Estimating Population Trends with Stratified Random Sampling Under the Pressures of Climate Change

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Abstract

An Abstract

Keywords

keyword 1, keyword 2

Introduction

The Northeast United States continental shelf spans from the Outer Banks of North Carolina to the Gulf of Maine. The region covers over 250,000 km^2 of ocean, extending over 200 km from shore in the largest areas in New England to just 30 km off shore in the southern regions. This ecologically diverse region contains approximately 18,000 vertebrate marine species. Commercial fisheries have been an important part of local economies for centuries. In 2019, New England fisheries produced $22 billion in sales, which sustained over 200,000 jobs ("Fisheries Economics of the United States: Data and Visualizations" n.d.). Maintaining a healthy ecosystem is therefore vital to sustained ecological health and economic prosperity of the region.

The NEFSC has conducted a bottom trawl survey since 1963 to support assessment and management of the fish and invertebrate populations in the region (Azarovitz 1981; Politis et al. 2014). The survey uses a stratified random design where bottom trawl sampling takes place in predefined strata along the eastern continental shelf. The survey has created a rich time series data set with many uses including species-specific habitat identification, analysis of how environmental conditions influence species abundance, and estimating yearly species abundance trends to help inform stock assessments and ultimately quota limits. The survey takes place twice each year- once in the spring and again in the fall. Most spatial analyses and projections of future distributions typically assume a constant survey catchability and availability over time. For this reason, NOAA's survey design includes sampling each strata in approximately the same 3-4 week time period in each season.

Stock assessment scientists choose from a number of approaches to obtain abundance estimates that are derived from the survey data. Methods range from traditional design-based estimates to model-based estimates that vary in complexity. Design-based estimators rely on the design of the sampling scheme with the underlying assumption that the data being collected is representative of the population of interest. These methods do not account for spatial variation in samples and are not able to account for environmental influences on survey values. Model-based abundance estimates use statistical models to measure the relationship between response variables (such as presence or abundance) and predictor variables (such as environmental factors). Model-based estimators, such as General Linear Models (GLM), General Additive Model (GAM), and General Linear Mixed Models (GLMM), help account for complex relationships between variables and can help overcome problems with sampling design.

Due to a combination of climate change and shifts in circulation, the Northeast United States continental shelf has experienced rapid warming in recent decades. The changes have resulted in a shift in spatial distributions of many species (Nye et al. 2009; Henderson et al. 2017; Kleisner et al. 2017). Since stock assessment models rely on accurate descriptions of population dynamics and contemporary patterns of spatial abundance, there is concern that rapid undocumented changes in spatial distributions of species will bias future stock assessments. More specifically, as fish populations shift their distributions over time, catchability and/or availability in the survey will change, altering the relationship between the index and the true population (Arreguín-Sánchez 1996; Langan et al. 2021). A species shifting its range beyond the survey area is an additional compounding factor to consider. Existing research has focused on temperature as the driver of such changes (Klein et al. 2017) and evidence suggests that failing to account for the impact of climate-induced change can lead to management challenges (Kerr et al. 2022). In these scenarios, management strategy evaluations have shown that unintended overfishing can occur resulting from misconceptions of stock status, which can ultimately have detrimental ecologic and economic impacts (Mazur et al. 2023). We are therefore interested in analyzing the impact of climate change on the accuracy of abundance estimates derived from NOAA's ongoing bottom-trawl survey along the East coast.

To test the ability of the bottom trawl survey to track population trends under shifting environmental conditions, we construct spatial models for fish where movement depend on temperature preferences. We consider the impact of climate change by comparing simulations that use a repeating water temperature pattern to those where temperature increases on average over time. In both cases we conduct stratified random sampling on model output and analyze the ability of the samples to track population trends. We compare yearly abundance estimates obtained from the stratified mean to estimates obtained from the Vector-Autoregressive Spatio-temporal (VAST) model. The stratified mean is a design-based approach that calculates the arithmetic mean catch per tow and has traditionally been used with stratified random sample designs. VAST is a spatial delta-generalized linear mixed model that estimates both abundance (biomass) and probability of occurrence (presence/absence) (Thorson 2019). If desired, VAST also allows users to include covariate data to better inform the model. Covariates can be static (eg. habitat preferences) or dynamics (eg. temperature). We explore whether including environmental predictors can help inform models and provide better abundance estimates, which is particularly relevant as climate change progresses.

Methods

We construct spatial models for Yellowtail Flounder, Atlantic Cod, and Haddock on Georges Bank, where movement of each species combine static species-specific habitat preferences with biologically-based temperature preferences. Model dynamics are driven by a time series of temperature gradients to create simulated data sets for each population where the true biomass is known. Using temperature gradients that repeat each year creates data sets with repeating spatial patterns, whereas using a temperature gradient that increases on average throughout the simulation leads to spatial distributions that shift over time. We conduct stratified random sampling on our simulation output to mimic the bottom trawl survey and use the samples to compare the ability of contemporary indexing methods to track population trends.

Population Model Formulation

We use the R package *MixFishSim* (MFS) to model our populations (Dolder et al. 2020). MFS is a discrete spatiotemporal simulation tool where users can model multiple species under varying environmental conditions. The package uses a delay-difference population model with discrete processes for growth, death, and recruitment of the population. We formulate the following inputs for the MFS package to address our research question.

Study Area

We obtained a shapefile for the 15 strata that comprise Georges Bank, where strata were partitioned based primarily on depth and secondarily by latitude (Politis et al. 2014). The region was discritized into a raster with 88 rows and 144 columns to use as our modeling environment. Each cell in our simulation domain represents approximately 8.7 km^2. A fish stock is considered to be a subpopulation of a species that has similar intrinsic parameters. Each of the species being modeled has multiple distinct stocks along the Atlantic coast resulting from local environmental conditions. Biological differences between species results in each stock inhabiting a different number of strata on Georges Bank. Haddock inhabit all 15 strata in the domain, Cod populate 13 strata, and Yellowtail can be found in 9 strata. Figure 1 shows the regions used in our models.

Population Dynamics and Recruitment

The time step for our models is one week. MFS uses a modified two-stage Deriso-Schnute delay difference equation that models the biomass in each cell in our study area (Dolder et al. 2020). Individual terms in the formulation account for growth of mature adults, mortality (natural and fishing), and the addition of new recruits. Recruitment is a function of the adult biomass that existed in the previous year and is added to the population incrementally throughout each species' predefined spawning period. Parameter inputs were either obtained from the literature or chosen to produce desired model dynamics. A full list of parameters used in our model can be seen below in Tables **??** and 4.

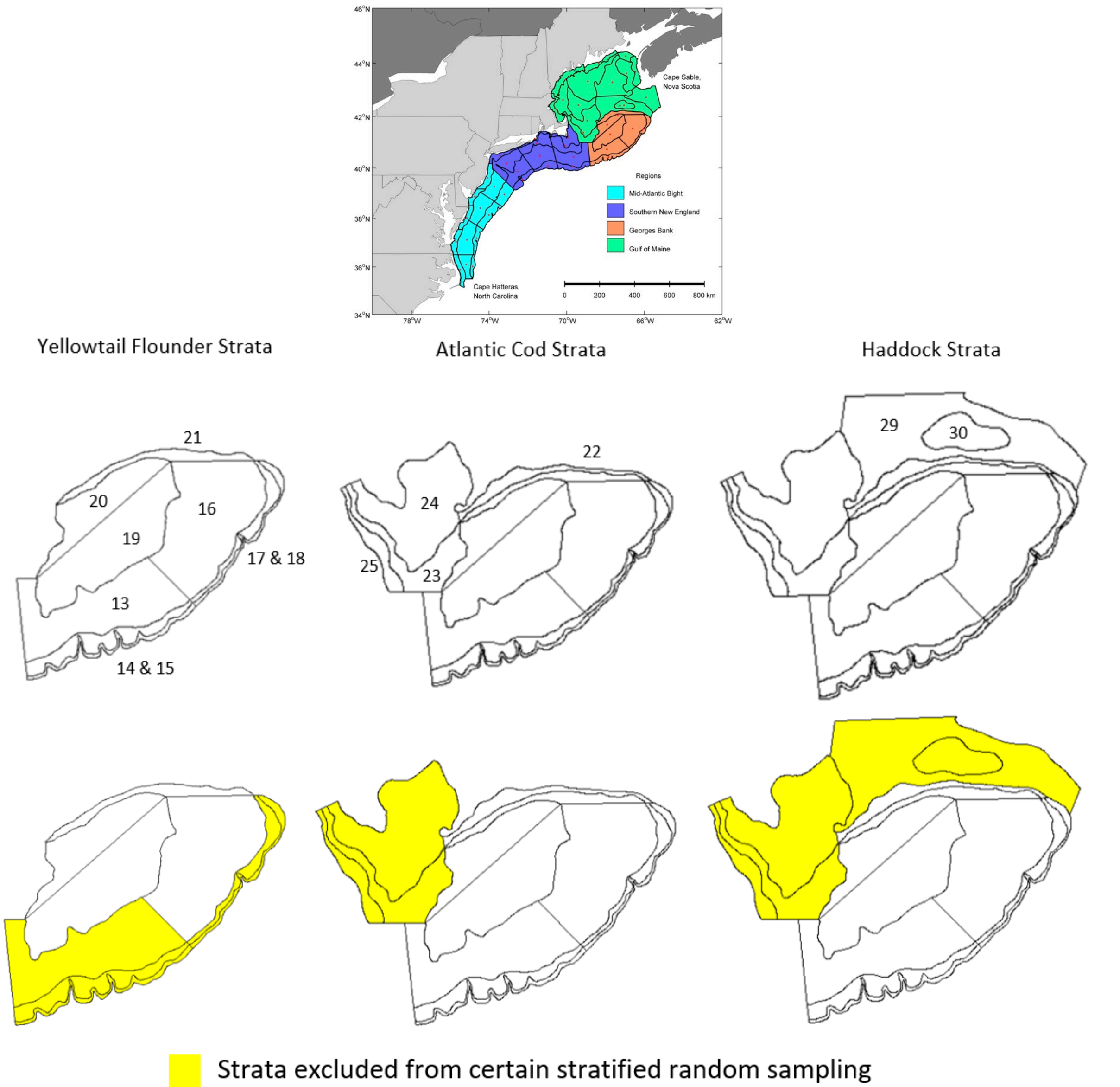

Figure 1: Strata inhabited by each species in our population models. All strata on the eastern US contintental shelf are shown in the first image with Georges Bank highlighted in orange. Stratum numbers used by the NEFSC bottom trawl survey are shown in the middle row. Strata that are excluded from certain stratified random sampling are shown in the bottom row in yellow.

Movement

The package combines species-specific temperature tolerances with habitat preferences to drive the probability of movement from cell I to cell J using the formulation

$$Pr(C_{wk+1} = J | C_{wk} = I) = \frac{e^{-\lambda \cdot d_{I,J}} \cdot (Hab^2_{J,s} \cdot Tol_{J,s,wk})}{\sum_{c=1}^{C} e^{-\lambda \cdot d} \cdot (Hab^2_{c,s} \cdot Tol_{c,s,wk})}, \tag{1}$$

where

$e^{-\lambda \cdot d_{I,J}}$ accounts for distance between cells I and J,

$Hab^2_{J,s}$ is the static habitat value for species s in cell J, and

$Tol_{c,s,wk}$ is the value from normally distributed temperature tolerance for species s in cell c in week wk.

The package was designed to generate hypothetical temperature gradients and theoretical habitat preferences using Gaussian Random Fields. The following sections describe how we formulated the habitat and temperature components to model real species in the western Atlantic Ocean.

Habitat Input

Species-specific habitat preferences were derived from niche model for each species using the *lrren* tool from the R package *envi* (Buller 2022). The *lrren* tool estimates an ecological niche using the relative risk function by relating presence/absence data to two covariate predictors. We used bottom trawl point data in from 2009-2021 as our presence/absence input by using a value of 0 for any tow that failed to catch the given species and weighting a successful catch by the biomass of the given tow. We combined data from both the fall and spring surveys to obscure the influence of temperature to allow the niche model to instead infer habitat preferences. Depth and mean sediment size were used as our covariate predictors.

Estimated depth for the region was obtained from FVCOM (Chen et al. 2006). The mean sediment size raster was interpolated in ArcMap using the natural neighbor interpolation method using point data collected by the United States Geologic Survey (USGS) (McMullen et al. n.d.). Since the values in $Hab_{J,s}$ are required to be between 0 and 1, we rescaled the spatial estimates from *lrren* to fall between these bounds. See Figure 2 for a visual representation of this process being applied to Cod. Figure 3 depicts habitat preferences $Hab_{J,s}$ for each species.

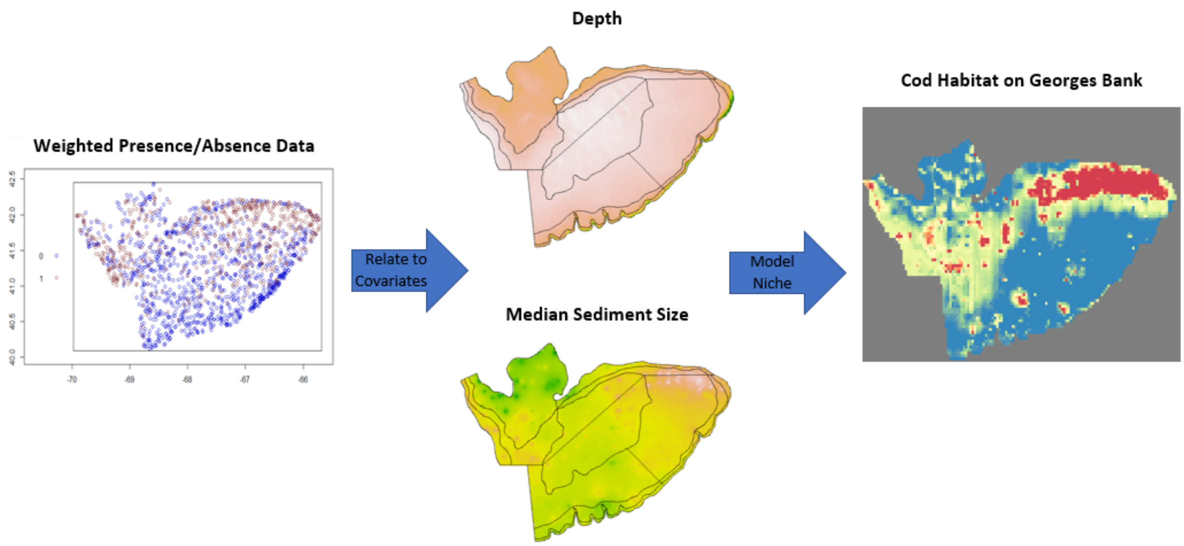

Figure 2: Visual representation of niche model for Cod.

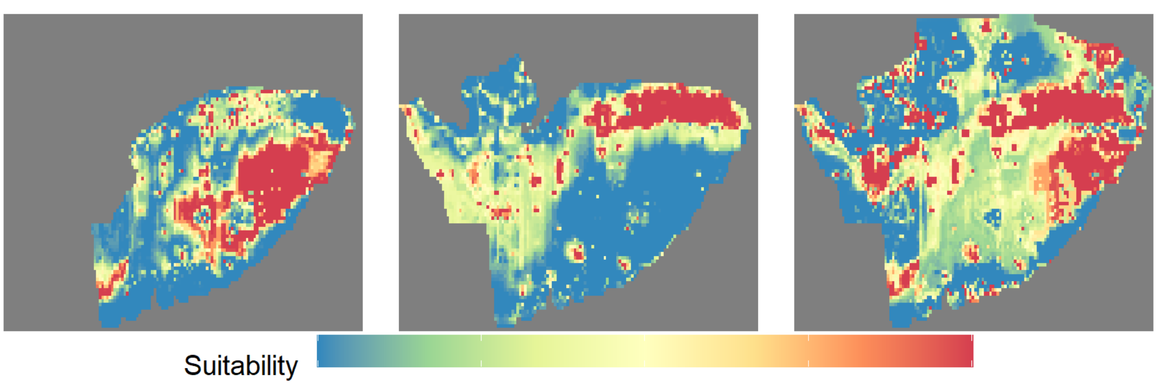

Figure 3: Static habitat preferences for each species in our population models. From left to right: Yellotwtail Flounder, Cod, and Haddock.

Temperature Input

Each species is assumed to have normally distributed temperature preferences ($N(\mu, \sigma)$).

Values were chosen by combining information in the literature with temperatures recorded in the bottom trawl survey. We assume Yellowtail Flounder's preferences are $N(8.75, 4.25)$, while Haddock and Cod have preferences $N(9, 4)$. Weekly estimated temperature data for the region for 2012 was obtained from FVCOM (Chen et al. 2006). We chose to repeat temperature estimates for a single year rather than use data for consecutive years to reduce the number of factors impacting model dynamics while still incorporating real data. The 2012 data was chosen because it displayed an average temperature pattern that consistently oscillated between maximum and minimum temperature values, allowing for a smooth repeating yearly temperature pattern for the constant temperature scenario. The 2012 temperature data was also transformed to create an oscillating pattern that increases 5 degrees Celsius on average over the duration of the simulation. We chose a 5 degree increase over a 20 year simulation to allow temperature change to have a meaningful impact on dynamics while remaining within reasonable computational limits in terms of the length of the simulation. Figure 4 depicts mean trends for the temperature scenarios used in our models. **dont forget to include animated gif in final submission**

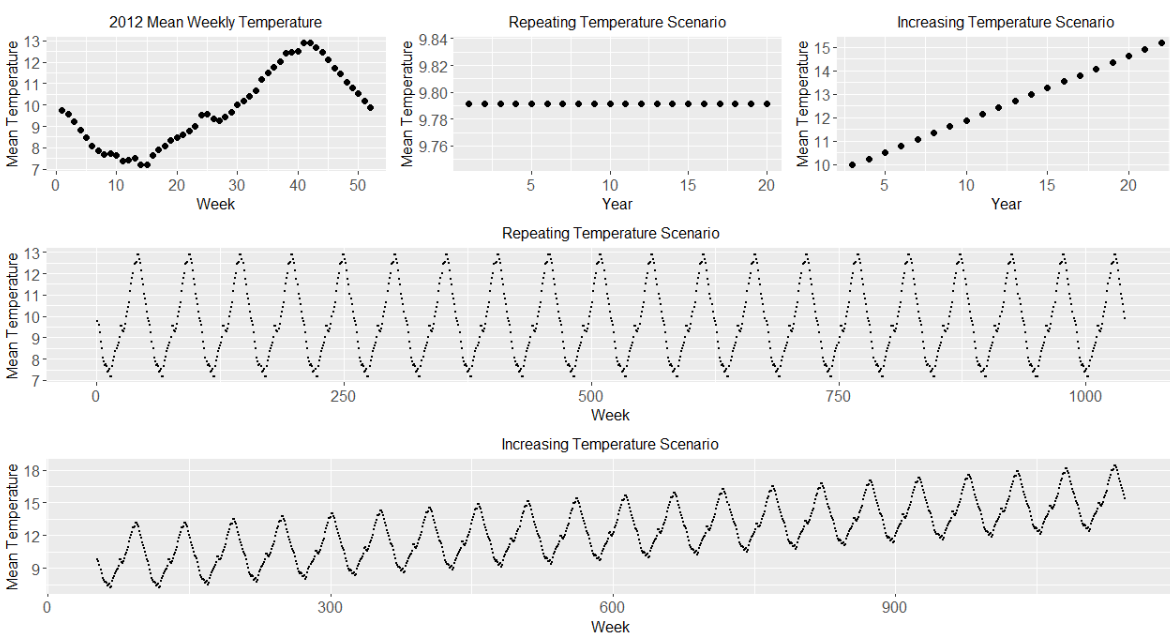

Figure 4: Mean trends of temperature data used in our model.

In equation (1), $Hab^2_{J,s}$ remains constant for each species for the duration of the simulation, while $Tol_{c,s,wk}$ changes each week with temperature fluctuations. Using a temperature gradient that repeats every 52 weeks produces the same spatial preferences in a given week each year, resulting in consistent spatial biomass patterns. Scenarios where the temperature increases over time creates spatial preferences that evolve as the water warms, producing spatial biomass patterns that shift in a given week over the duration of the simulation. Thus, stratified random samples in scenarios with a repeating temperature pattern will have constant survey catchability and availability over time, which may not be true for increasing temperature scenarios due to evolving spatial preferences.

We carry out 20 year simulations for each of our three species under various population scenarios. Historically, Atlantic Cod has seen significant decline over the last XXX years while Haddock has increased in abundance in recent year [[can cite the 2022 management track assessments, see https://apps-nefsc.fisheries.noaa.gov/saw/sari.php for when the document becomes available]] **cite**. For this reason we compare indexing estimates using stratified random samples from decreasing population scenarios for Cod and increasing population scenarios for Haddock. To provide a comprehensive analysis of population indexing methods we consider all possible scenario combinations for Yellowtail Flounder. Each of these scenarios is simulated twice: first with with an oscillating temperature gradient that repeats and second with a temperature gradient that increases roughly 5 degrees Celsius over the duration of the 20 year simulation, for a total of 10 simulated spatial datasets. The specific population trends used in our analyses can be see in Figure 5.

Simulating Bottom Trawl Survey and Population Indexing

After each simulation is complete, we mimic the bottom trawl survey by conducting stratified random sampling in each inhabited strata twice each year. We sample each strata in the same weeks in which the Spring and Fall surveys take place (weeks 13 & 14 in the Spring and 37 & 38 in the Fall). The number of the samples taken reflect true target values for each strata and sampling cells were randomly selected. We then use the biomass collected from

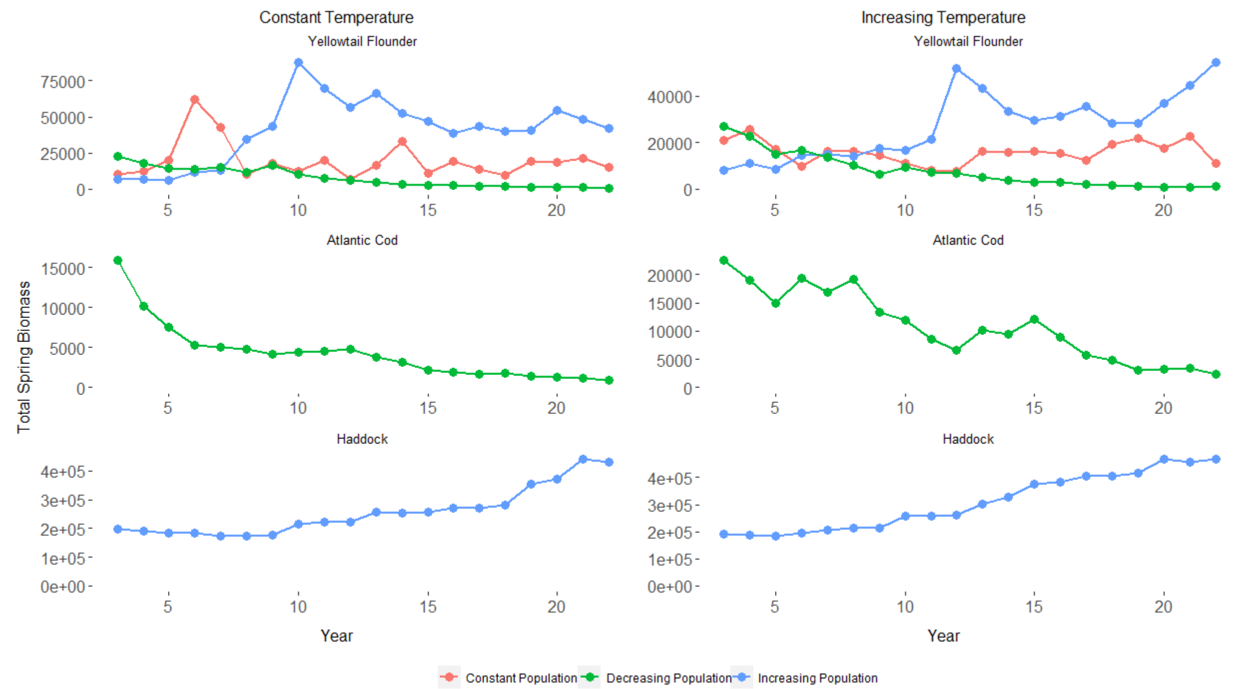

Figure 5: True population trends used in indexing analyses. Spring biomass plots are shown with fall values being very similar.

our samples in contemporary abundance indexing methods to estimate population trends. Knowing the true population values in our simulations allows us to compute and compare the absolute error calculated from each estimation method.

The design-based method we used is the stratified mean, which divides the inhabited domain into N disjoint strata based on relevant geographic and environmental information such as depth and latitude/longitude. The number of samples taken from each stratum S_j for $j = 1...N$ is relative to the given area. The stratified mean biomass $SM_{s,y}$ for a given season s and year y can then be calculated by through the weighted average

$$SM_{s,y} = \sum_{i=1}^{N} W_i \frac{\sum_{k=1}^{S_i} y_{k,i}}{S_i},$$

where $W_i = \frac{S_i}{\sum_{j=1}^{N} S_j}$ and $y_{k,i}$ represents the biomass in sample k of stratum i in season s and year y. These tow-dependent calculations are quick and easy to calculate, especially relative to the model-based VAST estimates.

We compare stratified mean estimates to those derived from the model-based VAST approach. VAST models both biomass $p_1(i)$ and presence/absence $p_2(i)$ for each observation i as linear predictors using a spatial delta-generalized linear mixed model. The equation representing the biomass predictor can be represented by

$$\text{temporal variation} + \text{spatial variation} + \text{spatio-temporal variation} + \text{vessel effects} + \text{habitat covariates} + \text{catchability co}$$

where more specific functional forms of each component are further described in (Thorson 2019). $p_2(i)$ takes on a similar form as $p_1(i)$. VAST models require numerous user inputs to determine how the linear predictors will be conditioned and solved. As a result, VAST models take on the order of hours to complete.

We follow the advice given in (Thorson 2019) to build VAST models that estimate biomass in our Georges Bank population models using stratified random samples from our model output. In addition to exploring different link functions and assumed distributions, our VAST model-building process involved testing the impact of including spatial and/or spatio-temporal variation in our models, considering varying number of knots in our mesh, and testing different forms of temporal correlation. We carried out the same model-building process using covariate information to inform our models as well as without covariates in our models. The covariates we considered were the dynamic temperature values and static habitat values ($Hab_{J.s}$) from our population models. When using covariates we ultimately decided to consider a best-case scenario by including both temperature and habitat covariates for both linear predictors in order to provide the most information to the model. Knowing the true population values in our models allowed us to calculate the absolute error of each VAST estimate to compare between potential settings. Through this process, and in consultation with the VAST package creator, we compared the performance of two sets of settings in our

VAST models, which can be seen in Table??. VAST Settings B were chosen after reviewing the information provided in the "Seasonal Model" section of VAST's online Github tutorial (Thorson, James T n.d.). After running models for each of our scenarios using these settings, we shared some of our results with the VAST package creator, James (Jim) Thorson. Jim reviewed our VAST model results and suggested we also consider the options shown in Settings A. Both settings use a Tweedie model and turn off the first linear predictor p_1 so that only biomass is being modeled. The difference between the two settings can be seen in the Rho Configuration, where RhoBeta2 = 0 in Settings B while RhoBeta2 = 3 in Settings A. The difference amounts to intercepts for the biomass predictor being a fixed effect (RhoBeta2=0) versus intercepts being constant among years as a fixed effect (RhoBeta2=3). According to Jim, the Settings A values are representative of what stock assessment scientists typically use in their analyses. As a result we will focus our analysis on VAST results obtained using Settings A.

Our goal is to determine indexing approaches and settings that are robust to changing environmental conditions and resulting spatial biomass patterns. An underlying assumption in all indexing methods is that individual random samples combine to accurately represent true abundance by a) containing a low enough noise level in the samples to allow for a discernible pattern and b) sampling all strata in which the population exists. These assumptions can be questioned given enough noise in the sampling process and/or climate change causing a population to move into previously uninhabited strata. To simulate the impact of noise, we compare indexing estimates after adding noise to our samples versus those using the true sampling values. Annual survey observations were simulated as log-normal deviations from the underlying "true" survey catches with a CV of 0.3 in the spring. The implication of a given population shifting its distribution into new habitat outside of the normal survey area is that stratified random sampling will fail to sample the entire geographic extend of the population. We therefore simulate the effect of populations moving into new habitat by comparing indexing estimates using samples from all strata inhabited by each species on

Table 1: Each index estimate chooses one condition from each of the following 7 columns.

Species	Population Trend	Temperature Scenario	Strata Included	Noise Added	Season	Covariates (VAST)
Yellowtail	Increasing	Repeating	All strata	No	Spring	No
Cod	Constant	Increasing 5°C	Subset	Yes	Fall	Yes
Haddock	Decreasing					

Georges Bank to those that only include a subset of the full spatial domain for each species. We chose strata to exclude for each species by reviewing how spatial preferences evolved in our increasing temperature scenarios and removing strata that each species either shifted into, or away from. Figure 1 shows all strata inhabited by each species as well as those that are removed from certain calculations using the spatial shifting trends shown in Figure 6. The yellow regions in Figure 1 depict the strata that were removed from certain stratified random surveys for each species.

Each scenario we consider is a combination of specific population trends for each species, differing temperature scenarios, altering seasons, and sampling possibilities (noise, strata, covariates), resulting in a large number of scenario combinations to consider. The columns in Table 1 show the choices that define each scenario.

Results

Figure 6 depicts the spatial shifting that occurs in each stratum within our population models, specifically during the bottom trawl survey in the spring (weeks 13 and 14) and fall (weeks 37 and 28). The left column in Figure 6 depicts the percent of population that exists in each stratum for each species when the temperature is a constant repeating pattern. In these scenarios we notice a small amount of shifting between successive years as the population aggregates on especially suitable habitat in the domain. More exaggerated shifting takes place in a larger number of strata when the temperature is increasing over time, as seen right column of Figure 6. This demonstrates how we were able to model shifting distributions due to climate change by running simulations with a temperature gradient that increased on average over time.

Tables 6, 7, 8, and 9 contain the absolute error between abundance estimates and model output for each of our abundance estimates. While the model-based results provided a slightly lower mean absolute error (0.34) compared to the stratified mean (0.38), the variance of all VAST absolute errors (0.10) was much larger than the stratified mean (0.02) highlighting the sensitivity of model-based estimates to the settings being used. When considering individual scenarios, $77/80 \approx 96\%$ had a VAST estimate with a lower relative error than the corresponding stratified mean estimate, with VAST models that include covariate information providing the lowest overall errors and standard deviations. Setting misspecification and/or a poor covariate response contribute to the large variance in VAST errors as illustrated by the fact that $\approx 63\%$ of individual scenarios contain a VAST estimate with a worst error than the corresponding stratified mean estimate. VAST models that included covariates had an average absolute error of 0.22, models that did not include covariate information had an average error of 0.46, and stratified mean estimates produces an average error of 0.39. When we reduce the number of strata that are included in indexing calculations to simulate species shifting into new territory, we typically see an increase in absolute error (as expected), though there are some scenarios where the impact is minimal. Furthermore, there are scenarios where including covariates in VAST models actually increases the absolute error, especially when we fail to sample the entire domain (e.g. in Table 9 rows 8 and 9, VAST models without covariates show lower errors than when covariates are included). We analyze these results further in the sections that follow.

Abundance Estimate Ratio Results

A simple visual analysis of all error plots for each species reveals that VAST estimates tend to provide abundance estimates that are above the true model value, while the stratified mean estimates are, on average, below the true model values. This can be further examined by examining yearly estimate:model ratio values, where we divide the yearly abundance estimates by the true model value. In doing so we see that VAST estimates tend to remain closer to the desired value of 1 compared to stratified mean estimates, which can estimate yearly abundance values as low as 0 at times and exhibit large yearly changes. A representative example of this trend for each species is shown on the log scale in Figure 8.

Analysis of individual yearly model:estimate ratios when all strata are included revealed that 73% of all yearly VAST ratios were above 1 (27% less than 1), with an average of 1.29 and a standard deviation of 0.21. On the other hand, just 33% of stratified mean estimate ratios were above 1 with an average of 0.874 and a standard deviation of 0.12. There were seasonal differences in estimate ratios for VAST with spring VAST ratios producing a mean value of 1.08 with a standard deviation of 0.12 while fall VAST ratios were larger with a mean of 1.50 and standard deviation of 0.38. Stratified mean ratios were more consistent between seasons with spring ratios resulting in a mean value of 0.91 with a standard deviation of 0.10, and fall values of providing a mean ratio of 0.84 with a standard deviation of 0.16. The breakdown for individual species followed a similar pattern.

When the entire domain is sampled, the stratified mean produced an average yearly ratio of 0.87 with a standard deviation of 0.12. Adding covariates in these scenarios brings the VAST estimate ratio closer to 1. Specifically, when all strata are sampled, adding covariates improved the VAST estimate ratio from a mean of 1.45 and standard deviation of 0.17 to a mean of 1.13 and standard deviation of 0.09. Failing to sample the entire domain predictably decreases each individual yearly estimate as the entire population is not being accounted for in the sampling process, which in turn decreases the corresponding estimate ratio. For example, failing to sample the entire domain decreased the estimate ratio for the stratified mean from 0.87 to 0.59 (standard deviation of 0.10). With a reduced number of strata, adding covariates to our VAST models decreased the average ratio results from a mean of 1.04 and standard deviation of 0.33 to a mean of 0.78 and standard deviation of 0.19. As discussed later, when we fail to sample the entire domain in VAST models adding covariates sometimes decreased the accuracy of VAST estimates, typically in the form of additional yearly overestimation.

Yellowtail Flounder Results

The top two panels in Figure 6 depict the results for Yellowtail Flounder with a repeating temperature gradient on the left (constant temperature) and a temperature gradient that increases over time on the right (increasing temperature). In both temperature scenarios we see the percent of Yellowtail Flounder in strata 13 decrease over the course of the time series in both seasons. The spring population in stratum 19 also decreases in both temperature scenarios as well. The percent of the population increases in stratum 16 in the spring over the duration of both time series, which implies the flow out of strata 13 and 19 in the spring are going into stratum 16. These dynamics occur in both temperature scenarios in weeks 13 and 14 because stratum 16 contains favorable habitat for Yellowtail Flounder that coincides with most of the areas we have designated as the species' spawning ground, which takes place in weeks 9-12. These spring changes are therefore related to the static habitat values in our model rather than the temperature preferences, which is why we seen the same dynamics with constant and increasing temperature. While we observe similar changes in the fall (weeks 37 and 38) in the constant temperature scenario, an increasing average temperature results in a decrease in the population in stratum 16 over time and corresponding increases in strata 17 and 18 (see Figure 6). These dynamics imply that an increase in temperature results in the more shallow strata 16 becoming less desirable than the deeper and more narrow outer strata 17 and 18. One noticeable seasonal difference in the constant temperature scenario for Yellowtail is how ~10% of the population exists in the narrow outer strata 17 in the fall, while seemingly none of the population exists in any of the strata near the edge of the domain (14, 15, 17, 18) in the spring.

Tables 6 and 7 contain the absolute error between our abundance estimates for Yellowtail Flounder comparing design-based approach (stratified mean) with two settings for a model-based approach (VAST A & B). In reviewing these Tables we can see VAST estimates generally provide lower errors relative to those derived from the stratified mean, with models that include covariate information typically providing the lowest errors. The settings used in VAST mattered with Settings B outperforming Settings A in $67/96 \approx 70\%$ of scenarios. When all strata are sampled, adding covariates greatly improved estimates in all scenarios. We still see an improvement in VAST estimates when certain strata are excluded from sampling, but the improvement was much less dramatic than with all strata included. There are several instances in which VAST failed to provide improved abundance estimates compared to the stratified mean during the fall season without covariate information, producing the largest errors seen in Tables 6 and 7. However, Including covariate information to each VAST model produced estimates with significantly lower error than their stratified mean counterparts.

Of all scenarios without covariates, $33/48 \approx 68\%$ had a VAST fit with a lower relative error compared to the stratified mean estimate. All 15 of the covariate-free VAST estimates that resulted in a higher error than the stratified mean were for the fall season and had a common theme of producing abundance estimates that are above the true model value. These 15 fall estimates span all other scenario variations. The implication of this is that our model-based approach without covariates struggles with the primary seasonal difference for Yellowtail Flounder, which is that a larger percentage of the population exists in the narrow strata toward the edge of the domain (18 and/or 17). This theory is further supported by the fact that the absolute error in the increasing temperature scenarios increased dramatically in the fall season, when the combined percentage of the population in the outer strata 17 and 18 increased to over 40% by the end of the simulation.

Including covariate information made a noticeable difference in our Yellowtail Flounder model-based VAST estimates. All of the VAST estimates that included covariate information produced a lower relative error than the corresponding VAST model that did not include covariates. The largest improvements were seen in the increasing temperature scenarios. When comparing to the design-based estimates, $47/48 \approx 98\%$ of the VAST estimates that included covariates information had a lower relative error than the corresponding stratified mean estimate. This implies that the covariate information helped our model-based estimate account for the design-based issues related to an increasing percentage of the population entering smaller strata, which can become exacerbated in the increasing temperature simulations.

We see diminished performance of our abundance estimates for Yellowtail under increasing temperature, with the most dramatic changes seen in our VAST estimates without covariates. One exception to this is when we use a stratified mean approach while the population is decreasing. Our analyses have found that the stratified mean tends to under estimate the true abundance and since these estimates are bounded below by zero, as the Yellowtail population decreases towards zero the difference between the estimate and the true value also decrease. That is, if the population is low enough, failing to appropriately sample the population in a design-based method produces the same result as appropriately sampling. In comparing abundances estimates calculated under the same conditions with the only difference being the temperature scenario, we see that an increasing average temperature had a larger impact on the model-based estimates compared to the design-based method. Specifically, when comparing the error of abundance estimates from the constant temperature scenario to the corresponding increasing temperature scenario, VAST increased by an average factor of 1.75 (both with and without covariates) while the stratified mean error increased by an average factor of 1.25.

Cod Results

In the constant temperature scenario for Cod, in both seasons the population decreases its presence in strata 19 and 20 over the duration of the simulation, while simultaneously increasing presence in stratum 16. However, we see a seasonal impact in stratum 16 during the increasing average temperature simulations where in the fall the population decrease presence in strata 16 and 21, and increase presence in 18, 22, and 24 (see Figure 3). Similar to the Yellowtail Flounder population, the favorable habitat in stratum 16 acts as an attractor in both temperature scenarios in the spring when the water temperature is cooler. When the temperature increases over time, the fall population compensates by shifting their preference to the adjacent strata that are deeper and/or further north than stratum 16.

Table 8 contains the absolute error between our abundance estimates for Cod and the true model values. The VAST settings performed comparably to each other with $18/32 \approx 57$ of estimates performing better with VAST Settings A. Of the abundance estimates without covariates, $12/16 = 75\%$ had a VAST fit with a lower relative error compared to the stratified mean estimate. VAST produced higher relative error compared to the stratified mean in scenarios that involved increasing temperature in the fall season without covariates. Similar to the Yellowtail results, this implies the model-based approach had seasonal trouble with populations shifting into smaller strata where fewer samples take place. Providing covariate information in these cases once again helped the model-based approach to provide improved absolute error estimates relative to the stratified mean. However, we see that adding covariates to VAST in the fall produces higher absolute error values when sampling reduced strata in the constant temperature scenario.

In comparing abundances estimates calculated under the same conditions with the only difference being the temperature scenario, we see that an increasing average temperature had a large negative impact on the model-based estimates. Specifically, when comparing the error of abundance estimates from the constant temperature scenario to the corresponding increasing temperature scenario for Cod, VAST increased by an average factor of 3.57 without covariates and 1.67 with covariates. In considering the average change in the error of stratified mean estimates between constant temperature scenarios and increasing temperature scenarios we surprisingly find an improvement in the error of abundance estimates, with an average decrease by a factor of 0.87.

Haddock Results

Figure 6 reveals some subtle seasonal differences in the percent of haddock in each strata. In the constant temperature scenarios, the spring shows a decrease in strata 19 and 20 that correspond to increases in 16, 24 and 29. This change represents a northward movement between larger centrally located strata. While strata 24 and 29 also increase in the fall under constant temperature, the corresponding decrease is primarily from strata 16 and 13. While similar results can be seen in the spring for the increasing temperature scenario, much more dramatic results exist in the fall under increasing temperature as we see a significant decreases in strata 13, 16, 21, and 22 that leads to the most noticeable increases in strata 17, 18, and 29. This shift represents movement from the shallower and more centrally located strata towards deeper strata located near the edge of the domain. Since stratum 16 contains very favorable habitat including much of the species' spawning ground, the strong shift out of 16 and into the northern most strata of 29 in the fall demonstrates a climate-driven change in movement preference.

Table 9 contains the absolute error between our abundance estimates for Haddock and the true model values. Absolute error values tended to be lower with VAST Settings B about $21/32 \approx 66\%$ of scenarios. We notice that the model-based VAST produced particularly large errors in spring compared to the stratified mean, with added covariates only improving to the level of the stratified mean. VAST shows improved results in fall relative to the stratified mean with added covariates producing extremely low errors in some cases. For Haddock results, adding covariates improves estimates only when all strata are included. That is, similar to Cod, when sampling a reduced domain adding covariates actually decreases VAST's accuracy. Since this occurs in all scenarios, it seems to again be related to failing to accurately monitor stratum 17 near the edge of the domain.

Of the scenarios without covariates, $10/16 \approx 63\%$ had a VAST fit with a lower relative error compared to the stratified mean estimate. The 6 covariate-free VAST estimates that resulted in a higher error than the stratified mean spanned all scenarios and seasons, with several fall errors being especially large (significant overestimates). Adding covariate information resulted in $14/16 \approx 88\%$ of VAST estimates having improved error compared to the stratified mean. The 2 scenarios that produced worse error spanned temperature scenarios, but were both in the spring season when the proportion of the population in each strata remained constant in each scenario. The average change in the error of abundance estimates between constant temperature scenarios and increasing temperature scenarios were 1.42 for VAST estimates without covariates, 1.80 for VAST estimates that included covariates, and 1.37 for stratified mean estimates.

Discussion

To test the impact of shifting populations on abundance estimates, we simulated known population data that included environmental forcing and compared biomass estimates derived from stratified random sampling to the true values. We carried out simulations for 3 species on Georges Bank that took into account different population trends, temperature scenarios, noise in survey samples, and seasonal variation. We compared a design-based estimation approach (stratified mean) with a model-based approach that allows for the inclusion of environmental covariates (VAST) when the entire domain was sampled as well as when a reduced number of strata were included. Our analysis included a comparison of absolute error values between 20-year estimates and consideration of the variation seen year-to-year displayed by each approach as well as the consistency between each 20-year estimate.

Our analysis showed that both approaches are capable of providing abundance estimates that track the true abundance trend. While VAST estimates tended to provide lower relative error values compared to the stratified mean, especially when covariate information was included in the models, VAST Settings A and B combined to produce over 30 abundance estimates with larger error values than the largest stratified mean error. This fact highlights how sensitive VAST is to the choices made regarding settings and data used in analyses. This problem is compounded by the lack of clear guidance regarding how to build and analyze models with the correct inputs. Even more concerning, a recent simulation study showed that the existing diagnostic tools available in VAST sometimes guide users towards using the wrong settings **cite Chris C paper**. The value of model-based approaches such as VAST are clear- they allow users to tailor the model to overcome issues related to the input data by and to account for factors such as environmental change. However, the many consequential decisions that must be made in a given model and the lack of clear criteria for making these decisions makes it challenging to make these choices and even more difficult to determine whether the choices are correct.

Spatial factors contributed to many of the scenarios that produced larger error values seen in our estimates. Flow from the shallow centrally located strata into the more deeper, smaller, and less-sampled eastern strata contributed to VAST failing to accurately modeling the abundance of yellowtail flounder without the addition of covariate information, the impact of which was greatly exacerbated in the increasing temperature scenarios. While adding covariates can help inform the model and improve the estimate as seen with the yellowtail flounder simulation results, including covariates can hinder the model in certain instances. For example, including covariates for haddock when the northern most strata were removed from the survey meant that the population was not being sampled in the coldest part of its domain which ultimately increased the error.

something about seasonal impact seen in all estimates with fall estimates typically noticeably worse. We explored this through the ratio plots. This was mostly a problem with VAST as SM showed more consistent estimates between seasons.

Impact of Covariates

As seen in Table **cite VAST setting table**, VAST models that included covariates used a linear combination of second degree polynomials for habitat and temperature to approximate species-specific covariate responses. Using the exact habitat and temperature covariate information from our population models typically resulted in improved estimates, with about

73% had a lower absolute error compared to the corresponding estimate without covariates (117/160 ≈ 73%), and 77/80 ≈ 96% of VAST models with covariates provided lower absolute error than the corresponding stratified mean estimate. There is more to explore with respect to the impact of covariates. For example, by including just one of the covariates individually, one could test which had a larger impact on abundance estimates. Adding noise to our covariate input would test how robust the model-based estimates are to uncertainty in the covariate information. One could also test the impact of assuming the wrong covariate response function (linear vs polynomial etc).

Of the ~27% of VAST models where covariates did not improve the VAST estimate, most provided a comparable error (for ex, 0.11 vs 0.13). The instances where including covariates provided a significant different in error took place scenarios that included either an increasing temperature and/or reduced sampling domain. More specifically, adding covariate information to our Yellowtail Flounder VAST models always decreased the absolute error in the resulting abundance estimates. However, when a reduced number of strata are sampled for Haddock and Cod, adding covariate information leads to a decrease in performance for fall estimates. The decline in performance can be explained by a failure to sample the full spectrum of temperature values where the species exists, leading to an incomplete estimation of the covariate response. Figure 1 shows the strata excluded from sampling and Figure 7 depicts the resulting covariate response for Yellowtail Flounder and Haddock for the same population scenario. Although strata were excluded for both species, the survey samples for Yellowtail Flounder still ranged across the species preferred values and thus fully formed the covariate response, while the Haddock covariate response did not contain enough samples from the lower temperature range due to the specific strata that were excluded from sampling (ie, northern strata). As a result, when projecting into those strata as seen in the lower portion of Figure 7, Yellowtail estimates with covariate information approximate the correct trend despite these strata being excluded from sampling, while the Haddock estimates that include strata provide that wrong trend and estimate the wrong magnitude of biomass.

Estimation methods that produce large variation between yearly estimates as displayed by the stratified mean can potentially lead to changes in catch limits that do not correspond to the true population trend, which could have a compounding effect. For example, a large, increasing biomass estimate when the population has actually decreased and is fairly low could potentially lead to a windfall catch limit that further reduces the total biomass available the following year. A second overestimate the following year could then have a detrimental impact by reducing the population even further. Conversely, an overly smoothed estimator could miss true signals of change in the population and delay needed management response to either sudden increases or decreases in the population. Our population model has assumed a constant total mortality that accounts for both fishing and natural death, and therefore will not account for impacts of such management decisions. This type of question can be best explored with a management strategy evaluation.

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Data and Code Availability

All data and code used in this work are available at https://github.com/Blevy2/READ-PDB-blevy2-MFS2.

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Tables

Table 3: Parameters used in all population models.

Parameter	Description	Unit	Yellowtail	Cod	Haddock	Source
<U+03C1>	Ford's growth coefficient	1/wk	4.48	4.43	4.49	
M	Natural mortality	1/wk	0.2064	0.2728	0.334	
W1	Weight of fully recruited fish	kg	0.39	2.95	1.12	
W2	Weight of pre-recruit fish	kg	0.13	0.39	0.19	
sigma	Variance in recruited fish	kg*kg	0.55	0.55	0.55	
lambda	Decay rate for movement	-	0.7	0.7	0.7	
spwn	Spawning weeks for species s	wks	9-12	8-13	11-14	
rec	Recruitment weeks for species s	wks	9-12	8-13	11-14	

Table 1. Parameters used in all population models. SAW 1: (NEFSC 2012), SAW 2: (NEFSC 2013), SAW 3: not out yet???

Parameter	Description	Unit	Yellowtail	Cod	Haddock	Source
ρ	Ford's growth coefficient	wk^{-1}	4.48	4.43	4.49	(Thorson 2020)
M	Natural Mortality	wk^{-1}	0.2064	0.2728	0.3340	(Thorson 2020)
F	Fishing Mortality	wk^{-1}	0.358	0.511	0.45	SAW 1, 2, 3
W_R	Weight of fully recruited fish	kg	0.39	2.95	1.12	SAW 1, 2, 3
W_{R-1}	Weight of pre-recruit fish	kg	0.13	0.39	0.19	SAW 1, 2, 3
σ^2	Variance in recruited fish	kg^2	0.55	0.55	0.55	assumed
λ	Decay rate for movement	-	0.7	0.7	0.7	assumed
$Spwn_s$	Spawning weeks for species s	wk	9-12	8-13	11-14	SAW 1, 2, 3
Rec_s	Recruitment weeks for species s	wk	9-12	8-13	11-14	SAW 1, 2, 3

Table XX. Settings for our two VAST models.

Parameter	Description	Settings A	Settings B
ObsModel	Link function and assumed distribution	c(10,2)	c(10,2)

Parameter	Description	Settings A	Settings B
FieldConfig	Specified spatial and/or spatio-temporal variation in predictors	c(Omega1=0, Epsilon1=0, Omega2=1, Epsilon2=1)	c(Omega1=0, Epsilon1=0, Omega2=1, Epsilon2=1)
RhoConfig	Specifying whether intercepts or spatio-temporal variation is structured among time intervals	c(Beta1=3, Beta2=0, Epsilon1=0, Epsilon2=4)	c(Beta1=3, Beta2=3, Epsilon1=0, Epsilon2=4)
X1_formula	Right-sided formula affecting the 1st linear predictor	N/A	X1_formula = ~ poly(Temp, degree=2)
X2_formula	Right-sided formula affecting the 2nd linear predictor	X2_formula = ~ poly(Temp, degree=2) + poly(Habitat, degree=2)	X2_formula = ~ poly(Temp, degree=2) + poly(Habitat, degree=2)

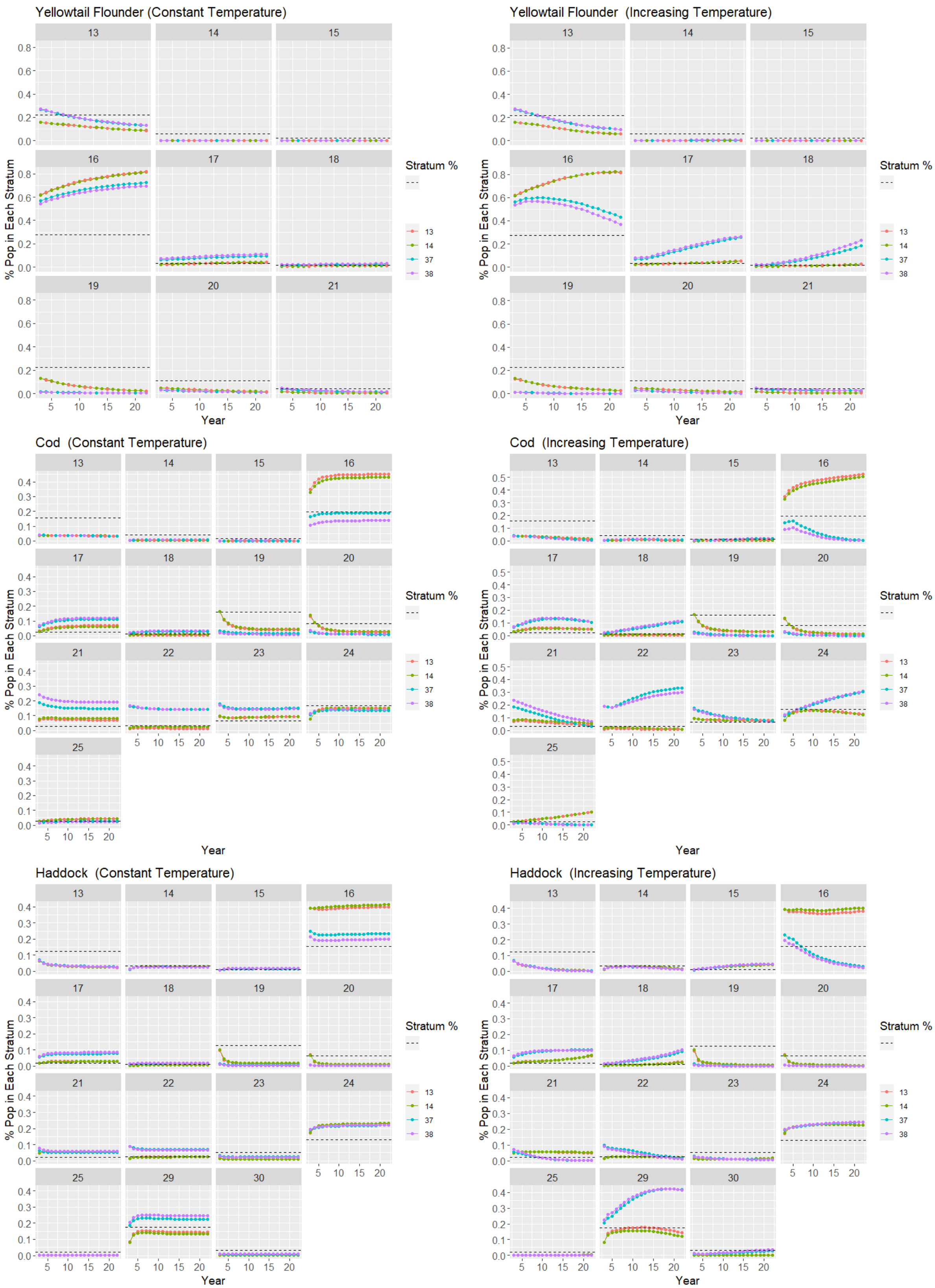

Figure 6: Percent of each species in each strata for during survey weeks in our spatial simulations. All constant temperature scenarios follow the patterns on the left while increasing temperature scenarios follow the patterns on the right. See Figure 1?? for a spatial reference of the Georges Bank strata.

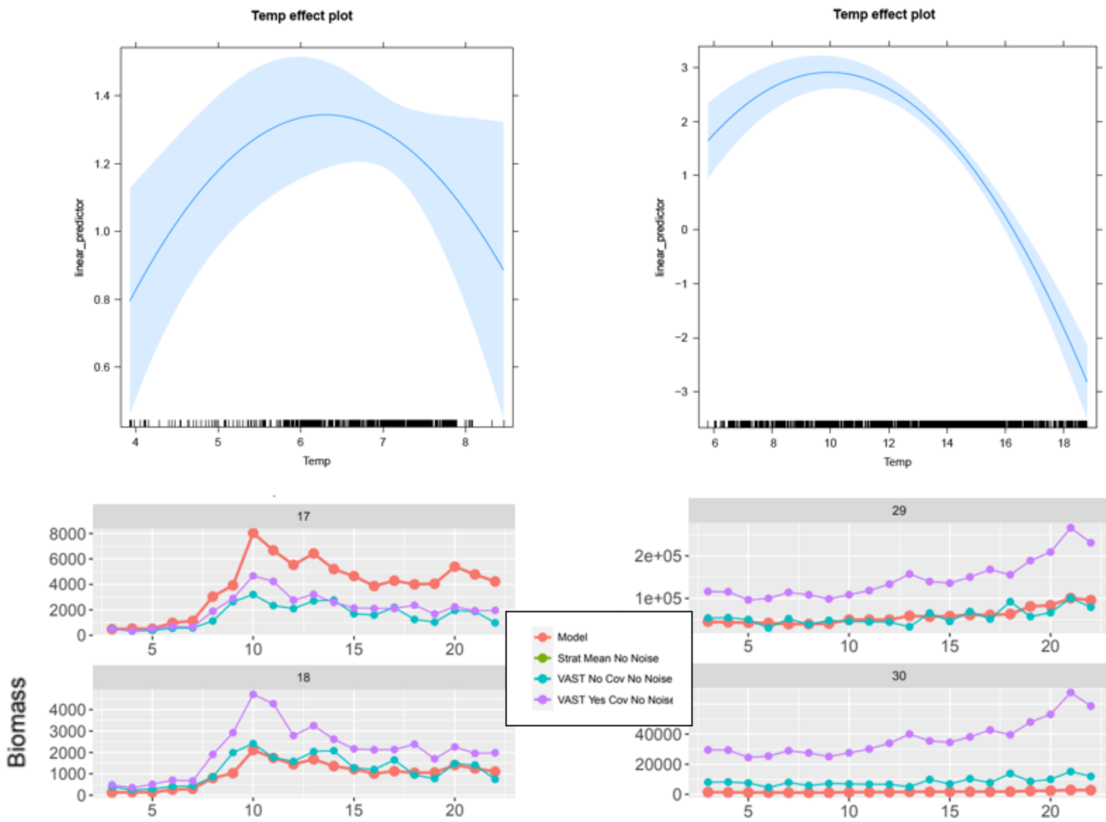

Figure 7: Temperature covariate response plots and resulting population estimate for Yellowtail Flounder on the left and Haddock on the right. In both cases the spatial simulations that were surveyed had an increasing population over time, increasing average temperature, and certain strata excluded from sampling, as shown in Figure 1**check**.

Table 4: Parameters used in population models for each scenario.

Parameter	Description	Unit	Yellowtail	Cod	Haddock
Constant Population					
M+F	Adjusted Mortality (Natural + Fishing)	1/wk	0.764	0.83	0.309
P0	Initial Biomass	kg	3190	21500	180000
a	Max recruitment rate	kg	30400	27900	73600
ß	Recruitment half saturation value	kg	4300	10500	40500
Decreasing Population					
M+F	Adjusted Mortality (Natural + Fishing)	1/wk	0.764	0.623	0.334
P0	Initial Biomass	kg	50000	21500	180000
a	Max recruitment rate	kg	1.07e+12	3.89e+08	4.97e+08
ß	Recruitment half saturation value	kg	2.3e+12	9.8e+08	2.08e+09
Increasing Population					
M+F	Adjusted Mortality (Natural + Fishing)	1/wk	0.564	0.372	0.134
P0	Initial Biomass	kg	3190	21500	180000
a	Max recruitment rate	kg	40000	45000	1e+05
ß	Recruitment half saturation value	kg	43000	62800	405000

Figure 8: Representative example of typical ratio trend for each species, as shown on a log scale.

Table 6: Yellowtail flounder error results with all strata included in calculations. Row colors correspond to the same settings applied in different seasons.

Temperature Scenario	Season	Covariate	Noise	VAST A	VAST B	Stratified Mean
Constant Population						
Constant	spring	no cov	no	0.13	0.11	0.21
Constant	spring	no cov	yes	0.14	0.16	0.25
Constant	spring	w/ cov	no	0.07	0.07	n/a
Constant	spring	w/ cov	yes	0.08	0.08	n/a
Constant	fall	no cov	no	0.63	0.68	0.32
Constant	fall	no cov	yes	0.80	0.77	0.31
Constant	fall	w/ cov	no	0.14	0.08	n/a
Constant	fall	w/ cov	yes	0.17	0.11	n/a
Increasing	spring	no cov	no	0.14	0.11	0.28
Increasing	spring	no cov	yes	0.18	0.15	0.28
Increasing	spring	w/ cov	no	0.05	0.06	n/a
Increasing	spring	w/ cov	yes	0.10	0.12	n/a
Increasing	fall	no cov	no	1.46	1.26	0.51
Increasing	fall	no cov	yes	1.40	1.38	0.5
Increasing	fall	w/ cov	no	0.21	0.23	n/a
Increasing	fall	w/ cov	yes	0.30	0.28	n/a
Decreasing Population						
Constant	spring	no cov	no	0.11	0.08	0.23
Constant	spring	no cov	yes	0.12	0.11	0.27
Constant	spring	w/ cov	no	0.07	0.06	n/a
Constant	spring	w/ cov	yes	0.11	0.07	n/a
Constant	fall	no cov	no	0.97	0.81	0.41
Constant	fall	no cov	yes	0.99	1.09	0.37
Constant	fall	w/ cov	no	0.16	0.08	n/a
Constant	fall	w/ cov	yes	0.29	0.18	n/a
Increasing	spring	no cov	no	0.17	0.15	0.22
Increasing	spring	no cov	yes	0.15	0.17	0.26
Increasing	spring	w/ cov	no	0.08	0.07	n/a
Increasing	spring	w/ cov	yes	0.16	0.10	n/a
Increasing	fall	no cov	no	1.17	1.06	0.28
Increasing	fall	no cov	yes	1.14	1.10	0.25
Increasing	fall	w/ cov	no	0.40	0.15	n/a
Increasing	fall	w/ cov	yes	0.40	0.20	n/a
Increasing Population						
Constant	spring	no cov	no	0.46	0.13	0.16
Constant	spring	no cov	yes	0.43	0.21	0.22
Constant	spring	w/ cov	no	0.06	0.06	n/a
Constant	spring	w/ cov	yes	0.08	0.07	n/a
Constant	fall	no cov	no	0.40	0.36	0.34
Constant	fall	no cov	yes	0.38	0.44	0.46
Constant	fall	w/ cov	no	0.11	0.08	n/a
Constant	fall	w/ cov	yes	0.24	0.17	n/a
Increasing	spring	no cov	no	0.16	0.13	0.32
Increasing	spring	no cov	yes	0.21	0.16	0.32
Increasing	spring	w/ cov	no	0.06	0.07	n/a
Increasing	spring	w/ cov	yes	0.12	0.10	n/a
Increasing	fall	no cov	no	0.71	0.66	0.3
Increasing	fall	no cov	yes	1.03	0.71	0.39
Increasing	fall	w/ cov	no	0.43	0.21	n/a
Increasing	fall	w/ cov	yes	0.51	0.37	n/a

Table 7: Yellowtail flounder error results with certain strata excluded from calculations. Row colors correspond to the same settings applied in different seasons.

Temperature Scenario	Season	Covariate	Noise	VAST A	VAST B	Stratified Mean
Constant Population						
Constant	spring	no cov	no	0.24	0.19	0.27
Constant	spring	no cov	yes	0.16	0.15	0.22
Constant	spring	w/ cov	no	0.19	0.19	n/a
Constant	spring	w/ cov	yes	0.12	0.14	n/a
Constant	fall	no cov	no	0.30	0.25	0.47
Constant	fall	no cov	yes	0.78	0.36	0.44
Constant	fall	w/ cov	no	0.22	0.19	n/a
Constant	fall	w/ cov	yes	0.24	0.17	n/a
Increasing	spring	no cov	no	0.23	0.17	0.31
Increasing	spring	no cov	yes	0.25	0.19	0.29
Increasing	spring	w/ cov	no	0.17	0.17	n/a
Increasing	spring	w/ cov	yes	0.62	0.15	n/a
Increasing	fall	no cov	no	2.22	0.75	0.64
Increasing	fall	no cov	yes	1.75	0.89	0.59
Increasing	fall	w/ cov	no	0.24	0.20	n/a
Increasing	fall	w/ cov	yes	0.59	0.13	n/a
Decreasing Population						
Constant	spring	no cov	no	0.31	0.19	0.25
Constant	spring	no cov	yes	0.27	0.16	0.27
Constant	spring	w/ cov	no	0.19	0.19	n/a
Constant	spring	w/ cov	yes	0.15	0.16	n/a
Constant	fall	no cov	no	0.53	0.24	0.55
Constant	fall	no cov	yes	0.53	0.36	0.53
Constant	fall	w/ cov	no	0.18	0.23	n/a
Constant	fall	w/ cov	yes	0.16	0.24	n/a
Increasing	spring	no cov	no	0.18	0.14	0.32
Increasing	spring	no cov	yes	0.37	0.15	0.29
Increasing	spring	w/ cov	no	0.21	0.22	n/a
Increasing	spring	w/ cov	yes	0.16	0.21	n/a
Increasing	fall	no cov	no	0.90	0.60	0.54
Increasing	fall	no cov	yes	0.84	0.62	0.48
Increasing	fall	w/ cov	no	0.32	0.31	n/a
Increasing	fall	w/ cov	yes	0.36	0.32	n/a
Increasing Population						
Constant	spring	no cov	no	0.22	0.15	0.2
Constant	spring	no cov	yes	0.19	0.11	0.22
Constant	spring	w/ cov	no	0.17	0.17	n/a
Constant	spring	w/ cov	yes	0.11	0.13	n/a
Constant	fall	no cov	no	0.19	0.11	0.41
Constant	fall	no cov	yes	0.26	0.21	0.46
Constant	fall	w/ cov	no	0.21	0.22	n/a
Constant	fall	w/ cov	yes	0.17	0.19	n/a
Increasing	spring	no cov	no	0.31	0.33	0.4
Increasing	spring	no cov	yes	0.30	0.26	0.38
Increasing	spring	w/ cov	no	0.30	0.30	n/a
Increasing	spring	w/ cov	yes	0.31	0.25	n/a
Increasing	fall	no cov	no	0.56	0.49	0.7
Increasing	fall	no cov	yes	0.58	0.48	0.69
Increasing	fall	w/ cov	no	0.48	0.53	n/a
Increasing	fall	w/ cov	yes	0.47	0.50	n/a

Table 8: Cod error results.

Strata	Noise	Season	VAST NC A	VAST NC B	VAST WC A	VAST WC B	Stratified Mean
Constant Temp.							
all	no	spring	0.11	0.11	0.13	0.12	0.36
all	yes	spring	0.14	0.12	0.09	0.15	0.35
all	no	fall	0.23	0.19	0.09	0.05	0.49
all	yes	fall	0.34	0.30	0.20	0.23	0.41
reduced	no	spring	0.25	0.17	0.22	0.24	0.41
reduced	yes	spring	0.25	0.20	0.14	0.23	0.46
reduced	no	fall	0.16	0.21	0.26	0.33	0.60
reduced	yes	fall	0.16	0.18	0.26	0.31	0.58
Increasing Temp.							
all	no	spring	0.12	0.12	0.16	0.15	0.25
all	yes	spring	0.16	0.19	0.23	0.19	0.27
all	no	fall	0.86	0.76	0.47	0.13	0.45
all	yes	fall	1.13	0.89	0.55	0.33	0.44
reduced	no	spring	0.29	0.26	0.22	0.21	0.34
reduced	yes	spring	0.32	0.19	0.19	0.11	0.33
reduced	no	fall	1.41	0.79	0.37	0.26	0.62
reduced	yes	fall	2.09	1.37	0.40	0.26	0.57

Table 9: Haddock error results.

Strata	Noise	Season	VAST NC A	VAST NC B	VAST WC A	VAST WC B	Stratified Mean
Constant Temp.							
all	no	spring	0.45	0.49	0.13	0.18	0.18
all	yes	spring	0.55	0.73	0.18	0.43	0.14
all	no	fall	0.31	0.28	0.05	0.05	0.26
all	yes	fall	0.45	0.41	0.15	0.06	0.27
reduced	no	spring	0.34	0.34	0.30	0.35	0.45
reduced	yes	spring	0.31	0.30	0.45	0.33	0.44
reduced	no	fall	0.34	0.36	0.46	0.48	0.54
reduced	yes	fall	0.29	0.33	0.41	0.46	0.50
Increasing Temp.							
all	no	spring	0.28	0.25	0.11	0.05	0.26
all	yes	spring	0.35	0.30	0.11	0.06	0.31
all	no	fall	0.82	0.89	0.23	0.23	0.40
all	yes	fall	1.01	1.04	0.29	0.35	0.39
reduced	no	spring	0.35	0.32	0.41	0.40	0.44
reduced	yes	spring	0.33	0.38	0.39	0.37	0.36
reduced	no	fall	0.48	0.44	0.61	0.64	0.72
reduced	yes	fall	0.49	0.42	0.60	0.62	0.70