Environmental Effects on Pelagic Fish Using Generalized Additive Models: *Clupea harengus*

Case Study

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Abstract

The Gulf of Maine (GOM) Atlantic herring (*Clupea harengus*) stock supports major commercial fisheries and is the main source of prey and bait for groundfish. Current stock forecasts neglect climate variables, but quantifying environmental effects on herring is critical in light of climate change as the recruitment, spawning patterns, and growth rates of herring are strongly dependent on environmental variables. An investigation was completed to improve GOM Atlantic herring spawning stock biomass (SSB) forecasts by accounting for relationships between SSB and environmental variables using generalized additive models (GAMs). For the period 1988-2018, Pearson's correlations were calculated between spring and fall SSB and lagged seasonal means of temperature, salinity, and climate indices. Climate-based GAMs were developed using past SSB and any combination of 3 environmental variables ($p<0.05$) and compared with controls that only used past SSB. The 6 climate-based models with the lowest REML values for each season were evaluated with hindcasting. The top spring and fall models explained 81% and 72% of the deviance in SSB and had root mean square errors (RMSEs) of 12% and 21%, while the spring and fall controls had RMSEs of 80% and 30%, respectively. The models can make 3-year climate-based forecasts of herring SSB using available climate data and can make longer-term predictions based on predicted values of environmental variables from climate models. The forecasts can be applied to harvest control rates to help minimize the effects of climate change. Similar modeling exercises can account for environmental effects on other fish stocks.

significantly affected by past climate change, as temperatures in the GOM have remained within its thermal tolerance, and the effects of short-term stressors are accounted for with increased fecundity while SSB is low, the stock is now near the southern end of its distribution and temperatures are approaching its upper thermal tolerance [4, 16]. The GOM is warming faster than 99% of global ocean and 7 times faster than the global average. Ice melt from Greenland has weakened the Atlantic Meridional Overturning Circulation, causing a northward shift in the Gulf Stream and a weakening of the Labrador current. GOM sea surface temperatures (SSTs) increase an average of 0.23°C/year since 2004, with an additional 3°C of warming expected through 2050. Fishing will magnify the effects of climate change and may lead to unexpected consequences when coupled with environmental effects [19-21]. Given the importance of the GOM Atlantic herring stock and its vulnerability to climate change, the introduction of climate stressors coupled with the recent decline in productivity necessitate improved climate-based GOM SSB forecasts to mitigate potentially catastrophic ecosystem-level impacts [15-18, 21-25].

Research on environmental effects on Atlantic herring in the Northwest Atlantic has been confined to experimental studies on growth, fecundity, behavior, and spawning patterns, with no research on quantitative effects on SSB [3, 4, 8, 10, 25, 26]. As a small forage fish, Atlantic herring SSB is highly variable due to the species' small size and low age of maturity [4, 6, 27]. Current management includes seasonal stock assessments for biomass and recruitment, which are used to determine seasonal quotas. Due to the poor understanding of the highly variable SSB, the current biomass-based management of the stock is ineffective which complicates stock forecasts [3-6, 21, 26]. The study aimed to improve Gulf of Maine (GOM) Atlantic herring spawning stock biomass forecasts by quantifying its response to environmental variables using generalized additive models (GAMs). The first objective was to identify environmental variables with the greatest influence on SSB for the period 1988-2018 based on Pearson's correlation coefficients. Variables analyzed included past SSB; temperature and salinity, which have been experimentally shown to affect Atlantic herring; and large-scale climate indices known to affect temperature, salinity current patterns, or other climate patterns in the GOM. The second objective was to use those variables to form a GAM capable of accurately forecasting GOM Atlantic herring SSB for management purposes while accounting for environmental effects. GAMs are one of the most powerful available types of models and are capable of explaining the complex and nonlinear relationships between environmental variables and SSB by using smooth functions of covariates designed to balance fit and smoothness [25, 28]. GAMs were successfully used in [29] to account for nonlinear relationships between temperature and biomass in forming species distribution models for river herring that predicted distribution and biomass shifts through 2100.

Table 1. *Abbreviations and descriptions of explanatory variables analyzed in relationship to spring and fall SSB.* Variables analyzed include those that are known to affect Atlantic herring based on experimental studies and those know to significantly affect environmental conditions in the GOM are listed in the left column, with their abbreviations listed in the middle column. Past SSB is abbreviated as SSB_{lag}. Brief descriptions of the basis of each variable is listed in the right column, if necessary.

Explanatory Variable	Label	Description
Past biomass	SSB_{lag}	Biomass in previous years
Temperature/Salinity		
Sea surface temperature	SST	Surface water temperature
Bottom temperature	BT	Water temperature at ocean floor
Surface salinity	SS	-
Salinity at a depth of 100m	S100	-
Salinity at a depth of 200m	S200	-
Environmental Indices		
Atlantic Multidecadal Oscillation	AMO	Temperature in North Atlantic
El Nino Southern Oscillation	ENSO	Water temperature in North Atlantic
East Pacific/North Pacific Oscillation	EP-NP	Water temperature in central equatorial Pacific
Gulf Stream North Wall Index	GSNW	Northern extent of the Gulf Stream
North Atlantic Oscillation	NAO	Pressure difference between Bermuda High & Icelandic low
Pacific Decadal Oscillation	PDO	Temperatures in the North and East Pacific
Pacific-North American Oscillation	PNA	Temperature patterns over North Pacific and North Atlantic

Methods

Data Acquisition

Herring. SSB data (in kg/tow) in the GOM for the period 1988-2018, and sea surface temperature (SST) and bottom temperature (BT) data for the period 1983-2018 were obtained from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey. The GOM region was defined by the following strata: 22-30, 34, 36-40, 56, 59-61, 64-66. Data before 1988 were omitted to minimize fishery impact as the GOM Atlantic herring stock-complex collapsed in the mid-1970s as a result of heavy exploitation and did not fully recover until 1988 [30]. For each data set, seasonal averages were calculated by averaging data from all stations within the GOM region for each of the variables analyzed. During the surveys, stratified random sampling was used throughout the Northeast US Continental Shelf Large Marine Ecosystem to collect data on the SSB of 85 species along with depth, temperature, and salinity. Data for spring surveys are available for the period 1968-2018 and data for fall surveys are available for the period 1963-2018. Salinity data were not collected until the mid-1990s, so they were not used in the study. Post 2016, fall surveys were no longer conducted for the Mid-Atlantic Bight and Southern New England regions [31]. Spring surveys were conducted from March to May and fall surveys were conducted from September to November. Measurements were taken in specific stations based on the stratified random sampling design. SSB was measured in kg/tow with otter trawls and buckets, while bucket thermometers measured SST and BT [32].

Temperature and Salinity. Salinity data were acquired from the Canadian Fisheries Hydrographic database for the period 1983-2018 in the GOM region, defined by the following strata: SS25, SS26, SS36-SS53, SS56, SS57. Since herring reside at depths of 1m-200m, queries were run at depths of 1m, 100m+/- 5m, and 200m +/- 5m, which corresponded to surface salinity

(SS), salinity at 100 meters (S100) and salinity at 200 meters (S200). Spring (March-April) and fall (September-October) averages were computed for each depth [33, 34].

Environmental Indices. Monthly time series data for the period 1983-2018 for the Atlantic Multidecadal Oscillation (AMO), El Nino Southern Oscillation (ENSO), East Pacific-North Pacific Oscillation (EP-NP), Gulf Stream North Wall Index (GSNW), North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), and Pacific North American Index (PNA) were downloaded from the NOAA Earth System Research Laboratory Physical Sciences division. 12 seasonal means were formed from 3-month running means of each variable to reduce noise [35, 36].

Variable Analysis

Pearson's correlations were computed between seasonal means of explanatory variables and spring and fall SSB for up to a 5-year lag to select the lag and seasonal mean with the strongest relationship with SSB for each explanatory variable while removing variables without significant correlations with SSB. Spring and fall SSB were considered separately as they represent discrete populations [34]. The lack of evident nonlinear relationships between variables along with the irregular distribution of data favored Pearson's correlations over Spearman's correlations [35]. Spring and fall temperature and salinity data were correlated with spring and fall SSB data, for a total of 60 covariates (5 variables, 2 seasonal means, and 6 lags). For large-scale environmental indices, each seasonal mean was correlated with spring and fall SSB, for a total of 504 covariates (7 variables, 12 seasonal means, and 6 lags). A total of 1128 correlations were performed (564 covariates and 2 seasons of biomass data). For each season, the lag and season of each variable with the strongest correlation with SSB was used in modeling if and only if the correlation was significant at 95% confidence [28, 38].

Modeling

GAMs were constructed for both seasons with the gam function in the Mixed GAM Computation Vehicle with Automatic Smoothness Estimation (mgcv) package in R using the explanatory variables chosen from variable analysis. All possible models incorporating past SSB and 3 environmental variables (165 models for spring and 120 models for fall) were formed. The general structure of GAMs is shown below:

```
gam1<-gam(SSB~s(SSBlag1,k=7)+s(var1,k=7)+s(var2,k=7)+s(var3,k=7),data=data,
method="REML",select=TRUE)
```

The s function formed thin plate regression spline-based smoothing. As suggested by [39], covariate selection was performed using the double penalty method, implemented with the select=TRUE command, and Restricted maximum likelihood (REML)-based penalization was implemented with the method= "REML" command. A full description can be found in [39]. Subset selection was performed to account for cases where the number of covariates is greater than the amount of data. Atlantic herring reach maturity at age 3-5, and 3 to 7-year-old fish form the dominant spawning population, so the dimensions of the smooth terms (k-values) were initially set to 7 to account for herring life history while keeping the number of predictors below the amount of data [39, 40]. After initial fitting, k-values were adjusted accordingly, if needed, to obtain the best REML values. Models were evaluated based on adjusted R^2 and REML values and the model with the lowest REML value for each season was selected. The top 5 models based on REML values for each season were refitted and calibrated to the period 1988-2012 to allow them to predict biomass for the period 2013-2018 and compare the predictions with the actual values [37]. Predictions were also made for the next several years by feeding the selected models available climate data. Adjusted R^2 values were calculated to determine to accuracy of predictions.

Results/Discussion

SSB was graphed for the period 1988-2018 to show the high variability and recent trends in SSB in the GOM. Fig. 2 confirms the high variability in SSB and the significant recent decline in SSB from 2016-2018. Spring and fall SSB were at their lowest level in 2018 in at least 10 and 20 years, respectively (Fig. 2).

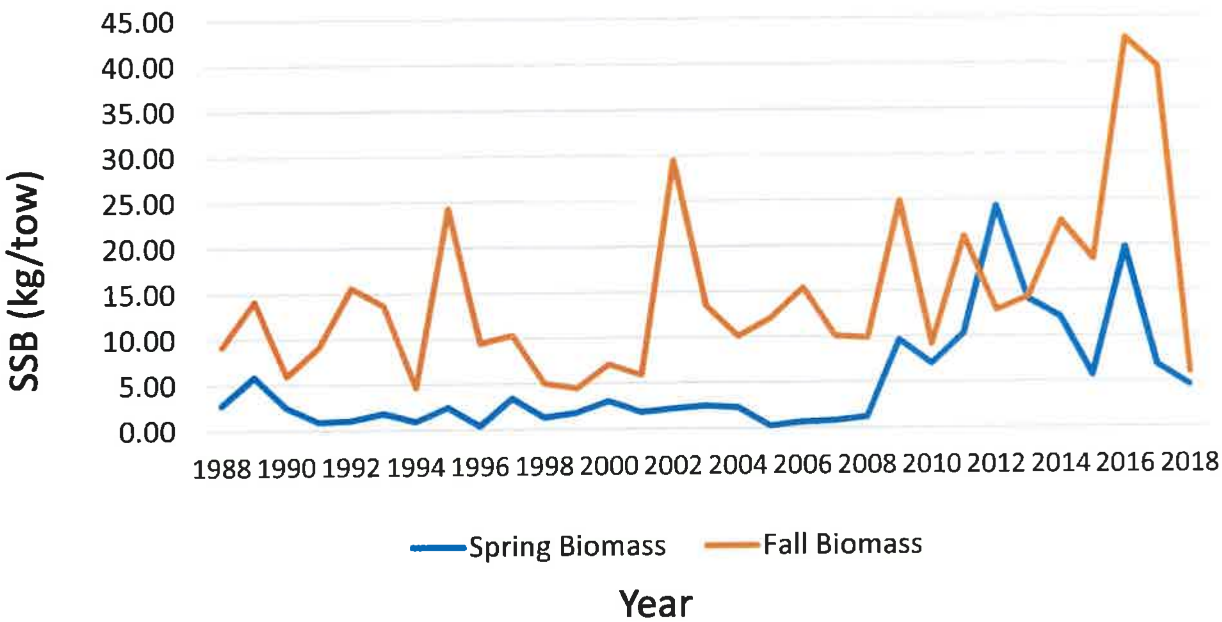


***Fig 2.* GOM Atlantic Herring SSB in kg/tow for the period 1988-2018.** Average spring (blue) and fall (orange) GOM Atlantic herring SSB in kg/tow, estimated from the NEFSC trawl survey are graphed for the period 1988-2018. SSB estimates are based on seasonally averaged SSB values measured at each station within the GOM.

This supports recent reports by the Northeast Fisheries Science Center that after further decline in 2019, the stock is at its lowest levels since its collapse in the late 1970s [26].

Seasonal means of explanatory variables with up to a 5-year lag were correlated with spring and fall SSB to find variables that would have the greatest explanatory power in models. With the exception of the ENSO and PNA, all environmental variables analyzed had significant correlations with both spring and fall SSB, so most variables were considered for modeling. This demonstrates the strong environmental influence on Atlantic herring and the importance of accounting for environmental variables in stock forecasts.

Table 2. ***Spring and fall Pearson correlations between explanatory variables and spring (a) and fall (b) SSB.*** Abbreviations of variables are listed on the left column. For each explanatory variable, the 3-month average/season and lag with the greatest correlation coefficient with spring and fall SSB is shown in the second column. Lags are shown in years. Lags for Nov-Jan means are based on the year of the Dec., while Dec-Feb means are based on the year of the Jan. R-values represent correlation coefficients to the nearest hundredth. p-values are calculated based on the correlation coefficients for each variable.

a) *Pearson correlations between spring SSB and explanatory variables*

Variable	Season	Lag	r value
SST	Spring	0	***0.72
NAO	Jun-Aug	4	***-0.60
BT	Fall	0	***0.59
S200	Spring	0	***0.58
SSB_{lag1}	Spring	1	***0.58
PNA	Aug-Oct	2	***0.57
EP-NP	Jan-Mar	4	**-0.55
AMO	Nov-Jan	5	**0.53
PDO	Mar-May	4	**-0.52
SS	Fall	5	*-0.42
GSNW	Sept-Nov	1	*-0.40
S100	Spring	1	*0.40
ENSO	Mar-May	4	-0.32

Note. *= p<0.05, **=p<0.0025, ***=p<0.001

b) Pearson correlations between fall SSB and explanatory variables

Variable	Season	Lag	r value
SST	Spring	3	***0.61
BT	Fall	1	***0.60
$SSB_{lag4.5}$	Spring	4	***0.60
NAO	Jun-Aug	5	**-0.54
PDO	Oct-Dec	0	**0.53
GSNW	Sept-Nov	1	**-0.52
SS	Spring	4	**-0.50
EP-NP	Jan-Mar	5	*-0.48
S100	Fall	3	*0.48
AMO	Feb-Apr	4	*0.47
S200	Spring	4	*0.46
PNA	Dec-Feb	1	0.33
ENSO	Jan-Mar	3	-0.33

Note. *=p<0.01, **=p<0.05, ** =p<0.0005

Based on Atlantic herring life history, lags of 0-2 years are associated with an effect on adults, while lags of 3-5 years correspond to effects on spawning, eggs, or larvae [30]. Past SSB had relatively low correlations for both seasons, demonstrating the unreliability of biomass-based forecasts. Both spring and fall SSB had the strongest correlation with spring SST. Warmer spring SSTs are more favorable for overwintering, increasing adult and larval survival [1]. Fall BT was positively correlated with spring and fall SSB, though the mechanism is unclear. The NAO and AMO had negative and positive correlations, respectively, with spring and fall SSB at lags of 4-5 years. The negative phase of the NAO and positive phase of the AMO feature warmer water temperatures, especially in spring, increasing larval survival [1, 41, 42]. Late summer PNA was positively correlated with spring SSB, but had weak correlations with fall SSB. The positive phase features significantly cooler water temperatures in fall and early winter, which benefits recruitment and adult survival. Average fall SSTs are 12-14°C, which is above the more favorable 9-12°C range for Atlantic herring [15, 43-45]. The winter EP-NP had negative correlations for both spring and fall SSB at lags of 4-5 years. The negative phase features warmer temperatures, particularly in winter and spring, which benefits larval survival [46]. Spring PDO_{lag4} was negatively correlated with spring SSB. The negative phase feature warmer temperatures, so warmer spring temperatures likely benefited larval survival, similar to what was argued in [47]. Fall PDO was positively correlated with fall SSB, likely because cooler fall water temperatures increase adult survival [48]. Fall $GSNW_{lag1}$ was negatively correlated with spring and fall SSB. A negative GSNW is associated with significantly cooler SSTs, especially in the southern GOM during fall, increasing adult survival [15, 49]. SS was negatively correlated with both spring and fall SSB, while S100 and S200 were positively correlated with spring and fall SSB. The mechanisms for these relationships are unclear but may be due to current patterns in the GOM. The strength of the Labrador Current, determines the degree of freshwater flow from ice melt in Greenland increases, so salinity may serve as a proxy for current patterns that affect larval drift and survival (Table 2a, Table 2b), [1, 62].

GAMs were constructed, each using past SSB and 3 environmental variables, to model spring and fall SSB. The selected models had significantly lower REML and significantly higher adjusted R^2 values than competing models. They explained around 90% of the variance in SSB, significantly outperforming the control models which only explained around 40% (Fig. 3a-3b).

Table 3. Spring (a) and fall (b) GAM statistics. For both seasons, statistics for the 8 models with the lowest REML along with the control model are shown. Lags of explanatory variable are shown in subscripts. All variables had spline-based smoothing with k=7. R^2 represents adjusted R^2 and REML represents the negative restricted maximum likelihood value.

a) Spring GAM statistics

Model	R^2	REML
$SSB_{lag1}+PNA_{lag2}+BT_{lag0}+SS_{lag5}$	**0.95**	**76.9**
$SSB_{lag1}+PNA_{lag2}+EP\text{-}NP_{lag4}+GSNW_{lag1}$	0.89	77.6
$SSB_{lag1}+PNA_{lag2}+BT_{lag0}+NAO_{lag4}$	0.90	77.8
$SSB_{lag1}+PNA_{lag2}+EP\text{-}NP_{lag4}+BT_{lag0}$	0.89	78.0
$SSB_{lag1}+PNA_{lag2}+GSNW_{lag1}+SST_{lag0}$	0.87	78.3
$SSB_{lag1}+PNA_{lag2}+SST_{lag0}+BT_{lag0}$	0.90	78.4
$SSB_{lag1}+PNA_{lag2}+BT_{lag0}+S200_{lag2}$	0.91	78.6
$SSB_{lag1}+PNA_{lag2}+PDO_{lag4}+SST_{lag0}$	0.88	78.8
SSB_{lag1} (control)	**0.38**	**92.1**

b) Fall GAM statistics

Model	R^2	REML
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+PDO_{lag0}$	**0.89**	**92.7**
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+S100_{lag3}$	0.86	94.8
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+EP\text{-}NP_{lag5}$	0.85	95.6
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+GSNW_{lag1}$	0.84	95.6
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+S200_{lag4}$	0.85	96.0
$SSB_{lag4.5}+SST_{lag3}+SS_{lag4}+PDO_{lag0}$	0.88	96.1
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+BT_{lag4}$	0.84	96.2
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+SS_{lag4}$	0.84	96.2
$SSB_{lag4.5}$ (control)	**0.41**	**106.8**

The best 8 spring models, based on REML values, all used PNA_{lag2} (Table 3a). The best fall models based on REML values used SST_{lag3}, and most used AMO_{lag4} (Table 3b).

Table 4 shows the approximate significance of smooth terms used in the selected models, which were generated with the summary function in the mgcv package in R. All smooth terms were significant for both models, justifying their use (Table 4a-4b).

Table 4. Spring (a) and fall (b) smooth term statistics. k values show the dimensionality of the smooth terms. Lags, in years, are shown in subscripts. F stat represents the F-statistic and p-values show the significance of the term.

a) Spring smooth term statistics

Formula: $SSB \sim s(SSB_{lag1}, k=7)+s(PNA_{lag2}, k=7)+s(BT, k=7)+s(SS_{lag5}, k=7)$

Smooth term	F stat	p-value
$s(SSB_{lag1})$	14.500	$2.07*10^{-11}$
$s(PNA_{lag2})$	8.590	$4.46*10^{-6}$
$s(BT)$	20.452	$9.14*10^{-12}$
$s(SS_{lag5})$	1.872	0.00452

b) Fall smooth term statistics

Formula: $SSB \sim s(SSB_{lag4.5}, k=7)+s(SST_{lag3}, k=7)+s(AMO_{lag4}, k=7)+s(PDO, k=7)$

Smooth term	F stat	p-value
$s(SSB_{lag4.5})$	5.438	$1.67*10^{-5}$
$s(SST_{lag3})$	6.611	$5.15*10^{-6}$
$s(AMO_{lag4})$	4.321	0.00011
$s(PDO)$	2.206	0.00127

BT was the strongest predictor of spring SSB (Fig. 4a), while SST_{lag3} was the strongest predictor of fall SSB (Fig. 4b). The variables with the strongest relationships with SSB in the best spring and fall models were generally consistent with the ones determined to have the strongest relationships based on tables 3a and 3b.

The modeled relationships between SSB and environmental variables were graphed for the best spring and fall models. Most variables had complex and nonlinear relationships. The generally narrow confidence intervals show the models' predictions are of high confidence.

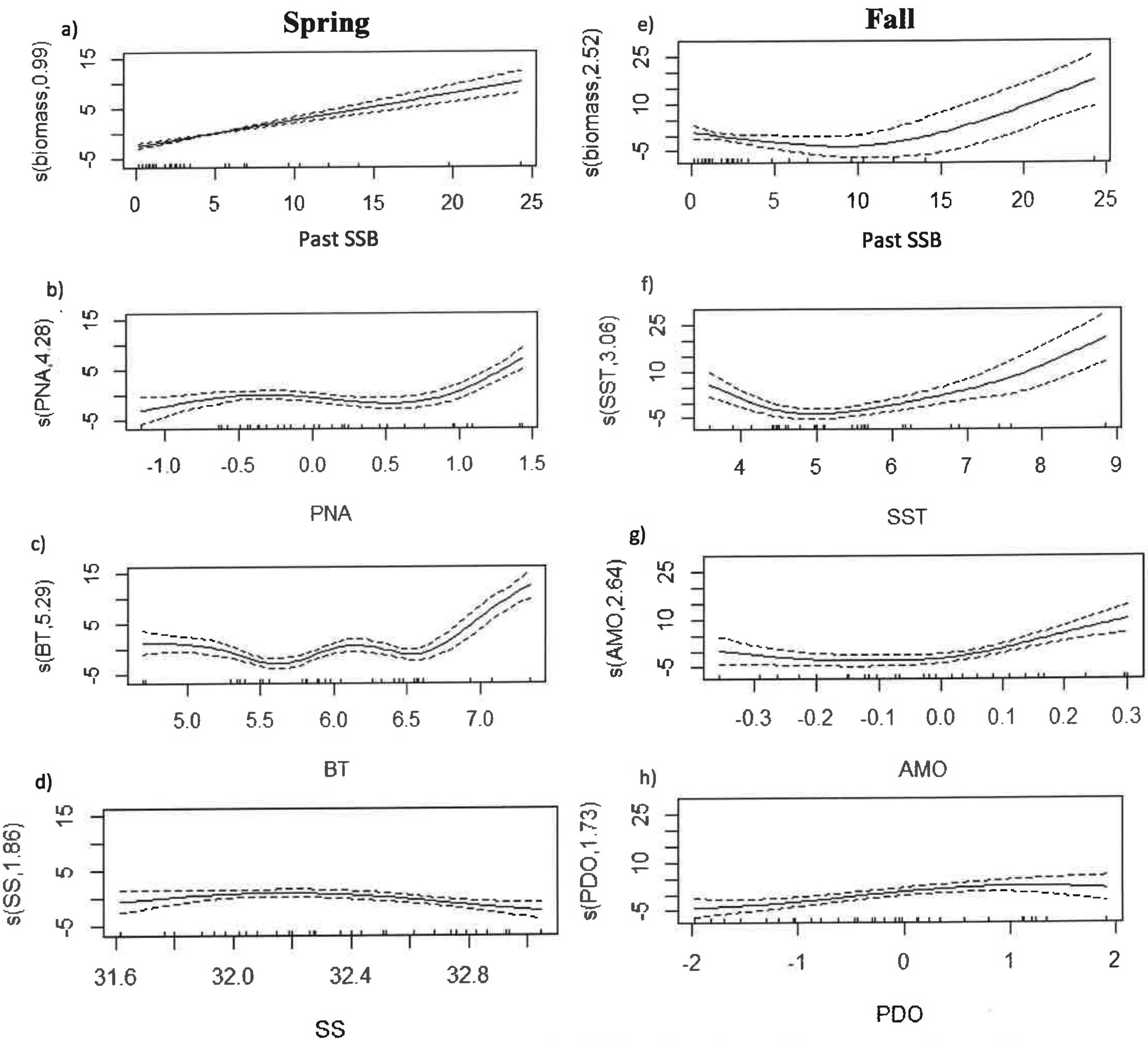


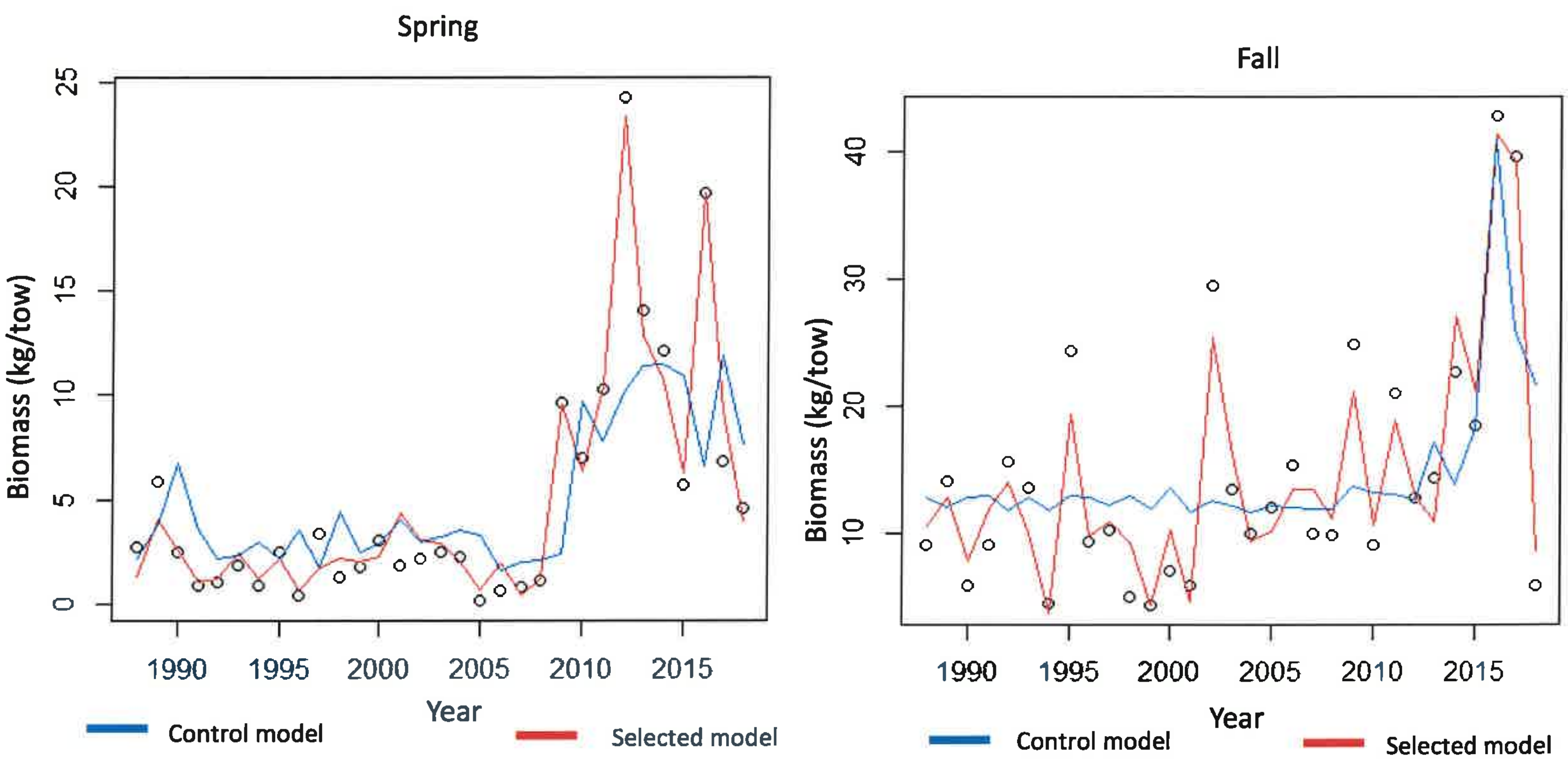
Fig 3. ***Relationships between explanatory variables and spring and fall SSB within the best models for spring (a-d) and fall (e-h).*** Vertical dashes just above the x-axis represent data points for the explanatory variable. The solid line represents actual predictions while the dashed lines are the upper and lower 95% confidence thresholds.

The best spring model incorporated past SSB, PNA, BT, and SS. SSB_{lag1} and SSB had an essentially linear relationship (Fig. 3a). SSB was lower in years with extremely low PNA and higher in years with extremely high PNA, but in years with a less extreme PNA, where the PNA was between -0.5 and 0.5, SSB was lower with higher PNA (Fig. 3b). The positive phase of the PNA corresponds with cooler temperatures over the GOM, especially in winter, providing less favorable overwintering conditions. SSTs are typically around 6-8°C in winter in the GOM, which is slightly cooler than the most favorable range of 9-12°C for Atlantic herring. In particular, larval survival declines with cooler waters, as larvae are more susceptible to cooler waters [44, 45]. A more pronounced PNA is also accompanied by warmer springs and cooler falls. SSTs are typically around 6-10°C and 12-14°C in spring and fall, respectively, so warmer springs and cooler falls put temperatures closer to the preferred temperatures of 9-12°C [43]. The relationship between spring BT and spring SSB was extremely complex and unclear. The high-confidence middle portion of the data where BT was 5.5-6.5°C indicates herring favor a BT of around 6°C for overwintering, though this relationship will need to be further investigated (Fig. 3c). Based on Fig. 3d, herring prefer an average fall SS in the GOM of 32.0-32.4 Practical Salinity Units (PSU). This is likely associated with benefits in spawning and egg/larval development based on the lag of 5 years.

The best fall model incorporated past SSB, SST, AMO, and PDO. Spring SSB_{lag4} and fall SSB unexpectedly had a negative relationship when spring biomass was less than 10 kg/tow. There was a positive relationship for years when spring SSB was above 10kg/tow, but this portion of the graph is of low confidence due to the lack of data (Fig. 3e). The spring and fall populations are likely distinct, as most herring in the GOM in fall migrate to the Georges Bank (GB) or Southern New England (SNE) areas for overwintering. The relationship between spring and fall SSB is unclear. SST and AMO had unexpected relationships with fall SSB and the mechanisms are unclear (Fig. 3f-3g). Fall SSB was generally greater during the neutral and positive phases of the PDO, and lower in the negative phase, when fall SSTs in the GOM are well above average (Fig. 3h), [48].

The predicted values of the selected and control models along with the actual biomass values were graphed for the period 1988-2018 to determine how the modeled values compared with the actual ones. For both seasons, the selected model made accurate predictions, while the control models did not even capture the general trends (Fig. 4).

Fig 4. ***Observed and modeled spring and fall GOM Atlantic herring SSB from 1988 to 2018.*** Actual SSB values (in kg/tow) obtained from the NEFSC bottom trawl survey, are shown in open circles. Predicted values for the selected models are shown in red and predicted values for the control models are shown in blue.



For spring, the selected GAM was more accurate than the control model 74% of the time. For fall, the selected GAM was more accurate than the control model 84% of the time (Fig. 4).

This demonstrates the importance of incorporating environmental variables into forecast models for Atlantic herring SSB as the models using environmental variables performed significantly better than the control models, which only used past SSB, supporting the hypothesis.

Hindcasting was performed on the 6 models for each season with the lowest REML values. The top climate-based spring models explained 80-90% of the variance in biomass while the control model that only used past SSB did not explain any (Table 5).

Table 5. Spring hindcast statistics. Lags, in years, are shown in subscripts. R^2 and RMSE values for the 6 spring models with the lowest REML values and the spring control are shown.

Spring hindcast statistics		
Model	R^2	RMSE
SSB_{lag1}+PNA_{lag2}+BT_{lag2}+SS_{lag5}	**0.81**	**12%**
SSB_{lag1}+PNA_{lag2}+$EP\text{-}NP_{lag4}$+$GSNW_{lag1}$	0.51	23%
SSB_{lag1}+PNA_{lag2}+BT_{lag2}+NAO_{lag4}	**0.87**	**10%**
SSB_{lag1}+PNA_{lag2}+$EP\text{-}NP_{lag4}$+BT_{lag2}	0.82	30%
SSB_{lag1}+PNA_{lag2}+$GSNW_{lag1}$+SST_{lag0}	**0.89**	**30%**
SSB_{lag1}+PNA_{lag2}+SST_{lag0}+BT_{lag2}	0.90	10%
SSB_{lag1} (control)	**-0.03**	**80%**

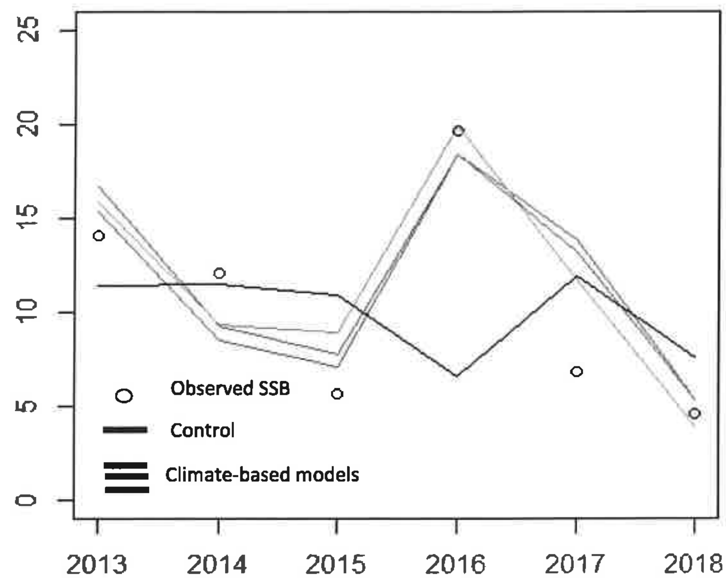


Fig 7. Observed and modeled spring GOM herring biomass from 1988-2018. Observed biomass values are shown in open circles, predicted values from the climate-based models are shown in red, green, and blue, while predicted values from the control are shown in black.

This is also supported by figure 7, where the predicted values of the climate-based models essentially matched the actual observed SSB while those of the control did not. This demonstrates the spring models can make accurate predictions several years out.

Similarly, the top fall climate-based models also explained 70-90% of the variance in biomass (Table 4). Based on figure 8, the control was completely useless even though it had a relatively high R^2 and low error as it predicted the same biomass every single year regardless of the input variables.

Table 6. Fall hindcast statistics. Lags, in years, are shown in subscripts. R^2 and RMSE values for the 6 fall models with the lowest REML values and the fall control are shown.

Fall hindcast statistics		
Model	R^2	RMSE
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+PDO_{lag0}$	**0.72**	**21%**
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+S100_{lag3}$	0.67	18%
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+EP\text{-}NP_{lag5}$	**0.86**	**29%**
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+GSNW_{lag1}$	**0.70**	**22%**
$SSB_{lag4.5}+SST_{lag3}+AMO_{lag4}+S200_{lag4}$	0.33	24%
$SSB_{lag4.5}+SST_{lag3}+SS_{lag4}+PDO_{lag0}$	0.78	28%
$SSB_{lag4.5}$ (control)	**0.68**	**30%**

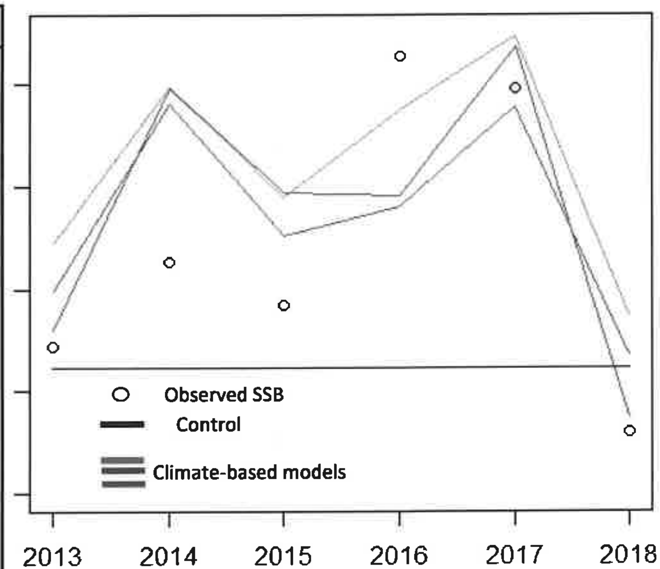
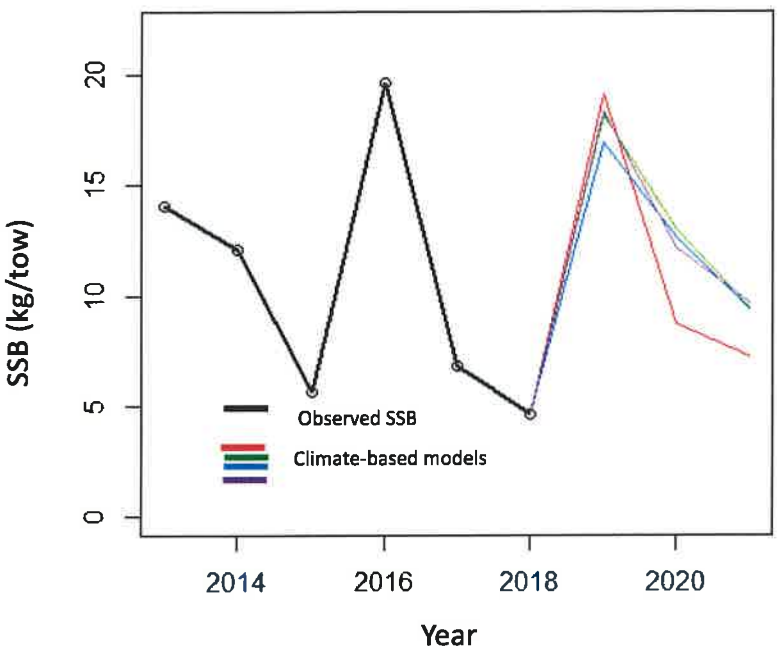
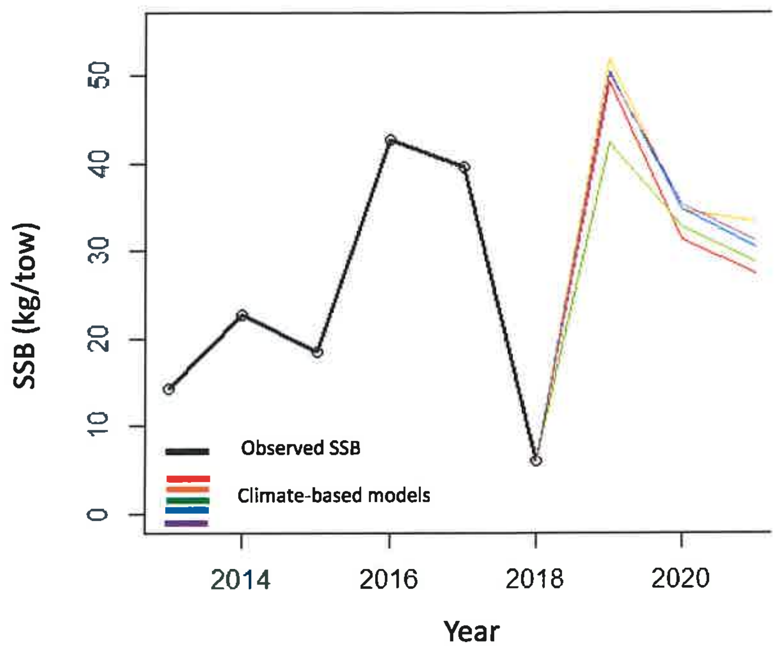


Fig 8. Observed and modeled fall GOM herring biomass from 1988-2018. Observed biomass values are shown in open circles, predicted values from the climate-based models are shown in red, green, and blue, while predicted values from the control are shown in black.

This demonstrates the fall climate-based models can make accurate predictions several years out. The other 10-30% of unexplained variance may simply be due to sampling inconstancies within the survey.

The top 4 models for each season were used to predict SSB through 2021. The models are in strong agreement, demonstrating they are capable of making high-confidence forecasts. The models are showing SSB will likely increase in 2019 followed by a steady decline through 2021.





The strong agreement of the models demonstrates that the forecasts are likely very accurate.

Conclusion

The study provided the first quantitative analysis of environmental effects on GOM Atlantic herring SSB. Environmental variables were shown to have strong relationships with SSB and high predictive power in models, and the use of GAMs helped quantify the complex, nonlinear relationships between environmental variables and SSB [25, 28]. The data provide models capable of accurately forecasting GOM spring and fall Atlantic herring SSB and account for environmental factors. Both models explained around 90% of the variance in the data, which is better than most models for herring in other regions [50-52]. They can be practically implemented for short-term fishery management as they use readily available and consistently updated data and can be run in relatively simple spreadsheet programs. This will aid short-term management as the stock's SSB is extremely difficult to predict and the stock is dangerously close to being overfished [49]. The procedures used in the study can be applied to form GAMs that effectively account for environmental variables for management of other stocks strongly affected by climate change.

Upon linkage to general circulation models (GCMs), the model can also help forecast the future biomass of the stock and provide a long-term direction for fishery management. To optimize the accuracy of long-term predictions, future research will need to investigate potential changes spawning patterns, and behavior of the species. These factors affect recruitment and survival could alter the interaction between SSB and environmental variables, changing the optimal variables and seasonal means and lags for modeling. Warmer temperatures support larval survival and juvenile growth but suppress adult survival [14, 15, 18]. This also forces fisheries to target increasingly younger fish, potentially causing an age truncation effect and altering spawning patterns [18, 53]. Future research will also need to account for ecosystem-level changes due to climate change, which have been shown to affect Atlantic herring due to its dynamic role within food webs [4, 9, 17, 54]. Also, the impacts of other anthropogenic stressors were not accounted for as their effects are difficult to discern from the effects of climate. Data before 1988 was omitted in an attempt to minimize the effects of fishing, but future research can still need to quantify the effects of the interaction of climate change and other anthropogenic stressors, such as pollution and ocean acidification [25, 55, 56]. With annual refitting and retesting, future investigations, and cautious use, the models can capture general long-term trends in GOM Atlantic herring SSB, providing a future direction for the fishery by accounting for the species' future response to climate change [57]. This will help minimize the effects of climate change [58]. Models specific to herring will greatly reduce risk of overfishing and/or collapse [59]. Predictions for all forage fish are currently very bad. By aiding short-term and long-term fishery management, this will help preserve the extremely important and vulnerable GOM Atlantic herring stock, and the entire GOM ecosystem [4, 5, 25]. Spatially explicit data with kriging can help with spatial distribution forecasts. Herring stocks are inherently resilient to short-term stressors. If properly managed, the GOM stock may be able to withstand much of the effects of climate change [61].

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