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

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Competing interests: The authors declare there are no competing interests.

[[Chris comments in double square brackets, search for them to see comments]]

Abstract

An Abstract

Keywords

keyword 1, keyword 2

Introduction

much of below is from https://apps-nefsc.fisheries.noaa.gov/nefsc/ecosystem-ecology/ or https://www.fisheries.noaa.gov/data-tools/fisheries-economics-united-states-data-and-visualizations

- The eastern continental shelf is ecologically diverse and economically important

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. Maintaining a healthy ecosystem is therefore vital to sustained ecological health and economic prosperity of the region.

- Bottom trawl survey is important for monitoring population trends

Fish stocks in this highly productive and economically important region are managed by the National Oceanic and Atmospheric Administration's (NOAA) Northeast Fisheries Science Center (NEFSC) in Woods Hole, Massachusetts. Federal scientists assess the health and abundance of each commercial fish stock using fishery-independent bottom trawl survey data that has been collected by NOAA throughout the region since 1963 (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. Since most spatial analyses and projections of future distributions typically assume a constant survey catchability and/or availability over time, NOAA's survey design includes sampling Georges Bank during approximately the same 3-4 week time period in each season.

- Climate change is happening

Due to a combination of climate change and shifts in circulation, the Northeast United States continental shelf has experienced rapid warming in recent decades, resulting in a shift in spatial distributions of many species. 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. We are therefore interested in analyzing the impact of climate change on the accuracy of future stock assessment models as measured by NOAA's ongoing bottom-trawl survey along the East coast.

use more info from initial proposal

- Briefly describe our study to test this

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 can then consider the impact of climate change by simulating scenarios with repeating temperature patterns and those where temperature increases on average over time. In both cases we analyze the ability of stratified random sampling to track population trends.

Methods

- Describe simulation study

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 temperature preferences. Model dynamics are driven by a time series of temperature gradients that were estimated from data 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 predictable, repeating spatial patterns, whereas using a temperature gradient that increases on average throughout the simulation leads to spatial distributions that shift over time, approximating the future distribution in the region under climate change. We conducting stratified random sampling on our simulation output to mimic the bottom trawl survey and compare the ability of contemporary indexing methods to track population trends.

Population Model Formulation

– Used MixFishSim.

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. 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 inhabit 13 strata, and Yellowtail exist in 9 strata. Figure 1 shows the regions used in our models.

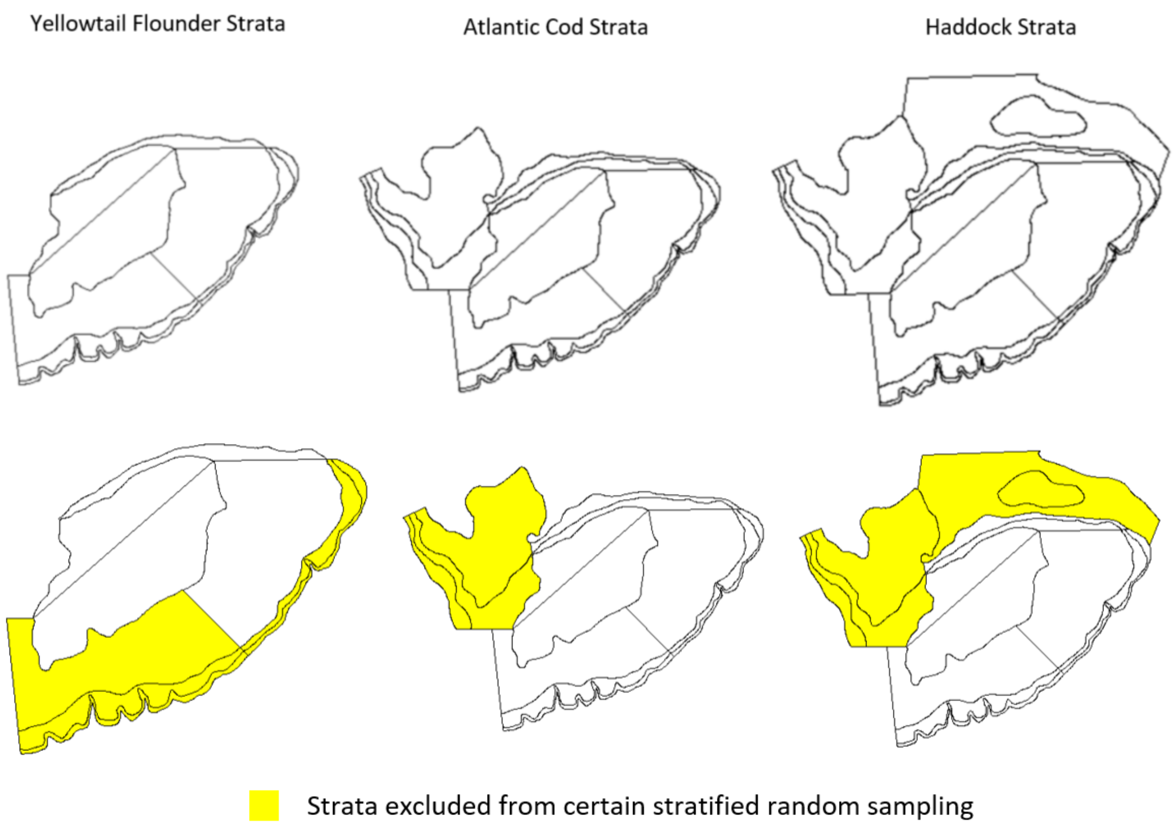

Figure 1: Strata inhabited by each species in our population models.

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, natural and fishing mortality, and the addition of new recruits. We chose to represent recruitment in the model using a Beverton-Holt formulation **cite**. 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.

Movement

The package was designed to generate theoretical habitat preferences using Gaussian Random Fields that combine with hypothetical temperature gradients 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 following sections describe how we formulated the habitat and temperature components to model real species on the northeast continental shelf.

Habitat Input

Species-specific habitat preferences were derived using the *lrren* tool from the R package *envi* (Buller 2022) to create a niche model for each species. 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 [[I don't think we need to cite the trawl data because we said we were using trawl data above]] **BL: Does trawl data ever get cited? It was not cited above. cite trawl data?**. We combined data from both the fall and spring surveys to obscure the influence of temperature so that the niche model would 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 **cite arcmap** using point data collected by the United States Geologic Survey (USGS) (McMullen et al. n.d.). Since the values in $Hab^2_{J,s}$ are required to be between 0 and 1, we transform 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 $Hab^2_{J,s}$ for each species.

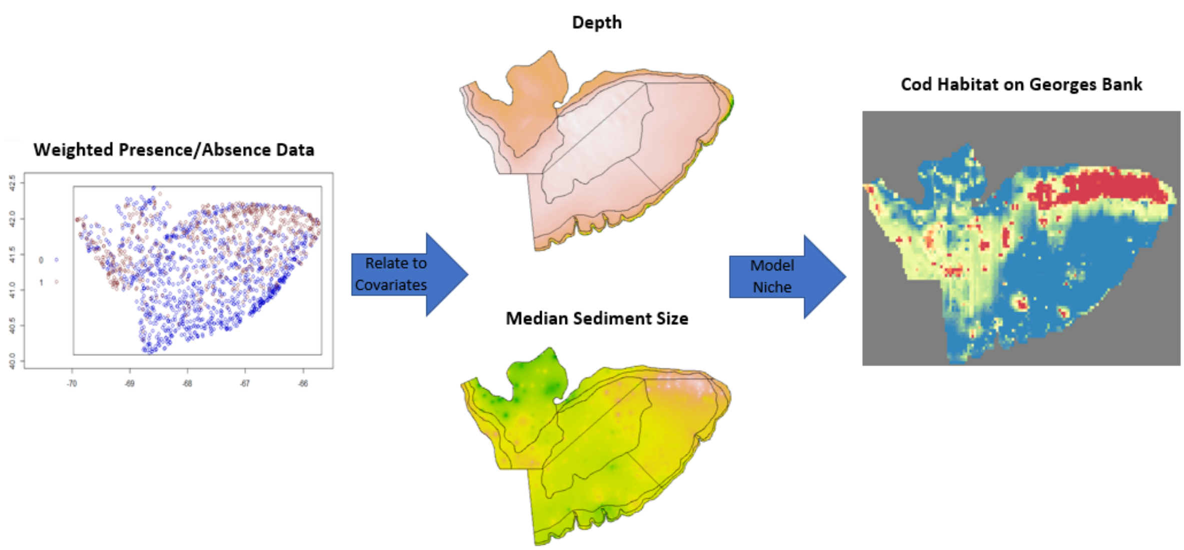

Figure 2: Visual representation of niche model for Cod.

Temperature Input

Each species is assumed to have normally distributed temperature preferences ($N(\mu, \sigma)$). We assume Yellowtail Flounder's preferences are $N(8.75, 4.25)$, while Haddock and Cod have preferences $N(9, 4)$. We chose these values by combining information in the literature with temperatures recorded in the bottom trawl survey. Weekly estimated temperature data for the region for 2012 was obtained from FVCOM (Chen et al. 2006). We chose to repeat

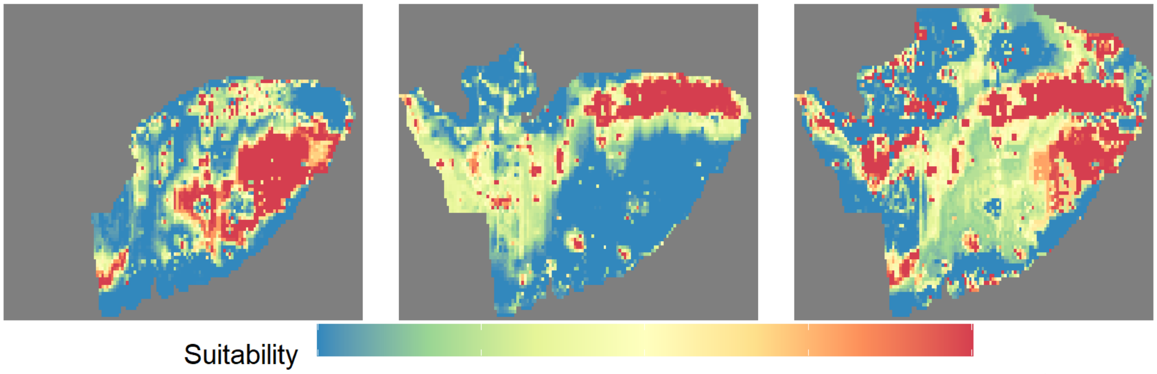

Figure 3: Static habitat preferences for each species in our population models (Yellotwtail, Cod, Haddock).

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 gif in final submission**

–Describe difference between increasing and constant temperature scenarios (images?)

In equation (1), $Hab^2_{J,s}$ is constant for the duration of the simulation, while $Tol_{c,s,wk}$ changes each week. 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

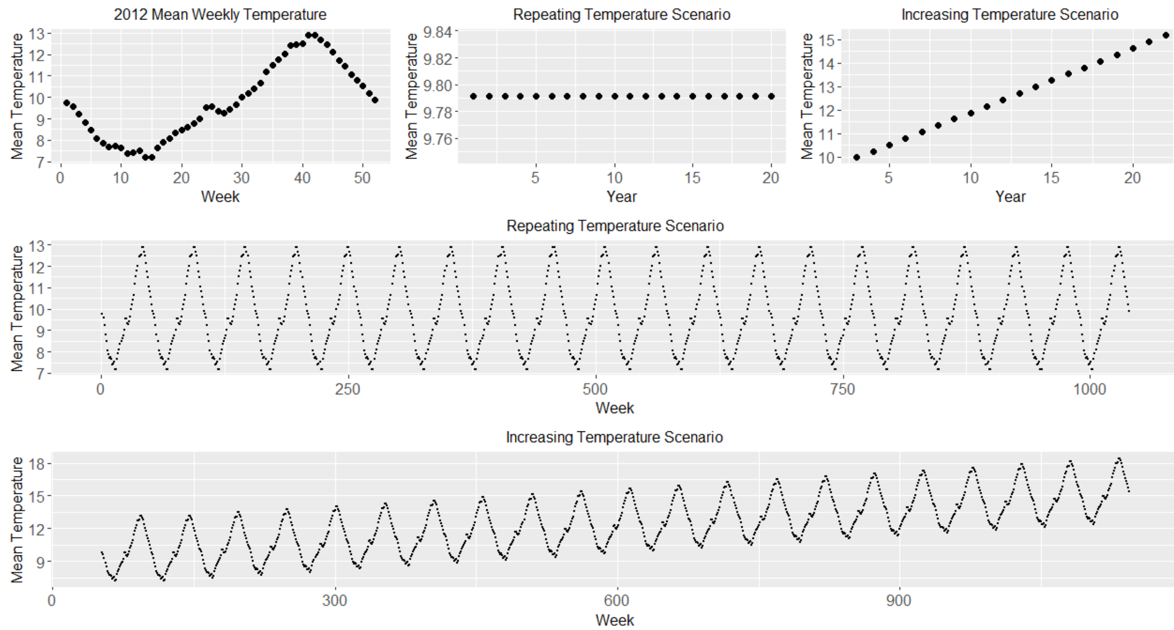

Figure 4: Mean trends of temperature data used in our model.

may not be true for increasing temperature scenarios due to evolving spatial preferences.

– Describe each scenario that is considered

We consider 20 year simulations under three population parameter scenarios for each of our three species- a scenario where parameters result in each population increasing over time, one where the populations are relatively constant over time, and a scenario where the parameter combination results in each population decreasing over time. Each of these three scenarios is paired with a temperature gradient that repeats as well as one that increasing roughly 5 degrees Celsius over the duration of the 20 year simulation. We therefore simulate 6 scenarios for each population.

Simulating Bottom Trawl Survey and Population Indexing

-Describe post hoc sampling process and how data is used

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, and the number of the samples taken reflect true target values for each strata. Most strata contain enough cells that we were able to generate a list of sampling locations without replacement, allowing us to sample a unique random cell in each survey over the duration of the simulation. For strata that contain small numbers of cells, we generate a random sampling locations with replacement of cells previously sampled. We then use the biomass collected from our samples in contemporary population indexing methods to estimate population trends. Knowing the true population values in our simulations allows us to compare the error calculated from each estimation method.

–Stratified mean vs VAST with and without covariates

Stock assessment scientists use samples from the bottom trawl survey to estimate the abundance for each fish stock. There are a number of approaches to obtain abundance estimates including traditional design-based estimates to model-based estimates that range 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 or allow the inclusion of environmental influences. 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.

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 geometric 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. The stratified mean calculations are straightforward and quick, while VAST models require numerous user inputs and can take on the order of hours to complete.

We follow the advice given in (Thorson 2019) to build VAST models to estimate biomass on Georges Bank 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 also carried out the same process running models without covariate information as well as including covariates in our model. We considered covariates in the form of dynamic temperature values and/or static habitat values ($Hab_{J,s}$) from our population model. When using covariates we ultimately decided to provide the most information to the model by including both temperature and habitat covariates for both linear predictors. 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 ultimately compared the performance of two sets of settings in our VAST models, which can be seen in Table**??**.

Our goal is to determine indexing approaches and settings that are robust to future 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 **cite?** and/or climate change causing a population to move into previously uninhabited strata. To simulate the impact of noise,

Table 1: Each index estimate chooses one condition from each of the following 7 columns. There are 3*3*2*2*2*2*2 = 288 VAST model combinations and 3*3*2*2*2*2 = 144 stratified mean estimates.

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					

we compare indexing estimates after adding noise to our samples versus those using the true sampling values. **BL: Help with correct notation for adding noise**. We simulate the effect of populations moving into new habitat by comparing indexing estimates using samples from all strata inhabited by each species on 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. Tabl XXX [[needs to be added]] lists all strata inhabited by each species, those that are removed from certain calculations, and the explanation of why these strata were removed.

When combining population trends for each species, differing temperature scenarios, altering seasons, and sampling possibilities (noise, strata, covariates) there are a large number of scenario combinations to consider. The columns in Table 1 show the choices that define each scenario.

Results

The goal of our project was to analyze the ability of contemporary population indexing methods to track population trends under a variety of conditions, as depicted in Table 1. 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. The specific population trends used in our analyses can be see in Figure 5.

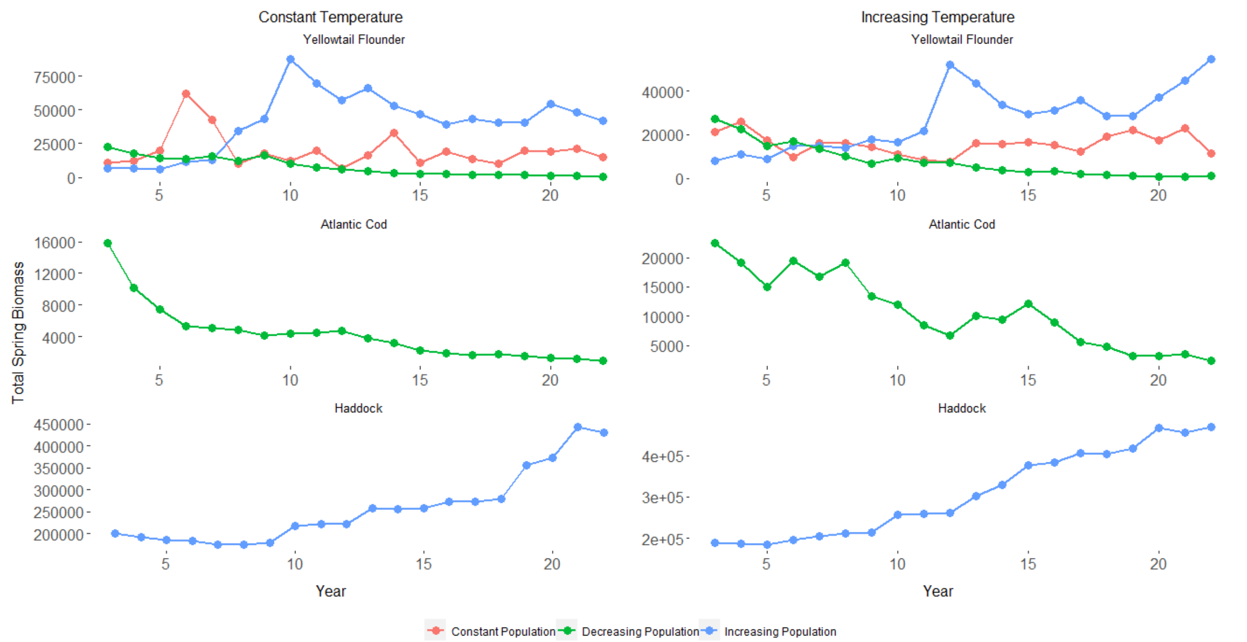

Figure 5: True population trends used in indexing analyses. Spring biomass plots are shown with fall values being very similar.

Tables 6, 7, 8, and 9 contain the results of our comparison between the absolute error of abundance estimates and model output. General themes are that VAST estimates provide lower errors relative to those derived from the stratified mean, with VAST models that include covariate information providing the lowest overall errors. We also see individual cases where the stratified mean produced the lowest absolute error and instances where including covariates in VAST models actually increase the absolute error. When we reduce the number of strata that are included in indexing calculations to simulation 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.

(see Table 8) In the Cod results, when using reduced strata adding covariates produces worst VAST results (though still better than stratified mean). VAST without covariates much worse than stratified mean in fall with increasing temperature and all strata, but adding covariates corrects this.

(see Table 9) For Haddock, VAST has a particularly hard time in spring regularly producing larger errors than 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.

In considering the Yellowtail Flounder results in Tables 6 and 7, 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. However, there are several instances in which VAST failed to provide improved abundance estimates during the fall season without covariate information, producing the largest errors seen in the Table. These errors are corrected by including covariate information allowing for an improved VAST estimate that are significantly lower than their stratified mean counterparts.

Notes on differences between VAST settings: For YTF, 29/96 ~ 30% of VAST runs with new settings were better (70% were worse). 80/96 ~ 83% of scenarios had a VAST run with a better error than the stratified mean. 15/16 of the times the stratified mean was better VAST was not using covariates. The 1 time that VAST was using covariates and was still worse than the stratified mean was IncPop_IncTemp_Allstrata_WCov_WNoise in the Fall (VAST had strong overestimate in the fall during IncPOP_IncTemP_allstrata for Had and YT). The overestimate in the fall only seems to be related to the way the population shifts between season. Looking at the percent shift plots, the population is shifting out of strata 16 in both seasons (large east strata). In the spring the population is shifting mostly into strata 17 (thin strata adjacent to 16), but in the fall they are shifting into both 17 and 18 (18 thin one adjacent to 17). Thus it seems like with much of the population concentrated in the really small outer most strata, VAST produces an underestimate, even with covariates

For Haddock (IncPop), 18/32 ~ 57% of VAST runs better with new settings. 24/32 = 75%

of scenarios had a VAST run with a better error than the stratified mean. 14/16 VAST were better with covariates (the two that were worse were essentially the same) while only 10/16 were better without covariates. Stratified mean tended to perform better when all strata were included in the calculation, while VAST tended to perform better when strata are removed.

For Cod (DecPop), only 11/32 ~ 34% of VAST runs were better with new settings. 28/32~ 88% of scenarios had a VAST run with a better estimate than the stratified mean. All 16/16 = 100% of VAST runs with a covariate were better than the stratified mean. 12/16 VAST were better without covariates. The 4 runs without covariates that were worse were all extremely large errors and all from increasing temp in the fall (with and without all strata and noise). In the fall the population is moving out of strata 16 (large eastern strata) and 21 (north large) and into a number of strata (22 (tiny north), 24 (large north), 18 (tiny north)). Might be having trouble tracking in to smaller strata again.

[[We'll want to expand the results section to focus on the impact of each factor one at at time within each species. This will be a bit dull, but it is important to walk through the results in words to ensure that readers get the message. They can of course examine the tables in detail and draw their own conclusions, but we should put our interpretation down on paper.]]

Cod Results

Of the scenarios without covariates, 12/16 = 75% had a VAST fit with a lower relative error compared to the stratified mean estimate. Including detailed covariate information in our Cod VAST estimates resulted in all 16/16 = 100% having a lower relative error than the corresponding stratified mean estimate. The 4 scenarios without covariates that had a higher VAST error were each overestimates for the fall season that involved an increasing temperature gradient. As seen in Figure XXX, Cod are shifting their spatial distribution much more in the fall than they are in the spring. While adding covariates to these fits allowed for an improved error relative to the stratified mean, the VAST abundance still display an overestimate early in the time series before covariates correct the trend, allowing for a lower overall absolute error **(show these plots? IncTemp fall scenarios)**.

Haddock Results

$10/16 \approx 63\%$ of the scenarios without covariates 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 procedure 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.**why?? doesnt make sense. the values with cov are about the same as SM** Qualitatively, including covariate information has a larger impact on decreasing the relative error compared to the stratified mean compared to failing to include covariates.

Yellowtail Flounder Results

Of the 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. These 15 Fall estimates span all other scenario variations and had a common theme of producing abundance estimates that are well above the true model value. Including detailed covariate information made a noticeable difference in our Yellowtail Flounder VAST estimates. Of the VAST estimates that included covariates information, $47/48 \approx 98\%$ had a lower relative error than the corresponding stratified mean estimate. **For discussion: clearly our perfect covariate information made a big difference here, but the question is could we achieve similar results without "perfect" information? Which covariate is best?**

Good question for future research

A more careful visual analysis of all error plots for each species reveals that VAST estimates tend to provide error estimates that are too high, while the stratified mean estimates are, on average, too low. Additionally, model/estimate ratio plots for all VAST estimates remain much closer to the desired value of 1 compared to stratified mean estimates, which can range as high as 10 and exhibit large yearly changes.

Discussion

Estimation methods that have large, inaccurate swings (stratified mean) can lead to changes in quotas that do not correspond to the true population trend, which could have a compounding effect (can lead to quotas that are too high/low given an incorrect assumption of increase/decrease in biomass). Our model has a constant assumed mortality that accounts for fishing and natural death and will not account for impacts of these decisions. VAST may provide more consistent biomass predictions(?)

[[some things that I think we'll need to address, in addition to those mentioned above are (in no particular order): number of simulations done for each scenario - time required to do them and analyses pros and cons of using VAST with covariates in a changing environment implications for current practice of using stratified mean (not horrible, but might be able to do better with model-based using covariates if enviro changing, note we don't want to say stratified mean should not be used because that will draw a lot of tomato throwing) future work - some of the ideas we've discussed already could be mentioned limitations to our study perhaps for discussion, but we should mention somewhere that MFS only tracks biomass not age structure, the latter is important for stock assessments but not considered in this paper]]

Acknowledgements

[[we should thank Jim (obviously), but also those who helped you with the habitat data (robyn, david Chev.) and others? also should note that funding provided by Climate-Groundfish source (I'll dig up the official name of the funding source)]]

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	

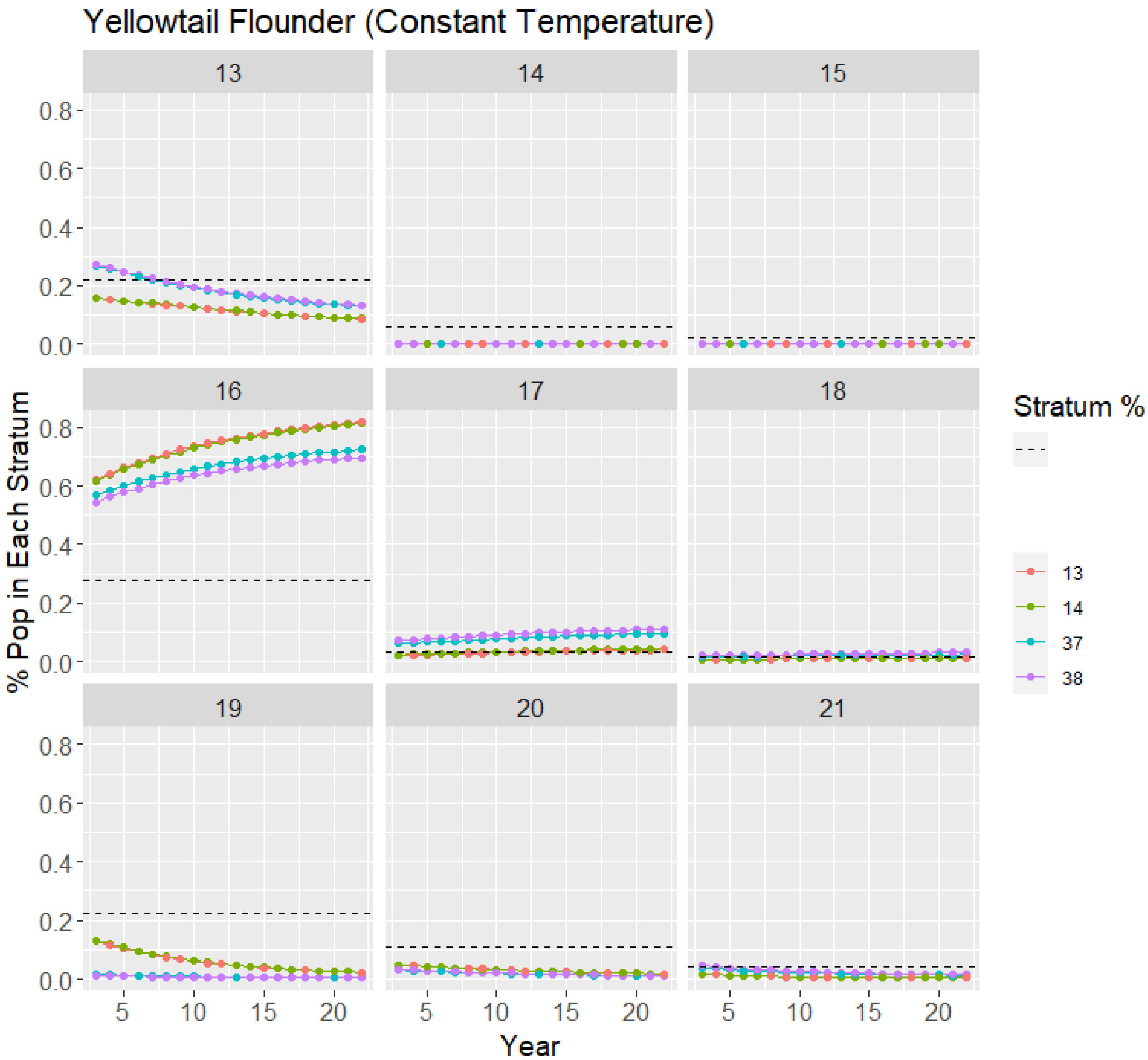
Table 1. Parameters used in all population models.

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

Table XX. Parameters used in all VAST models.

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

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


Yellowtail Flounder (Constant Temperature)
13
14
15
16
17
18
19
20
21
0.0
0.2
0.4
0.6
0.8
% Pop in Each Stratum
5
10
15
20
Year
Stratum %
13
14
37
38

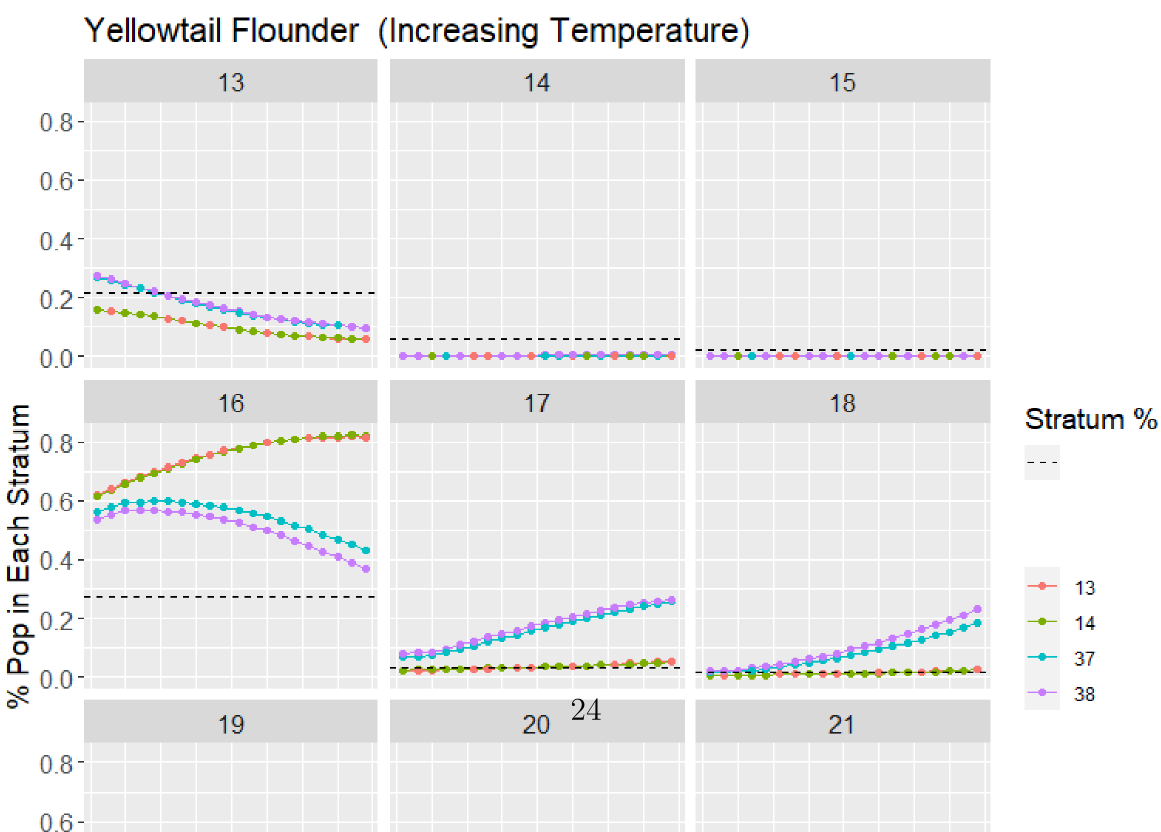

Yellowtail Flounder (Increasing Temperature)
13
14
15
16
17
18
19
20
21
0.0
0.2
0.4
0.6
0.8
% Pop in Each Stratum
Stratum %
13
14
37
38

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

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	0.21
Constant	spring	w/ cov	yes	0.08	0.08	0.25
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	0.32
Constant	fall	w/ cov	yes	0.17	0.11	0.31
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	0.28
Increasing	spring	w/ cov	yes	0.10	0.12	0.28
Increasing	fall	no cov	no	1.46	1.26	0.51
Increasing	fall	no cov	yes	1.40	1.38	0.50
Increasing	fall	w/ cov	no	0.21	0.23	0.51
Increasing	fall	w/ cov	yes	0.30	0.28	0.50
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	0.23
Constant	spring	w/ cov	yes	0.11	0.07	0.27
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	0.41
Constant	fall	w/ cov	yes	0.29	0.18	0.37
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	0.22
Increasing	spring	w/ cov	yes	0.16	0.10	0.26
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	0.28
Increasing	fall	w/ cov	yes	0.40	0.20	0.25
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	0.16
Constant	spring	w/ cov	yes	0.08	0.07	0.22
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	0.34
Constant	fall	w/ cov	yes	0.24	0.17	0.46
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	0.32
Increasing	spring	w/ cov	yes	0.12	0.10	0.32
Increasing	fall	no cov	no	0.71	0.66	0.30
Increasing	fall	no cov	yes	1.03	0.71	0.39
Increasing	fall	w/ cov	no	0.43	0.21	0.30
Increasing	fall	w/ cov	yes	0.51	0.37	0.30

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	0.27
Constant	spring	w/ cov	yes	0.12	0.14	0.22
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	0.47
Constant	fall	w/ cov	yes	0.24	0.17	0.44
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	0.31
Increasing	spring	w/ cov	yes	0.62	0.15	0.29
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	0.64
Increasing	fall	w/ cov	yes	0.59	0.13	0.59
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	0.25
Constant	spring	w/ cov	yes	0.15	0.16	0.27
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	0.55
Constant	fall	w/ cov	yes	0.16	0.24	0.53
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	0.32
Increasing	spring	w/ cov	yes	0.16	0.21	0.29
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	0.54
Increasing	fall	w/ cov	yes	0.36	0.32	0.48
Increasing Population						
Constant	spring	no cov	no	0.22	0.15	0.20
Constant	spring	no cov	yes	0.19	0.11	0.22
Constant	spring	w/ cov	no	0.17	0.17	0.20
Constant	spring	w/ cov	yes	0.11	0.13	0.22
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	0.41
Constant	fall	w/ cov	yes	0.17	0.19	0.46
Increasing	spring	no cov	no	0.31	0.33	0.40
Increasing	spring	no cov	yes	0.30	0.26	0.38
Increasing	spring	w/ cov	no	0.30	0.30	0.40
Increasing	spring	w/ cov	yes	0.31	0.25	0.38
Increasing	fall	no cov	no	0.56	0.49	0.70
Increasing	fall	no cov	yes	0.58	0.48	0.69
Increasing	fall	w/ cov	no	0.48	0.53	0.70
Increasing	fall	w/ cov	yes	0.47	0.50	0.69

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