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

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. [@nefmc20]

- 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 (cite survey paper). 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 **just listed a few uses of survey. change/add others?**.

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 during approximately the same 2-3 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. The implication of this is that the bottom trawl survey is actually sampling the population during a different life cycle stage than was originally assumed, which can lead to biased stock assessments. 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.

- say something about our study species? Past abundance history, biological characteristics, others? Maybe better suited in below section

use more info from initial proposal

- Fish are changing spatial distribution and have altered life stages (?) because of climate change NYE paper
- Population indexing methods may be becoming biased as a result
- 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 George's 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. 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. Describe edits made to package

We use the R package *MixFishSim* (MFS) to model our populations [@dolder2020highly]. 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 George's Bank to use as our modeling environment. We discritized the region into a raster with 88 rows and 144 columns. 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.

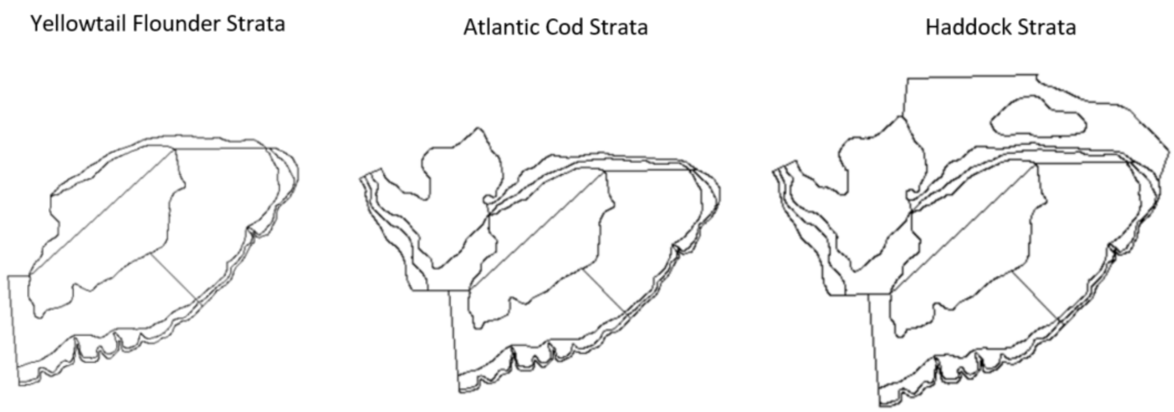

Figure 1: Strata inhabited by each species in our population models.

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 [@dolder2020highly]. 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 7.

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* [@envi] 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 **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 [@chen2006unstructured]. The mean sediment size raster was interpolated in ArcMap using the natural neighbor interpolation method **cite arcmap or more?** using point data collected by the United States Geologic Survey (USGS) [@mcmullen2005usgs]. 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.

Temperature Input

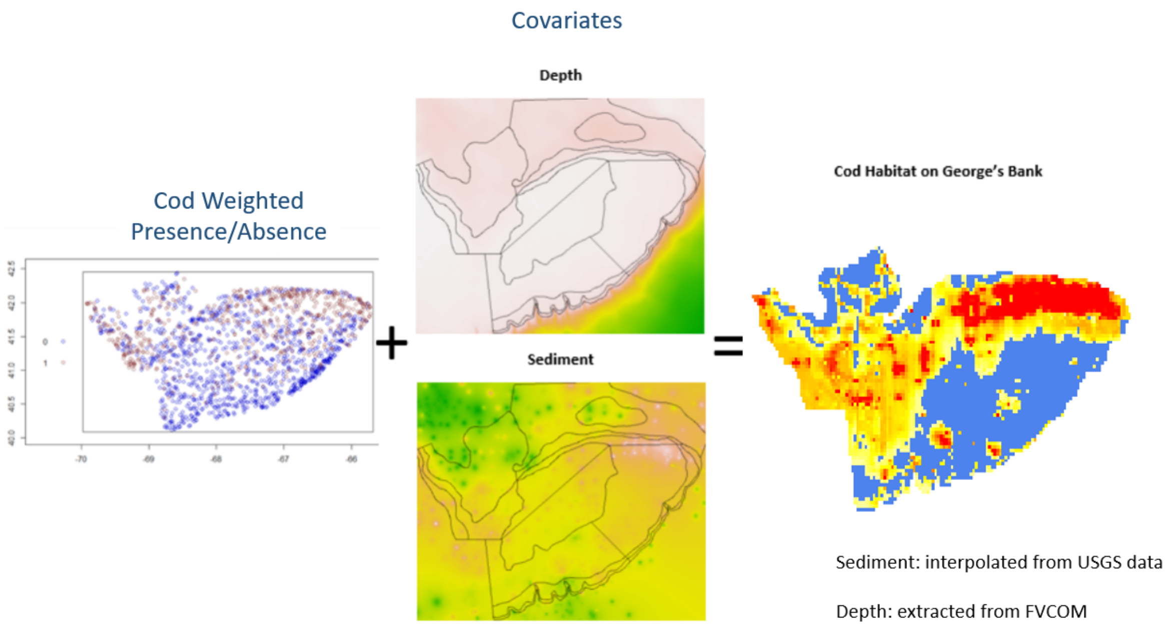

Figure 2: Visual representation of niche model for Cod.

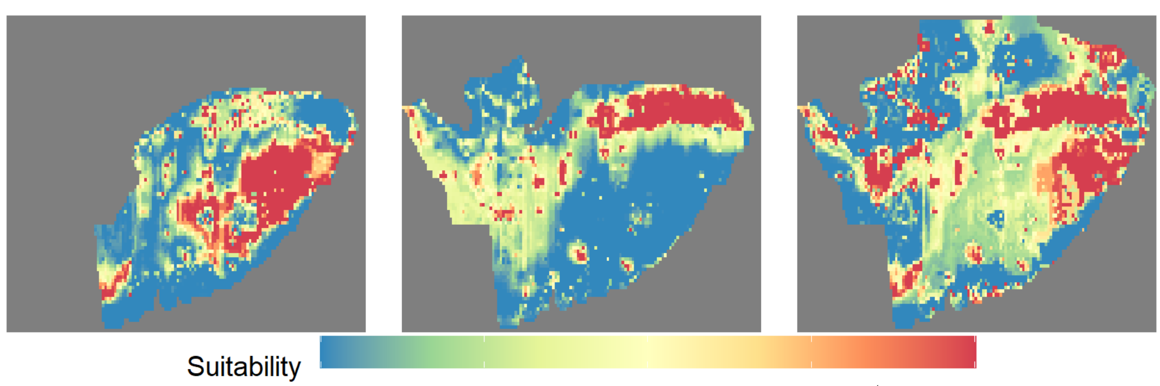

Figure 3: Static habitat preferences for each species in our population models (Yellotwtail, Cod, Haddock).

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 [@chen2006unstructured]. We chose 2012 because the data displayed an average temperature pattern that consistently oscillated between maximum and minimum temperature values. This data was also transform to create an oscillating pattern that increases 5 degrees Celsius on average over the duration of the simulation. **show images of temperature and/or and/or temp videos??? and/or average temperature oscillations?**

–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 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 a total of 6 scenarios. **show line plot of population for each?**

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 in the same weeks that the Spring and Fall surveys take place and the number of the samples taken in each strata reflect true values. Most strata contain enough cells to sample a unique location in each survey over the duration of the simulation. For smaller strata we must repeat some sample locations. 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

We compare the yearly estimated of abundance obtained from the stratified mean to estimates obtained from the Vector-Autoregressive Spatio-temporal (VAST) model. The stratified mean is a typical survey-based approach that scales individual samples to the strata-level by considering the area of each strata, before scaling to the region-level based on the relative size of each strata. VAST is a spatio-temporal statistical framework that models both abundance (biomass) and probability of occurrence (presence/absence). 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). The stratified mean calculations are straightforward and quick, while VAST models require numerous user inputs and take on the order of hours to complete.

We follow the advice given in [@thorson2019guidance] to build VAST models to estimate biomass on George's Bank using stratified mean samples from our model output. In addition to exploring different link functions and assumed distributions, our VAST model-building process included 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 both including covariates in our model as well as running models without covariate information. We considered covariates in the form of dynamic temperature values and/or static habitat values from our population model. When using covariates we ultimately decided to provide the most information to the model by including both covariates for both linear predictors. Since we know the true population values in our models we 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 determined setting that allowed VAST models to converge for all of our scenarios while also providing the lowest absolute error values. Settings for our VAST models 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 that individual random samples combine to accurately represent true abundance by a) sampling all strata in which the population exists and b) low enough noise level in the samples to allow for a discernible pattern. This assumption can be questioned given enough noise in the sampling process **cite?** and/or shifting spatial preferences driven by climate change causing a population to move into a previously uninhabited strata. To simulate the impact of noise, indexing estimates after adding noise to our samples versus those using the true sampling values. To evaluate the effect of populations moving into new habitat, we compare indexing estimates using samples from all strata versus those that only include a subset of the full spatial domain for each species.

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 COMBOS show the choices that define each scenario.

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

Species	Population Trend	Temperature Scenario	Strata Included	Noise in Data	Covariates (VAST only)	Season
Yellowtail	Increasing	Repeating	All strata	No Noise	No Covariates	Spring
Cod	Constant	Increasing 5°	Subset	Yes Noise	Temp + Habitat	Fall
Haddock	Decreasing					

Results

The goal of our project was to analyze how well different contemporary population indexing methods can track population trends under a host of conditions, as depicted in Table COMBOS. Historically, Atlantic Cod has seen significant decline over the last XXX years while Haddock has increased in abundance in recent year **cite**. For this reason we compare indexing estimates using stratified random samples from decreasing population scenarios for Cod and increasing population scenarios for Haddock. We consider all possible scenario combinations for Yellowtail Flounder to provide a comprehensive analysis of population indexing methods.

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 temperture and all strata, but adding covariates corrects this.

For Haddock, VAST has a particularly hard time in spring regulalry producing larger errors than the stratified mean with added covariates only improving to the level of the stratifie dmean. VAST shows imrpoved results in fall relative to the stratified mean with added covaraites producing extremely low errors in some cases.

Table 2: Yellowtail error results

X	X.1	X.2	X.3	X.4	Constant.Population	X.5	Increasing.Population	X.6
Temp	Covariate	Strata	Noise	season	Stratified Mean	VAST Estimate	Stratified Mean	VA
const	no cov	all	no	spring	0.21	0.11	0.16	0.1
const	no cov	all	yes	spring	0.25	0.16	0.22	0.2
const	w/ cov	all	no	spring	0.21	0.07	0.16	0.0
const	w/ cov	all	yes	spring	0.25	0.08	0.22	0.0
const	no cov	all	no	fall	0.32	0.68	0.34	0.3
const	no cov	all	yes	fall	0.31	0.77	0.46	0.4
const	w/ cov	all	no	fall	0.32	0.08	0.34	0.0
const	w/ cov	all	yes	fall	0.31	0.11	0.46	0.1
const	no cov	reduced	no	spring	0.27	0.19	0.2	0.1
const	no cov	reduced	yes	spring	0.26	0.15	0.22	0.1
const	w/ cov	reduced	no	spring	0.27	0.19	0.2	0.1
const	w/ cov	reduced	yes	spring	0.26	0.14	0.22	0.1
const	no cov	reduced	no	fall	0.47	0.25	0.41	0.1
const	no cov	reduced	yes	fall	0.49	0.36	0.46	0.2
const	w/ cov	reduced	no	fall	0.47	0.19	0.41	0.2
const	w/ cov	reduced	yes	fall	0.49	0.17	0.46	0.1
increasing	no cov	all	no	spring	0.28	0.11	0.32	0.1
increasing	no cov	all	yes	spring	0.28	0.15	0.34	0.1
increasing	w/ cov	all	no	spring	0.28	0.06	0.32	0.0
increasing	w/ cov	all	yes	spring	0.28	0.12	0.34	0.1
increasing	no cov	all	no	fall	0.51	1.26	0.3	0.6
increasing	no cov	all	yes	fall	0.5	1.38	0.39	0.7
increasing	w/ cov	all	no	fall	0.51	0.23	0.3	0.2
increasing	w/ cov	all	yes	fall	0.5	0.28	0.3	0.3
increasing	no cov	reduced	no	spring	0.31	0.17	0.4	0.3
increasing	no cov	reduced	yes	spring	0.29	0.19	0.41	0.2
increasing	w/ cov	reduced	no	spring	0.31	0.17	0.4	0.3
increasing	w/ cov	reduced	yes	spring	0.29	0.15	0.41	0.2
increasing	no cov	reduced	no	fall	0.64	0.75	0.7	0.4
increasing	no cov	reduced	yes	fall	0.66	0.89	0.69	0.4
increasing	w/ cov	reduced	no	fall	0.64	0.2	0.7	0.5
increasing	w/ cov	reduced	yes	fall	0.66	0.13	0.69	0.5

In considering the Yellowtail Flounder results in Table XXX, 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.

Table 3: Cod error results

Temp	Strata	Noise	season	VAST.No.Cov	VAST.w..Cov	Stratified.Mean	X	X.1
const	all	no	spring	0.11	0.12	0.36	NA	
const	all	yes	spring	0.12	0.15	0.35	NA	Cod
const	all	no	fall	0.19	0.05	0.49	NA	Decreasing Population
const	all	yes	fall	0.30	0.23	0.41	NA	
const	reduced	no	spring	0.17	0.24	0.41	NA	
const	reduced	yes	spring	0.20	0.23	0.46	NA	
const	reduced	no	fall	0.21	0.33	0.60	NA	
const	reduced	yes	fall	0.18	0.31	0.58	NA	
increasing	all	no	spring	0.12	0.15	0.25	NA	
increasing	all	yes	spring	0.19	0.19	0.27	NA	
increasing	all	no	fall	0.76	0.13	0.45	NA	
increasing	all	yes	fall	0.89	0.33	0.44	NA	
increasing	reduced	no	spring	0.14	0.22	0.32	NA	
increasing	reduced	yes	spring	0.15	0.21	0.29	NA	
increasing	reduced	no	fall	0.60	0.31	0.54	NA	
increasing	reduced	yes	fall	0.62	0.32	0.53	NA	

Table 4: Haddock error results

Temp	Strata	Noise	season	VAST.No.Cov	VAST.w..Cov	Stratified.Mean	X	X.1
const	all	no	spring	0.49	0.18	0.18	NA	
const	all	yes	spring	0.73	0.43	0.21	NA	Haddock
const	all	no	fall	0.28	0.05	0.26	NA	Increasing Population
const	all	yes	fall	0.41	0.06	0.27	NA	
const	reduced	no	spring	0.34	0.35	0.45	NA	
const	reduced	yes	spring	0.30	0.33	0.46	NA	
const	reduced	no	fall	0.36	0.48	0.54	NA	
const	reduced	yes	fall	0.33	0.46	0.52	NA	
increasing	all	no	spring	0.25	0.05	0.26	NA	
increasing	all	yes	spring	0.30	0.06	0.31	NA	
increasing	all	no	fall	0.89	0.23	0.40	NA	
increasing	all	yes	fall	1.04	0.35	0.42	NA	
increasing	reduced	no	spring	0.32	0.40	0.44	NA	
increasing	reduced	yes	spring	0.38	0.37	0.37	NA	
increasing	reduced	no	fall	0.44	0.64	0.72	NA	
increasing	reduced	yes	fall	0.42	0.62	0.70	NA	

Discussion

Acknowledgements

Data and Code Availability

All data and code used in this work are available at https://github.com/cmlegault/IBMWG.

References

Tables

Table 6: 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	NA
M	Natural mortality	1/wk	0.2064	0.2728	0.334	NA
W1	Weight of fully recruited fish	kg	0.39	2.95	1.12	NA
W2	Weight of pre-recruit fish	kg	0.13	0.39	0.19	NA
sigma	Variance in recruited fish	kg*kg	0.55	0.55	0.55	NA
lambda	Decay rate for movement	-	0.7	0.7	0.7	NA
spwn	Spawning weeks for species s	wks	9-12	8-13	11-14	NA
rec	Recruitment weeks for species s	wks	9-12	8-13	11-14	NA

Table 7: 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 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	Input/Value
ObsModel	Link function and assumed distribution	c(10,2)
FieldCOnfig	Specified spatial and/or spatio-temporal variation in predictors	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=3, Epsilon1=0, Epsilon2=4)
X1_formula	Right-sided formula affecting the 1st linear predictor	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)

Scenario	Temp	Covariate	Strata	Noise	Season	Stratified Mean	VAST Estimate
Constant Population	constantant	no cov	all	no	spring	0.21	0.11
Constant Population	constantant	no cov	all	yes	spring	0.25	0.16
Constant Population	constantant	w/ cov	all	no	spring	0.21	0.07
Constant Population	constantant	w/ cov	all	yes	spring	0.25	0.08
Constant Population	constantant	no cov	all	no	fall	0.32	0.68
Constant Population	constantant	no cov	all	yes	fall	0.31	0.77
Constant Population	constantant	w/ cov	all	no	fall	0.32	0.08
Constant Population	constant	w/ cov	all	yes	fall	0.31	0.11
Constant Population	constant	no cov	reduced	no	spring	0.27	0.19
Constant Population	constant	no cov	reduced	yes	spring	0.26	0.15
Constant Population	constant	w/ cov	reduced	no	spring	0.27	0.19
Constant Population	constant	w/ cov	reduced	yes	spring	0.26	0.14
Constant Population	constant	no cov	reduced	no	fall	0.47	0.25
Constant Population	constant	no cov	reduced	yes	fall	0.49	0.36
Constant Population	constant	w/ cov	reduced	no	fall	0.47	0.19
Constant Population	constant	w/ cov	reduced	yes	fall	0.49	0.17
Constant Population	increasing	no cov	all	no	spring	0.28	0.11
Constant Population	increasing	no cov	all	yes	spring	0.28	0.15
Constant Population	increasing	w/ cov	all	no	spring	0.28	0.06
Constant Population	increasing	w/ cov	all	yes	spring	0.28	0.12
Constant Population	increasing	no cov	all	no	fall	0.51	1.26
Constant Population	increasing	no cov	all	yes	fall	0.50	1.38
Constant Population	increasing	w/ cov	all	no	fall	0.51	0.23
Constant Population	increasing	w/ cov	all	yes	fall	0.50	0.28
Constant Population	increasing	no cov	reduced	no	spring	0.31	0.17
Constant Population	increasing	no cov	reduced	yes	spring	0.29	0.19
Constant Population	increasing	w/ cov	reduced	no	spring	0.31	0.17
Constant Population	increasing	w/ cov	reduced	yes	spring	0.29	0.15
Constant Population	increasing	no cov	reduced	no	fall	0.64	0.75
Constant Population	increasing	no cov	reduced	yes	fall	0.66	0.89
Constant Population	increasing	w/ cov	reduced	no	fall	0.64	0.20
Constant Population	increasing	w/ cov	reduced	yes	fall	0.66	0.13
Decreasing Population	constant	no cov	all	no	spring	0.23	0.08
Decreasing Population	constant	no cov	all	yes	spring	0.27	0.11
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]