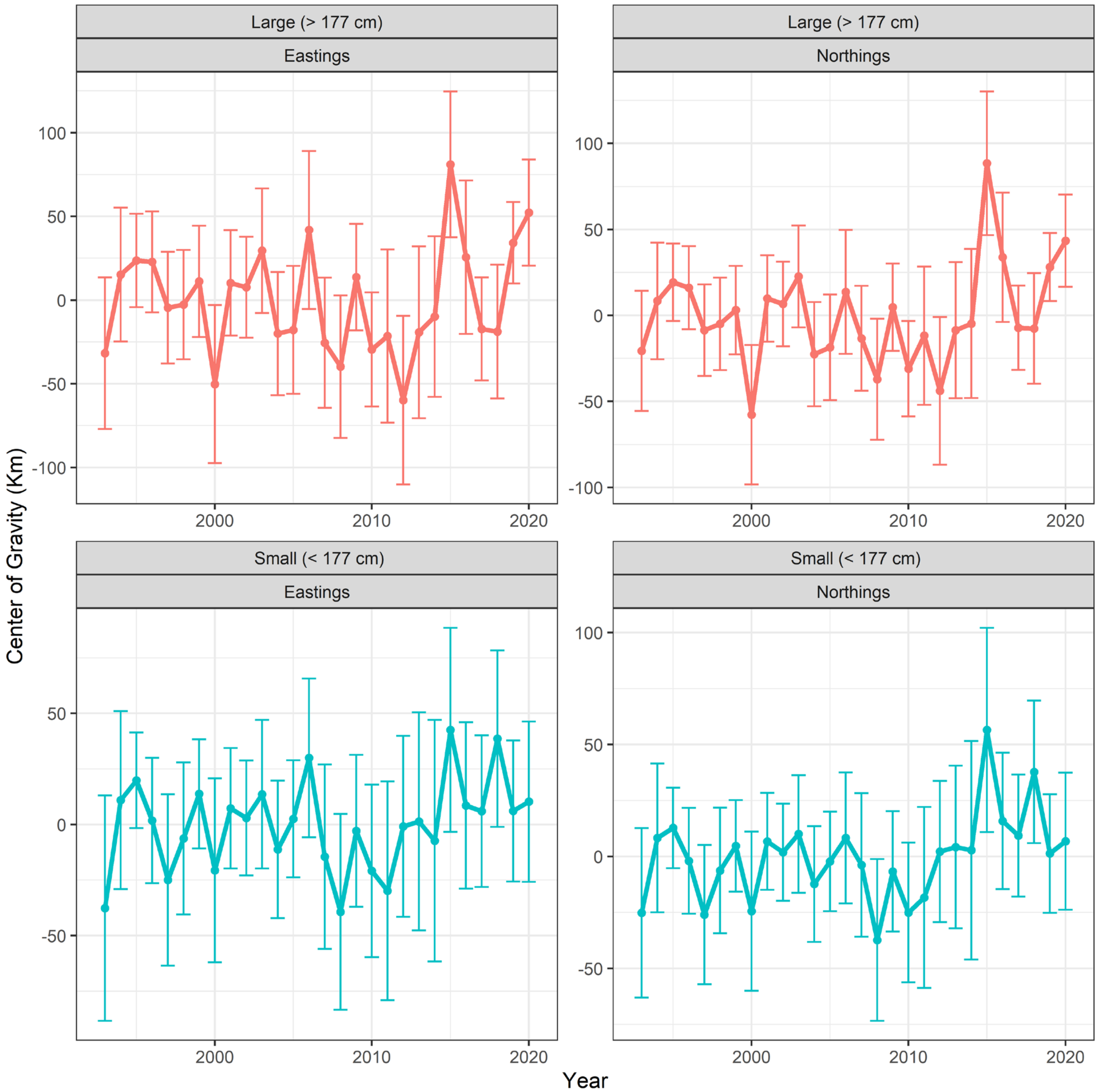

Figure 7. VAST spatial distribution changes estimates for large and small Atlantic bluefin tuna. The model is fit with Gaussian Markov random fields and all covariates (SST, AMO, herring abundance).

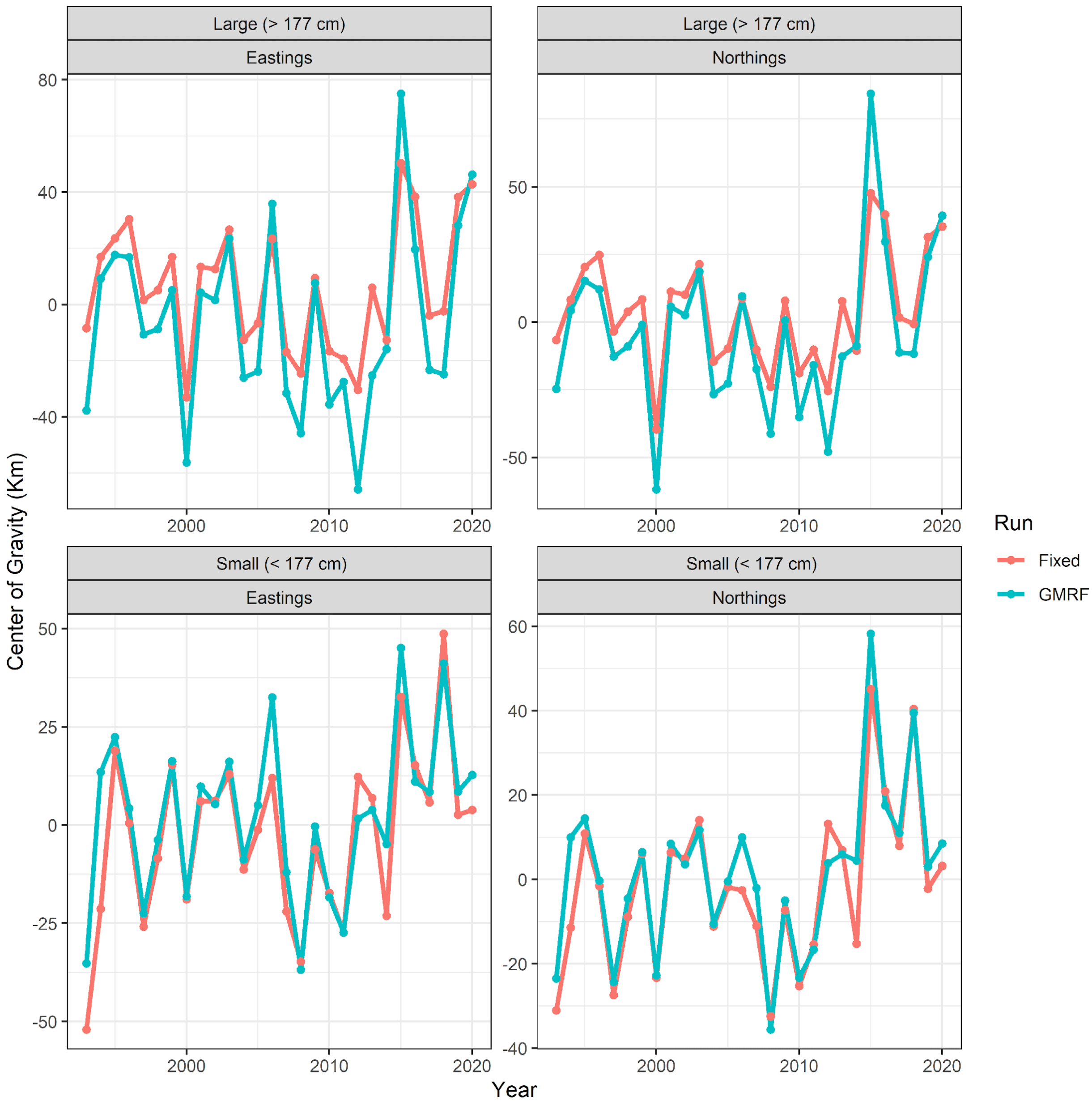

Figure 8. Counterfactual analysis exploring if covariates can explain observed distribution shifts. Blue represents VAST model runs used to estimate distribution shifts and fit with the Gaussian Markov random fields (GMRF), while red is the model run with only covariates (fixed effects).

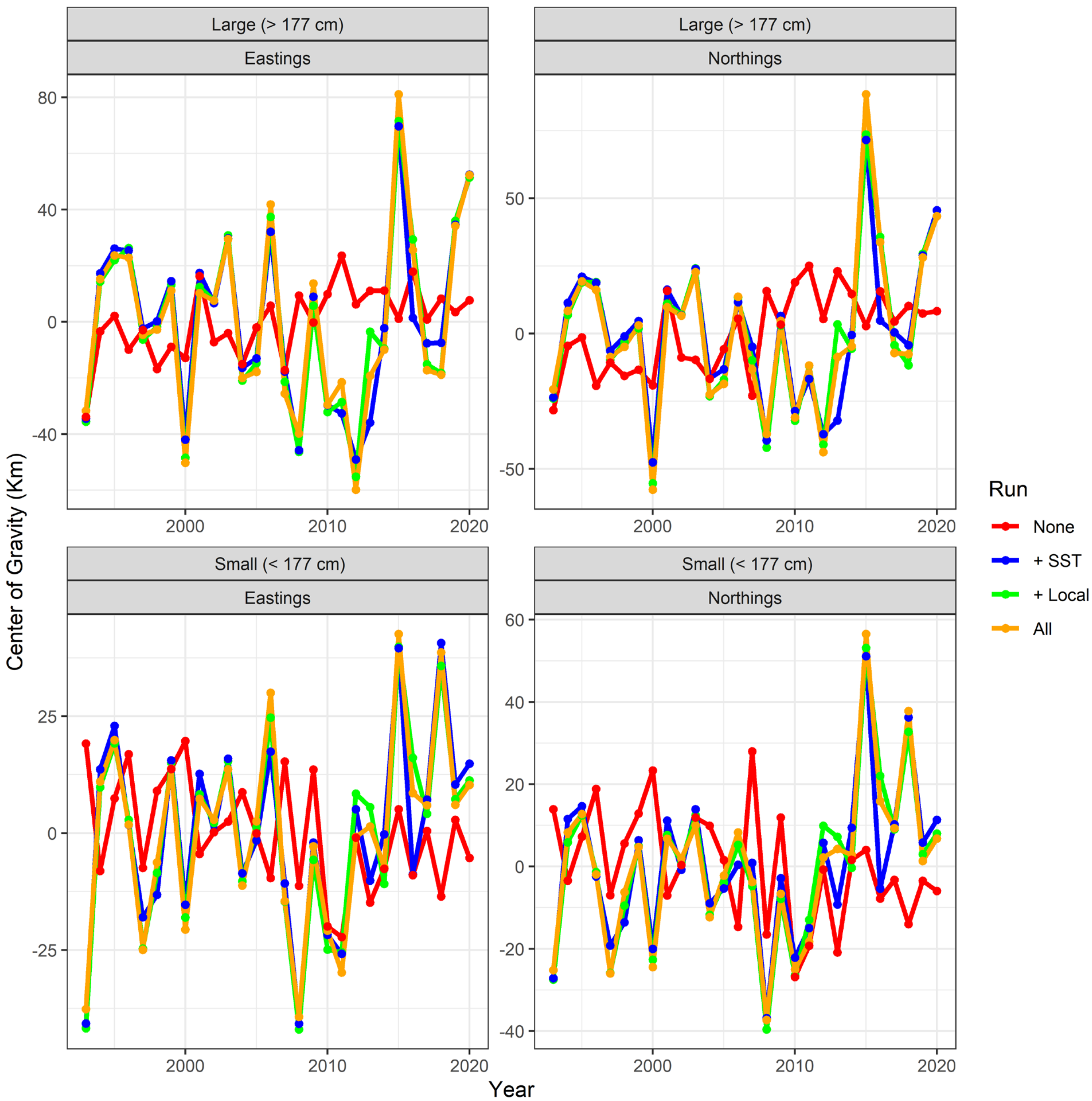

Figure 9. Counterfactual analysis sensitivity runs. Red is a VAST model without Gaussian Markov random fields (GMRF) and covariates. Following model runs continuously add covariates, blues adds sea surface temperature (SST), green adds local covariates (SST and depth), orange adds local and regional (AMO and herring abundance) covariates.

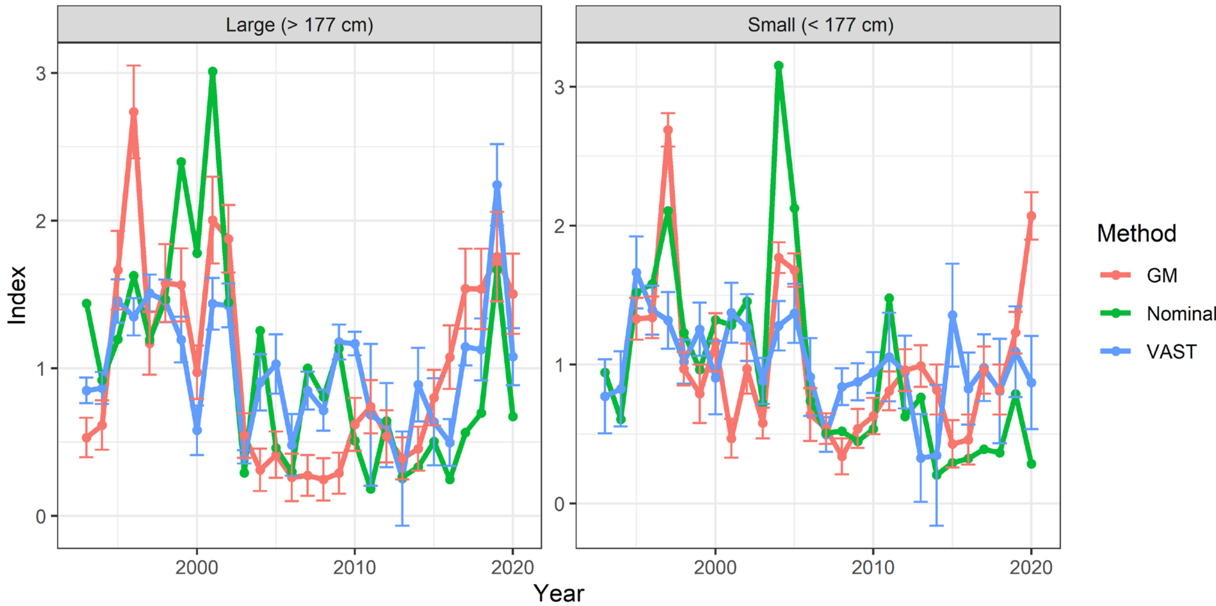

Figure 10. For Atlantic bluefin tuna, standardized indices of abundance from previous generalized models (GM) and the spatio-temporal VAST model. Error bars are +/- two standard error. The VAST model includes SST as an effect on density.