Working Paper 3

Environmental Influences on Atlantic Cod (*Gadus morhua*) Stock Dynamics

A working paper submitted to the 2023 Cod Research Track Stock Assessment

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Background

In the northwestern Atlantic, temperature is considered one of the most influential environmental parameters for many species and may affect a species' growth, maturity, survival, metabolism, recruitment, or other aspects of life history (Nye et al. 2010; Runge et al. 2010; Lesser 2016). In the Gulf of Maine region, annual temperature averages have increased approximately 1.6 °C since 1895 at the surface (Fernandez et al. 2020) and 0.68 °C since 1982 at the bottom (Kavanaugh et al. 2017). Fish population dynamics are strongly influenced by these changing ocean conditions and Northeast groundfish have exhibited sensitivity to changing thermal conditions with associated changes in productivity and distribution (Brodziak and O'Brien 2005, Nye et al. 2009, Hare et al. 2016, Pershing et al. 2021). Atlantic cod (*Gadus morhua*) are a benthopelagic fish whose range in the northwestern Atlantic extends from Greenland to Cape Hatteras, North Carolina, with the majority of biomass in United States waters in the western Gulf of Maine (GOM) and Georges Bank (GBK) regions (Fahay, Michael P. and Northeast Fisheries Science Center (U.S.) 1999). Changes in ocean conditions have been documented to affect key life history processes, including recruitment, distribution, and growth of Atlantic cod (see detailed description in ToR 1 chapter of WG report).

The historical productivity of cod fisheries has been high, but has experienced substantial population declines since the 1990s. Including ecosystem variables in stock assessments may lead to more precautionary advice (CAUSES 2019; Lynch et al 2018). To help achieve more sustainable fisheries management, these climate and ecosystem shifts should be closely tracked and considered. Therefore, it is important to explore the ways in which ecosystem and climate changes are affecting distributions, stock dynamics, and other life history characteristics of species such as cod in the GOM and GBK regions. Understanding how cod respond to ecological and climate drivers will likely help to reduce uncertainties related to estimates of stock size and composition. These benefits may help to better inform or improve management.

The goal of this work was to conduct exploratory modeling to examine the relationship between key aspects of Atlantic cod stock dynamics (i.e., recruitment, distribution, and growth) and ocean climate variables. The literature review, combined with fishermen's ecosystem knowledge informed the selection of environmental drivers to explore in these analyses (see TOR1 report chapter). Time series of relevant environmental variables included sea surface (SST) and bottom temperature anomalies, the Gulf Stream Index (GSI), zooplankton abundance anomalies for *Calanus finmarchicus* and *Pseudocalanus spp.*, and mean cumulative heatwave index. Spawning stock biomass (SSB) was also included to account for density dependence. These environmental and climatic variables were related to time series of stock variables which included age 1 abundance and recruits per spawning stock biomass (R/SSB) as proxies for recruitment, mean population depth and latitude of occurrence as proxies of distribution, and mean relative condition and weight at age (WAA) anomaly as proxies of growth. These analyses were used to inform the environmental covariates considered in performance testing of climate-integrated stock assessment modeling of Atlantic cod (see ToR 4 section of WG report).

Methods

Data Sources

Atlantic Cod Data

We estimated recruitment success using seasonal (fall & spring) indices of abundance at age 1 from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey between the years 1982-2019. The timing of the seasonal NEFSC varies by region, with the fall survey generally running from September-December, and the spring survey running from February-May. These data represent the standardized stratified mean number per tow of age 1 Atlantic cod, in strata 1380 and 1390 for Eastern Gulf of Maine (EGOM), 1090, 1100, 1230-1280, 1370, and 1400 for Western Gulf of Maine (WGOM), 1130-1220 for Georges Bank (GBK), and 1010, 1020, 1050, 1060, 1690, 1730, and 1740 for the Southern New England (SNE) stock area (Figure 1).

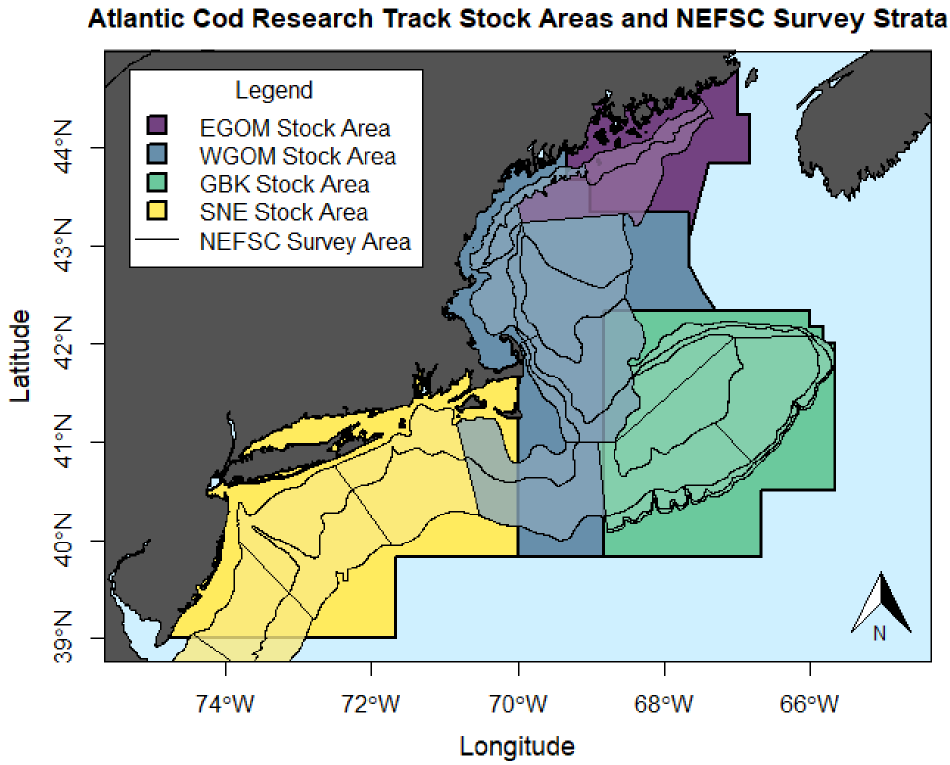


Figure 1. Atlantic Cod Research Track Stock Areas and Northeast Fisheries Science Center (NEFSC) Trawl Survey Strata Overlap. Legend abbreviations include “EGOM”= Eastern Gulf of Maine, “WGOM”= Western Gulf of Maine, “GBK”= Georges Bank, “SNE”= Southern New England, “NEFSC”= Northeast Fisheries Science Center. These stock areas serve as the study area for these analyses. NEFSC survey areas have been colored to match the stock area they were assigned to.

Atlantic cod age 1 indices exhibited a decreasing trend over time in most stock areas. Specifically, in the EGOM region, there was an overall decreasing trend over time in abundance in both the spring and fall surveys, with a spike in observed abundance recorded in the spring survey of 2000 (Supplemental Figure 1). WGOM and GBK regions also exhibited generally decreasing trends in both fall and spring surveys, with GBK numbers at age demonstrating slight increases in abundance in the past decade. The NEFSC survey did not capture a lot of age 1 data for the SNE region for either season, where the majority of recorded years showed an abundance of 0 age 1 fish, with the exception of the spring 2004 survey (Supplemental Figure 1).

Spawning stock biomass (SSB) data were estimated using spring and fall NEFSC bottom trawl survey numbers at age and weights at age for cod ages 4+. The aggregate biomass for these indices was calculated for each year (1982-2019) and for each season, in units of kg/tow. Annual abundance of age 1 fish from the NEFSC trawl survey were used for recruitment data and recruits per spawner was used as a metric of recruitment success (Perretti et al. 2017; Supplemental Figure 2) and calculated as recruitment = index of abundance at age 1 in year *t* per SSB in year *t-1* , e.g., R_t/SSB_{t-1}. Atlantic cod SSB data were also used as independent variables to explain recruitment (abundance of age 1 fish), as well as in the distribution and growth analyses, but not in the recruits per spawner (R/SSB) recruitment analysis as SSB is already incorporated into the dependent variable.

Distribution analyses used cod-weighted mean population depth and mean population latitude (geographic center) time series of cod from the NEFSC bottom trawl survey as response variables. Data were sourced from the NOAA Fisheries Distribution Mapping and Analysis Portal (https://apps-st.fisheries.noaa.gov/dismap/DisMAP.html). Because the DisMAP analysis considered all cod observations in the NMFS Bottom Trawl Survey as a unit population, we preserved this data structure and analyzed cod distribution as a unit instead of separating it into the stock regions. Metrics were calculated as biomass-weighted averages of depth and latitude, weighted by the interpolated biomass at each depth or latitude for each year (1982-2019) and season (fall, spring; DisMAP Technical Report 2022). Cod depth increased slightly over time in the spring, with a large increase in depth observed around 1995, whereas in the fall, depth was variable but consistently became shallower over time (Supplemental Figure 3). Mean latitude of occurrence of cod in the spring generally increased (moved northward), while in the fall cod were observed more southward over time (Supplemental Figure 3).

Growth analyses utilized cod relative condition and weight-at-age (WAA) data. Relative condition index data were calculated as the ratio of observed weight to predicted weight at a given length from the fall and spring NEFSC trawl surveys from 1992-2019 (2022 State of the Ecosystem New England report). Atlantic cod WAA anomalies were calculated from the NEFSC Bottom Trawl survey for ages 1-9+ from 1982-2019. Weight at age data were limited, especially for SNE and EGOM stocks. Only stocks and ages which had >30 years of data were used and 1982-2011 base-periods (or as close to that range as possible while still maintaining 30 years for a base period) were used to calculate the means for the anomaly calculations. WAA anomaly data included in the growth analysis for the fall used ages 1-6 for WGOM, age 2 for EGOM, and ages 1-5 for Georges Bank. WAA anomaly data used for the spring growth analysis included ages 1-7 for WGOM, age 1 for EGOM, and ages 1-7 for GBK. There were not enough WAA data for SNE to include a model in this region for this growth analysis.

Relative condition data varied greatly by stock area. EGOM showed an overall increase in spring relative condition and decrease in fall over time (Supplemental Figure 4). WGOM demonstrated a general and consistent slight increasing trend in relative condition over time in both fall and spring surveys. GBK showed contradicting trends compared to EGOM, where the spring GBK relative condition decreased over time and generally increased in the fall. SNE relative condition data were sparse and variable, especially in the spring (Supplemental Figure 4).

For WAA data, EGOM age 1 and age 2 data trends were consistent over time, whereas WGOM showed decreasing patterns in WAA over time in the spring with more consistency over time in the fall (Supplemental Figure 5). In GBK, both fall and spring exhibited general decreasing trends over time. In all stocks, older ages exhibited more variation in WAA over time than younger ages (Supplemental Figure 5).

Environmental Data

Sea surface temperature (SST) data were sourced from the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Laboratory. Optimum Interpolation Sea Surface Temperature (OISST) data were used, a long-term record of climate data that utilizes multiple data collection platforms into a global grid. Data were masked to cod stock regions and a monthly spatial average was calculated for each stock area. For the recruitment analyses, SST data were averaged over a four month recruitment period, which was temporally aligned with the beginning of the peak spawning period of the previous year for each stock area. 4-month means were chosen as cod eggs are buoyant and range between 90-150 days in settlement timing (McBride and Smedbol 2022). For the growth and distribution analyses, SST data were averaged over the six months preceding the start of the respective seasonal survey for each stock region. 6-month means were chosen in an effort to capture enough signal from the variable, while limiting the potential of washing out signals from selecting a period length too long. Years

1982-2011 of the corresponding 4- and 6-month time periods were used as the reference base period to calculate the final SST anomaly datasets for each season.

Bottom water temperature data were sourced from the high-resolution, long-term bottom temperature product for the Northeast U.S. continental shelf, as described in du Pontavice et al. (2023). Means over the six months prior to the start of each seasonal survey were used in all stock dynamic analyses (recruitment, growth, and distribution). Temperature anomalies were calculated for the years 1982-2019, using 1982-2011 as a reference baseline period for comparison.

Gulf Stream Index (GSI) data were obtained from the R package, *ecodata* (Bastille K, Hardison S 2022). Gulf Stream indices were calculated from the monthly data provided in the ecodata "gsi" dataset. These data characterize a 200-m depth 15°C isotherm derived GSI and were recorded at monthly time intervals for years 1954-2020. The leading mode of the Gulf Stream's temperature variability is equivalent to a 50-100 km north-south shift, and represents approximately 50% of the interannual seasonal variance between 75°W and 55°W for which it's estimated (Joyce et al. 2019) and thus the Gulf Stream Index is recorded in terms of the Gulf Stream position anomaly (degrees latitude). For recruitment analyses, 6-month means were taken from the monthly dataset and aligned with the beginning of the peak spawning timing for each stock area, as the Gulf Stream Index is associated with egg and larval cod retention (Bundy and Gamble 2018). For growth and distribution analysis, 6-month means were estimated using the 6 months prior to the start of the seasonal survey for each stock area.

Annual cumulative marine heatwave data were provided by the Northeast Fisheries Science Center via *ecodata* (Bastille K, Hardison S 2022). The marine heatwave dataset was masked to the Atlantic cod research track working group stock regions, as shown in Figure 1. This dataset can be found under "ESP_heatwave_cod" in the *ecodata* R package. These data were provided as annual means and were lagged one year in all models, with the exception of the fall distribution and growth models, where same-year data were used. The decision to lag spring models was due to the timing of the spring survey, as inclusion of several months of data that occur after the survey is not appropriate. This is less of an issue for fall models, as the fall survey generally runs near year-end (September-December), depending on stock area. However, heatwave data were lagged for the fall recruitment models to better align with the environment during the spawning timing.

Zooplankton abundance data were sourced from the NOAA Ecosystem Monitoring (EcoMon) program. Abundance anomalies for the copepods *Calanus finmarchicus* and *Pseudocalanus spp.* were included as separate covariates, as they are important species for cod larvae (Kane 1984; Heath and Lough 2007; Jacobsen et al. 2020). For the EGOM & WGOM stock area models, summer zooplankton survey months (June-August) were used, and in GBK and SNE stock area models, spring zooplankton survey months (March-May) were used as these time periods align with the start of, or begin just after, the peak spawning period for cod, when cod larvae would likely be feeding on zooplankton (Kane 1984; Heath and Lough 2007; Jacobsen et al. 2020). All zooplankton data were lagged one year and were subsetted to match cod stock areas, as shown in Figure 1. Detailed descriptions of how these data were derived can be found in Kane (2007).

Generalized Additive Model Development & Fitting

Pearson correlation coefficient and variance inflation factor (VIF) tests were conducted prior to model development to test for variable independence and multicollinearity. Correlated variables varied by season and stock area datasets examined, but high (≥.70, Nettleton 2014) correlation between bottom temperature anomaly & SST anomaly, SST anomaly & mean cumulative heatwave, and bottom temperature anomaly & GSI were commonly found. Correlated variables were not both included as covariates in any tested model, as well as variables with VIF numbers >3 (Zuur et al. 2009). All potential covariates were tested in each model but only unique (non-correlated) and significant (<0.05 p-value) variables that explained the most variance were kept in final models to avoid effects of multicollinearity.

Each of the dependent variables were modeled independently using Generalized Additive Models (GAMs; Hastie and Tibshirani 1986). A GAM is an extension of a generalized linear model (GLM), with the addition of a smooth function. GAMs use spline functions to estimate relationships between independent and dependent variables, which allows them the flexibility to model nonlinear relationships beyond the parametric forms that GLMs are commonly bound to (Wood 2017; Yee and Mitchell 1991). Nonlinear mechanisms are often observed in ecology. In this study, GAMs were used to evaluate the relationships between Atlantic cod population dynamics (i.e., recruitment, distribution, and growth) and environmental variables. Final model selection criteria was based upon covariate significance ($p < 0.05$), Akaike Information Criterion (AIC; Akaike 1974), and model residual diagnostics using function *gam.check()* from the package *mgcv* in R (Wood 2017). We used the default tensor product basis spline and evaluated if the number of knots for each model was appropriate. These criteria were used in tandem to build and select the best fitting model for each population dynamic × season × stock area group. An example GAM equation for the recruitment analysis, including all potential variables before eliminating variables due to collinearity, non-significance, duplicates, etc. can be written as:

$$Recruits/SSB = s(GSI) + s(Bt) + s(SST) + s(Heatwave) + s(Calanus) + s(Pseudocalnus)$$

where *s* is a spline smoother, and *GSI, Bt, SST*, *Heatwave, Calanus*, and *Pseudocalnus* are the independent variables representing the Gulf Stream Index, mean bottom temperature anomalies, mean sea surface temperature anomalies, mean cumulative heatwave indices, mean *Calanus finmarchicus* abundance anomalies, and mean *Pseudocalanus spp.* abundance anomalies, respectively. Similar GAM equations were constructed for the distribution and growth analyses based upon these methods. Tweedie distributions were chosen in all final recruitment models due to the zero-inflated recruitment data, while gaussian distributions were chosen for all growth and distribution models.

Each stock dynamic examined utilized two different dependent variables to serve as proxies of either recruitment, distribution, or growth. For recruitment, logged age 1 abundance and R/SSB were used as proxies of recruitment and recruitment rate, respectively. For the logged age 1 abundance models, some seasonal surveys observed 0 abundance of age 1 fish some years. Thus to avoid logging a 0 value, +1 was added to all abundance data prior to logging for this recruitment analysis. For the recruitment rate analysis, R/SSB values were estimated as described in the *Atlantic Cod Data* methods section. Mean population depth and mean population latitude (geographic center) were used as proxies of distribution and for growth analyses, cod relative condition and mean weight-at-age (WAA) data were used.

Results

Recruitment Analysis Results

For each proxy of recruitment (R/SSB and log age 1 abundance +1), recruitment models were run for each stock area x season, for a total of 16 models tested. 8 models revealed at least 1 significant environmental driver (Table 1). Model results are described below.

Recruitment Rate Models

There were three recruitment rate (R/SSB) stock area x season models that revealed significant environmental drivers: WGOM Spring, WGOM Fall, and EGOM Spring (Table 1). Bottom temperature anomaly and SST anomaly were the only significant drivers returned in recruitment rate models. The SST anomaly variable was significant in both the EGOM spring and WGOM fall recruitment rate models, while bottom temperature anomaly was significant in the WGOM spring model. Both temperature drivers exhibited general negative relationships with WGOM recruitment rate, suggesting that as temperature anomalies increase in WGOM, Atlantic cod recruitment success decreases (Figures 2a, 2b). The spring EGOM model exhibited a curvilinear response with SST anomaly such that anomaly values <0.0 Δ°C and >1.5 Δ°C reveal a negative relationship with recruitment rate while anomaly values between 0.0-1.5 Δ°C demonstrate a positive relationship with recruitment rate. This suggests the presence of thermal thresholds at both colder (<0.0 Δ°C) and warmer than average (>1.5 Δ°C) spring sea surface temperatures in EGOM, where recruitment success of cod is either positively or negatively impacted, respectively (Figure 2c).

Table 1. Significant environmental drivers revealed in recruitment GAM analysis by season and stock area. If a season or stock area is not listed, that indicates that model either did not have any significant environmental drivers identified or that there was not enough data to run the analysis. Each row of table represents a different season x stock area model run. Relationship trends listed are generalized and represent trends over where the majority of the observations occur. In models where multiple significant independent variables were returned as significant, relationship trend patterns are listed respective to the variable order in the "Independent Variable" column.

Season	Stock Area	Dependent Variable	Independent Variable	Deviance Explained	Relationship Trend
Spring	EGOM	R/SSB	SST Anomaly	68.8%	Varies
Spring	EGOM	Log Age 1	SST Anomaly + Calanus abundance anomaly	45.8%	Negative, Constant
Spring	WGOM	R/SSB	Bottom temperature Anomaly	18.6%	Negative
Spring	WGOM	Log Age 1	Heatwave	50.9%	Negative
Fall	EGOM	Log Age 1	SST Anomaly	22.4%	Negative
Fall	WGOM	R/SSB	SST Anomaly	10.7%	Negative
Fall	WGOM	Log Age 1	Bottom temperature Anomaly	38.6%	Negative
Fall	GBK	Log Age 1	SSB	23.1%	Positive

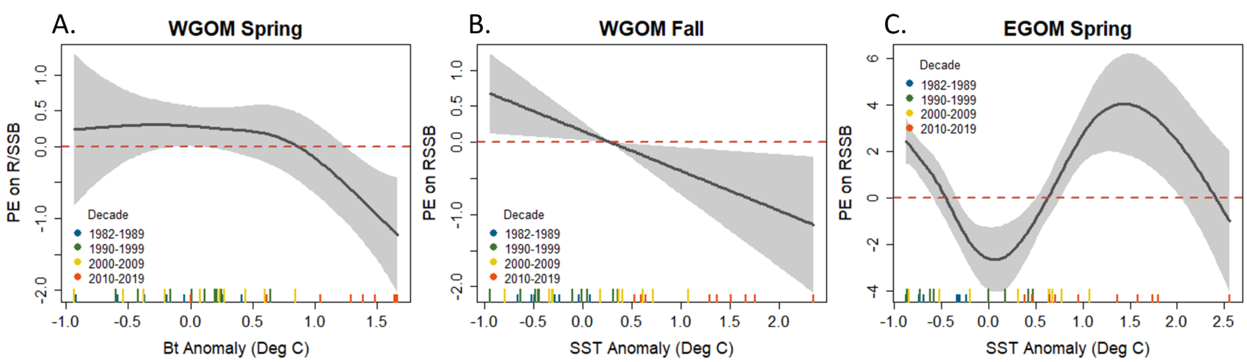


Figure 2. GAM response curves in WGOM spring (A.), WGOM fall (B.), and EGOM spring (C.) recruitment rate models. “PE” denotes the partial effect the independent variable has on the dependent variable, recruitment rate (R/SSB). Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade as denoted in the legend. Shaded regions indicate the standard error confidence intervals.

Recruitment Models

There were 5 stock area x season models that revealed significant environmental indicator(s) with recruitment data (log of age 1 abundance+1; Table 1). The recruitment models revealed similarities in significant environmental drivers to the recruitment rate models. SST and bottom temperature anomaly variables were significant in EGOM and WGOM models here too, however the recruitment models also revealed the calanus abundance, heatwave, and SSB drivers as significant in some season x stock area models as well (Table 1). SST anomaly drivers were significant in both spring and fall EGOM models, where bottom temperature anomaly and heatwave variables were significant in the fall WGOM and spring WGOM models, respectively. SST anomaly, bottom temperature, anomaly, and heatwave are all indicators of temperature change, and all model response curves for these variables displayed an overall negative relationship with recruitment (Figure 3), suggesting decreases in recruitment under warming temperatures. See Table 1 for a list of all recruitment and recruitment rate models which returned significant environmental drivers.

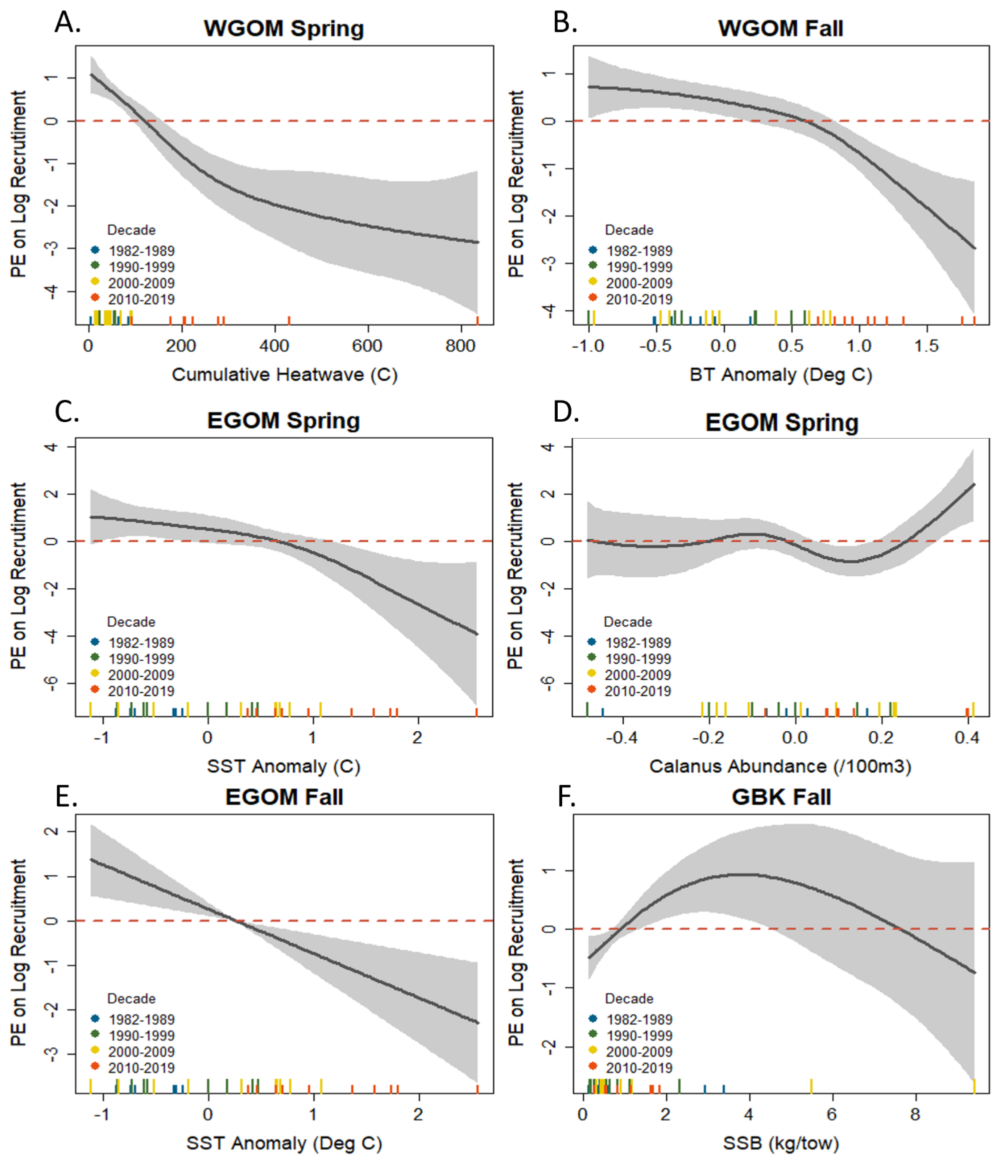


Figure 3. GAM response curves in WGOM spring (A.), WGOM fall (B.), and EGOM spring (C. and D.), EGOM fall (E.), and GBK fall (F.) recruitment models. "PE" denotes the partial effect the independent variable has on the dependent variable, recruitment (log of age 1 abundance+1). See Figure 2 description for further figure details.

Distribution Analysis Results

Distribution models were run for unique seasons (fall and spring), but were not run on unique stock areas. See Methods: Atlantic Cod Data section for reasoning. Thus 4 models in total were run for the distribution analysis: 1) population depth fall, 2) population depth spring, 3) population latitude fall, and 4) population latitude spring. All 4 models revealed significant environmental drivers.

Geographic Center: Population Depth Models

Spawning stock biomass and Calanus abundance were significant in the depth distribution models. SSB was significant in the spring model and demonstrated a negative relationship with depth (Figure 4a), suggesting that as mean cod SSB increases, cod occupy shallower waters. Calanus abundance anomaly was significant in the fall depth model and although the GAM relationship was curvilinear overall, the relationship was negative over the majority of the data observations (-1.25-0.25 (Δ abundance/100m^3); Figure 4b). This suggests that as calanus abundance anomalies increase, cod occupy shallower waters.

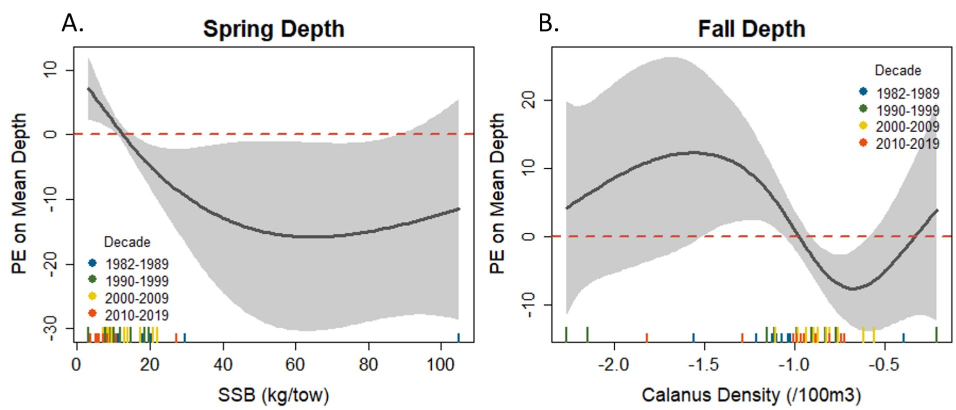


Figure 4. GAM response curves in spring depth (A.), fall depth (B.) distribution models. “PE” denotes the partial effect the independent variable has on the dependent variable, mean population depth (m), where negative depth values indicate shallower waters. See Figure 2 description for further figure details.

Geographic Center: Population Latitude Models

Spawning stock biomass and mean cumulative heatwave were significant in the latitude distribution models. SSB was significant in the fall model and demonstrated a positive relationship with latitude (Figure 5a), suggesting that cod are likely to shift northward as SSB increases. Mean cumulative heatwave was significant in the spring model and also showed a positive relationship with latitude, indicating that cod are also likely to shift northward in distribution under warming temperatures (Figure 5b). See Table 2 for a list of all distribution models and associated significant environmental variables identified.

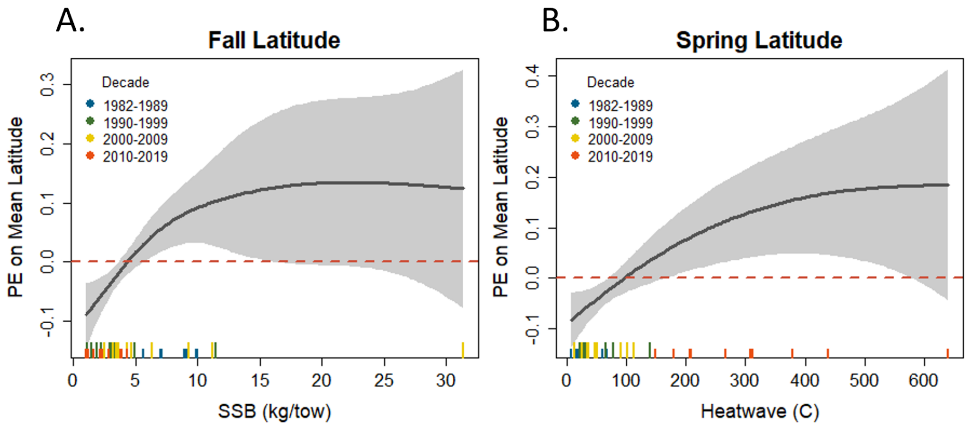


Figure 5. GAM response curves in fall (a) and spring (b) latitude distribution models. “PE” denotes the partial effect the independent variable has on the dependent variable, mean latitude of population occurrence, where more positive values indicate more northward latitudes.See Figure 2 description for further figure details.

Table 2. Significant Environmental drivers revealed in distribution GAM analysis by season. Distribution models utilized averaged environmental data across all stock areas. Relationship trends listed are generalized and represent trends over where the majority of the observations occur.

Season	Dependent Variable	Independent Variable	Deviance Explained	Relationship Trends
Spring	Depth	SSB	26.7%	Negative
Fall	Depth	Calanus	31.7%	Negative
Spring	Latitude	Heatwave	29.1%	Positive
Fall	Latitude	SSB	30.8%	Positive

Growth Analysis Results

Relative condition growth models were performed by stock area x season, for a total of 8 models tested. 4 stock area x season relative condition models revealed significant driver(s) (Table 3) which are described below. Weight at age (WAA) growth models were performed by stock area x season x age when enough data was available (see Methods: Atlantic Cod Data for description), for a total of 27 models initially tested. 16 stock area x season x age WAA models revealed significant driver(s) (Table 4) which are described below.

Relative Condition Models

Bottom temperature anomaly, Pseudocalanus abundance, GSI, and SST anomaly were all significant drivers in the relative condition growth models, with no clear pattern in indicators identified across stock areas or by seasons. Bottom temperature anomaly was significant in the fall EGOM model where a negative relationship demonstrates that as bottom temperature increases, relative condition of cod decreases (Figure 6a). For the WGOM stock area, GSI was significant in the spring model, with a relatively consistent trend, with the exception of a decrease around -0.25 degrees latitude (Figure 6b). This suggests that when the north wall of the Gulf Stream is nearing 0.25 degrees south of its average latitude, cod relative condition is lower than average. SST anomaly was significant in the fall WGOM model and exhibited a positive relationship (Figure 6c), indicating that as SST increases, cod relative condition also increases in this region and season. Pseudocalanus abundance was significant in the Georges Bank spring model only, where Pseudocalanus abundance revealed a positive relationship (Figure 6d), suggesting that as Pseudocalanus abundance increases, cod relative condition increases as well. There were no significant drivers identified in the GBK fall model, and both the SNE spring and fall models did not have enough relative condition data to support this analysis in this region. See Table 3 for a list of all relative condition models and associated significant environmental variables identified.

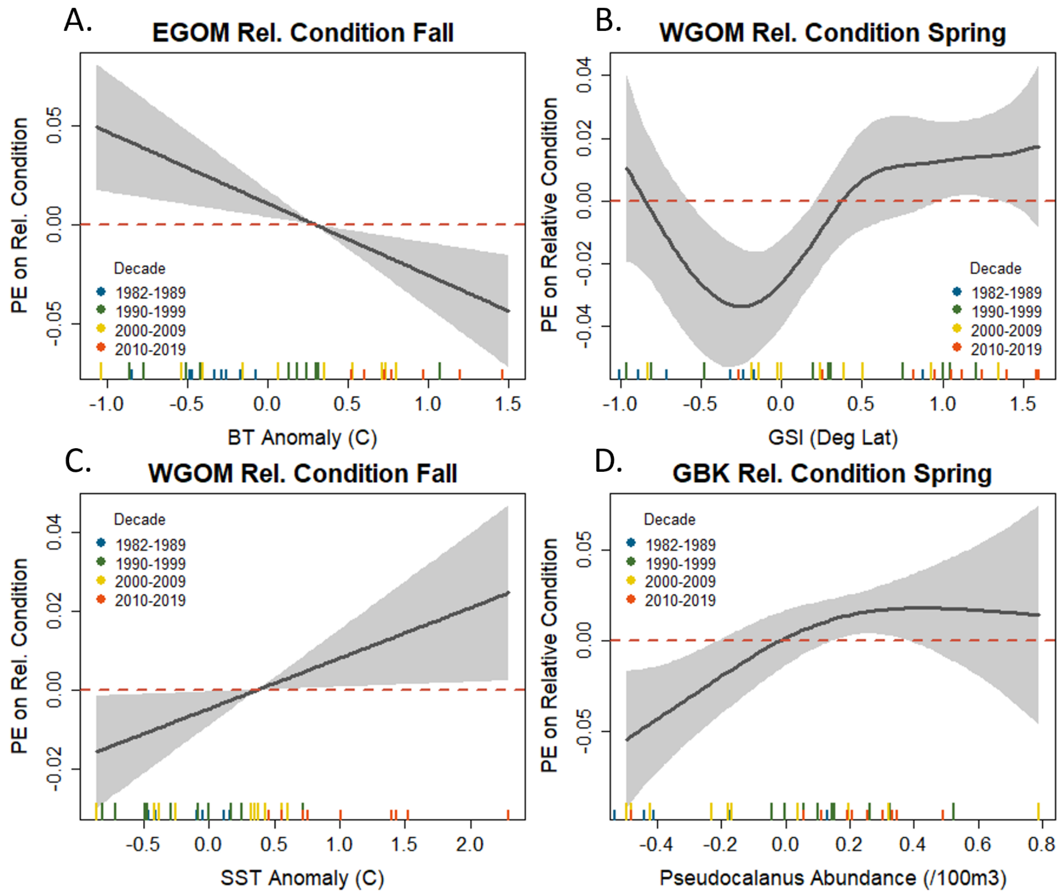


Figure 6. GAM response curves in relative condition growth models. Each Figure panel represents a different season x stock area model: EGOM fall (A), WGOM spring (B), WGOM fall (C), GBK spring (D). "PE" denotes the partial effect the independent variable has on the dependent variable, relative condition. See Figure 2 description for further figure details.

Table 3. Significant Environmental drivers revealed in Relative Condition Growth GAM analysis by season and stock area. If a season or stock area is not listed, that indicates that model either did not have any significant environmental drivers identified or that there was not enough data to run the analysis. Relationship trends listed are generalized and represent trends over where the majority of the observations occur. In models where multiple significant independent variables were returned as significant, relationship trend patterns are listed respective to the variable order in the "Independent Variable" column.

Season	Stock Area	Dependent Variable	Independent Variable	Deviance Explained	Relationship Trend

Spring	WGOM	Relative Condition	GSI	47.2%	Varies
Spring	GBK	Relative Condition	Pseudocalanus	28.6%	Positive
Fall	EGOM	Relative Condition	Bottom Temperature Anomaly	28.5%	Negative
Fall	WGOM	Relative Condition	SST Anomaly	15.8%	Positive

Weight at Age Anomaly Models

There were no significant drivers found in the EGOM fall, EGOM spring, and SNE spring WAA anomaly growth models. Additionally, there were not enough WAA data to run this analysis for the SNE fall model.

Georges Bank

Ages 2-5 for the spring GBK WAA anomaly models revealed significant drivers. For ages 4 and 5, heatwave was the best fitting indicator (Figure 7), whereas SST anomaly was significant at age 2 and bottom temperature anomaly was significant at age 3. For all 4 of these indicators of temperature, a negative relationship with WAA was apparent (Figure 7), which indicates that increasing spring temperatures are associated with decreases in cod weight at age in Georges Bank. In addition to bottom temperature anomaly, the GBK spring model for age 3 also had calanus abundance anomaly as a significant driver. The calanus abundance variable for this model also displayed a negative relationship (Figure 7c) that suggests decreases in WAA as calanus abundance increases.

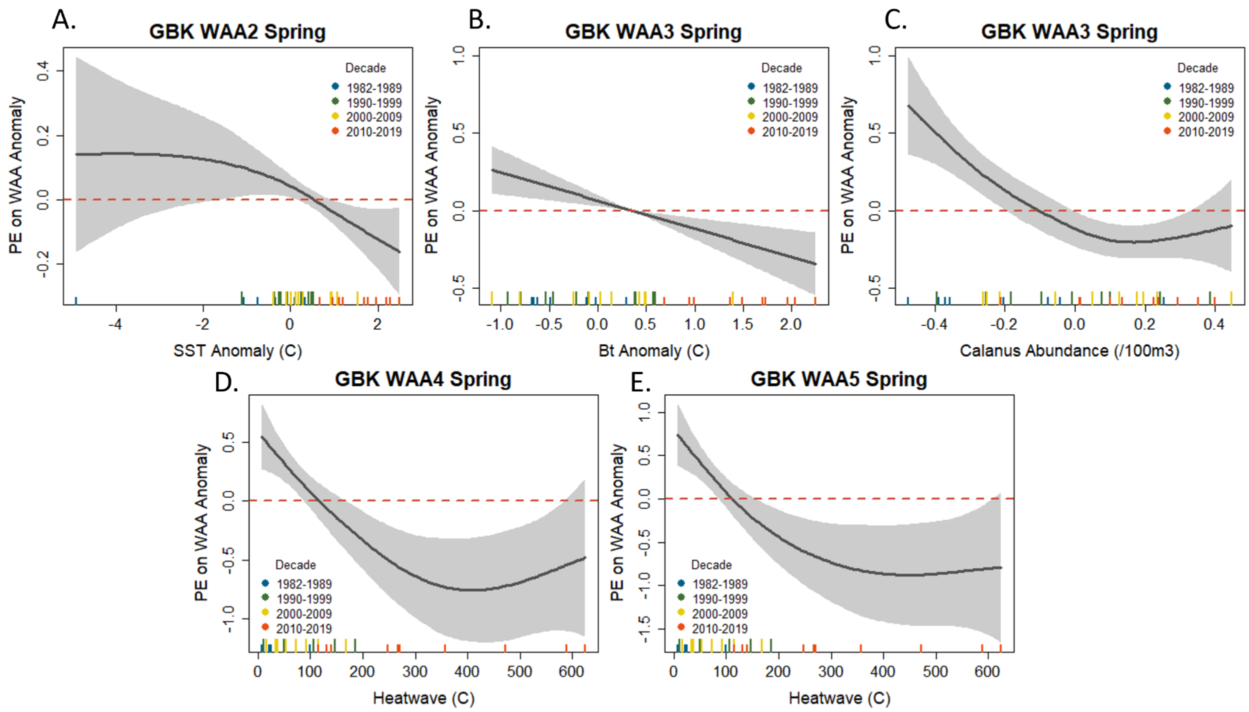


Figure 7. GAM response curves for Georges Bank spring weight at age growth models. Each Figure panel represents a different age model: age 2 (A), age 3 (B and C), age 4 (D), age 5 (E). "PE" denotes the partial effect the independent variable has on the dependent variable, weight at age anomaly. See Figure 2 description for further figure details.

For the fall GBK WAA anomaly models, calanus abundance and SST anomaly were found to be significant in the Georges Bank fall age 2 model. Heatwave and calanus abundance anomaly indicators were significant in age 3 and 4 models, respectively. All relationship curves were negative (Figure 8), suggesting that as the indicators of temperature (SST anomaly & heatwave) as well as calanus abundance increase, weight at age anomaly for cod decreases in the fall GBK region. See Table 4 for a list of all WAA anomaly models and associated significant environmental variables identified.

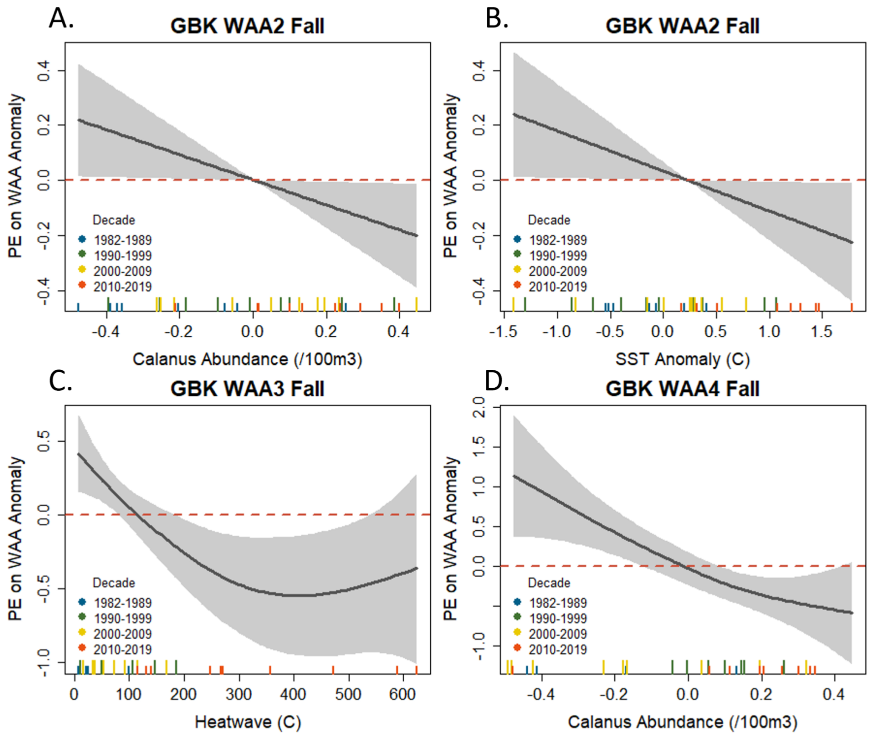


Figure 8. GAM response curves for Georges Bank fall weight at age growth models. Each Figure panel represents a different age model: age 2 (A and B), age 3 (C), age 4 (D). "PE" denotes the partial effect the independent variable has on the dependent variable, weight at age anomaly. See Figure 2 description for further figure details.

Western Gulf of Maine

Ages 2-6 for the spring WGOM WAA anomaly models revealed significant drivers. Calanus and pseudocalanus abundance anomaly indicators were significant in the age 2 and age 3 models, where the WAA anomaly relationships with calanus were negative over the majority of the data (-0.2-0.3 calanus/100m^3; Figures 9c and 9d), and where the relationships with pseudocalanus were both positive (Figure 9b and 9e). GSI was significant in the age 4 model, where GSI displayed a negative relationship with WAA anomaly (Figure 9f), suggesting that as the Gulf Stream north wall moves northward, WAA anomaly decreases. Ages 5 and 6 models both showed significance with mean cumulative heatwave, and both relationships were negative (Figures 9g and 9h), meaning that under more extreme heatwave temperature conditions, WAA anomaly for age 5 and 6 fish decreases in WGOM in the spring.

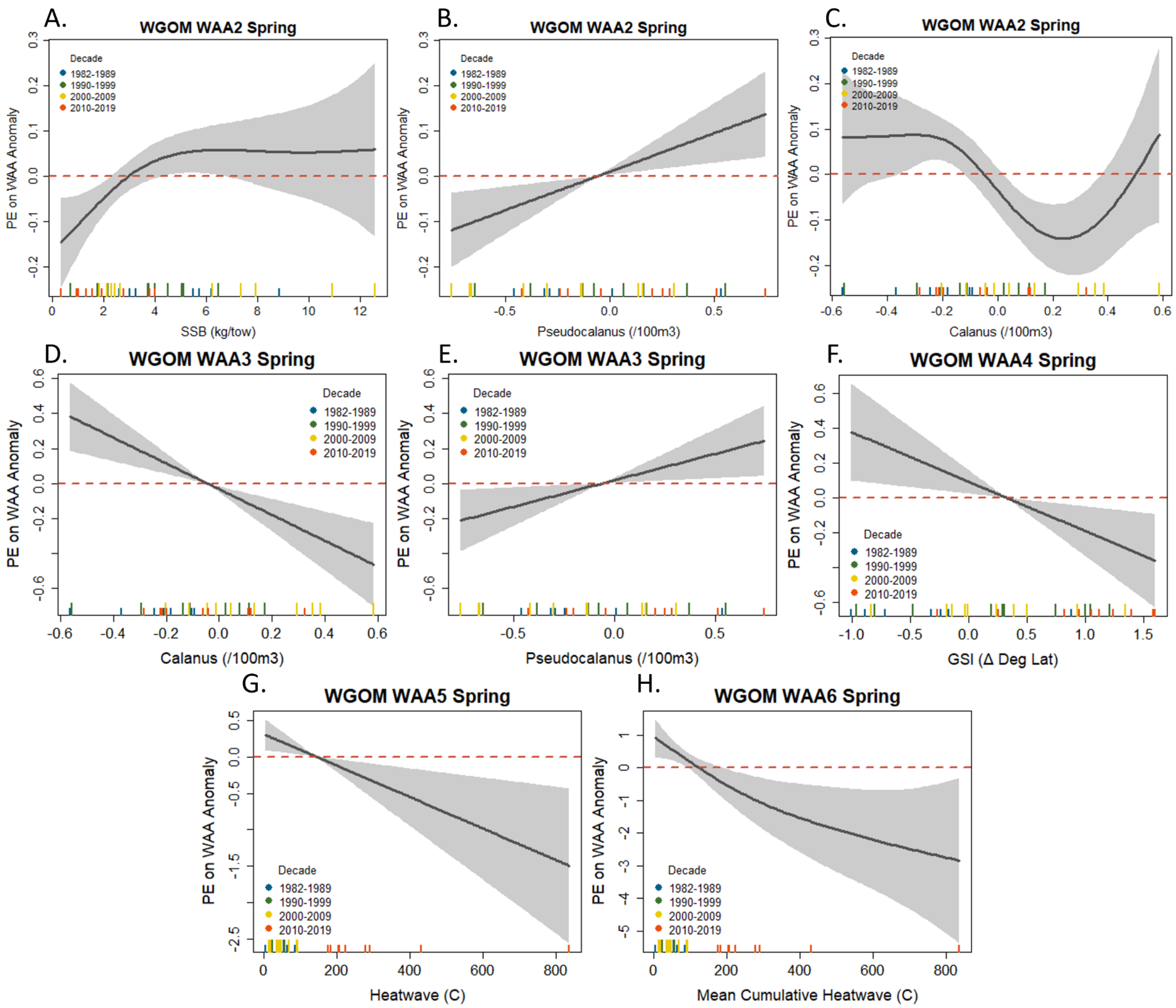


Figure 9. GAM response curves for Western GOM spring weight at age growth models. Each figure panel represents a different age model: age 2 (A, B, and C), age 3 (D and E), age 4 (F), age 5 (G), and age 6 (H). "PE" denotes the partial effect the independent variable has on the dependent variable, weight at age anomaly. See Figure 2 description for further figure details.

For the WGOM fall models, ages 1, 4, 5, and 6 had significant covariates. Age 1 was significant with GSI, where the relationship was relatively stable until extreme high latitude shifts (>1.5° northward) where a positive relationship occurred (Figure 10a). The age 4 model was significant with *Pseudcalanus spp*. abundance anomalies, where a positive relationship was revealed (Figure 10b), suggesting that as *Pseudocalanus spp*. abundance increases, weight at age 4 cod also increases. Mean cumulative heatwave was significant in the age 5 model, where an overall negative relationship was revealed, especially over the majority of the data observations (0-200

°C; Figure 10c). This suggests growth for age 5 cod declines under increasing heatwave conditions. SST anomaly was significant in the age 6 model, where a right-skewed normal distribution can be seen, where peak SST influence on WAA anomaly occurs around 0.25 °C (Figure 10d). This suggests the presence of some thermal threshold that age 6 cod experience in WGOM in the fall, where SST has a positive effect on WAA until 0.25 °C, and after this suggested thermal threshold, cod WAA is negatively impacted. See Table 4 for a list of all WAA anomaly models and associated significant environmental variables identified.

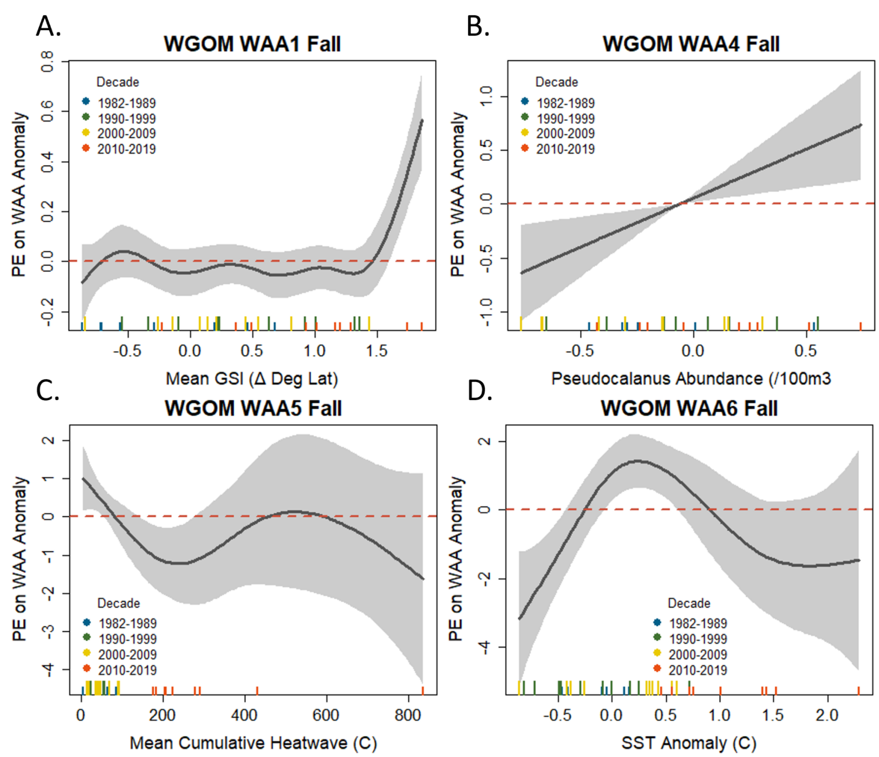


Figure 10. GAM response curves for Western GOM fall weight at age growth models. Each figure panel represents a different age model: age 1 (A), age 4 (B), age 5 (C), and age 6 (D). “PE” denotes the partial effect the independent variable has on the dependent variable, weight at age anomaly. See Figure 2 description for further figure details.

Table 4. Significant Environmental drivers revealed in WAA Anomaly Growth GAM analysis by season, stock area, and age. If a season, stock area, or age combination is not listed, that indicates that model either did not have any significant environmental drivers identified or that there was not enough data to run the analysis. Relationship trends listed are generalized and represent trends over where the majority of the observations occur. In models where multiple significant independent variables were returned as significant, relationship trend patterns are listed respective to the variable order in the "Independent Variable" column.

Season	Stock Area	Age	Dependent Variable	Independent Variable	Deviance Explained	Relationship Trend
Spring	WGOM	2	WAA Anomaly	Calanus + Pseudocalanus + SSB	61.2%	Negative, Positive, Positive
Spring	WGOM	3	WAA Anomaly	Calanus + Pseudocalanus	36.6%	Negative, Positive
Spring	WGOM	4	WAA Anomaly	GSI	16.9%	Negative
Spring	WGOM	5	WAA Anomaly	Heatwave	22.8%	Negative
Spring	WGOM	6	WAA Anomaly	Heatwave	32.3%	Negative
Spring	GBK	2	WAA Anomaly	SST Anomaly	19.5%	Negative
Spring	GBK	3	WAA Anomaly	Bottom Temperature Anomaly + Calanus	59.2%	Negative, Negative
Spring	GBK	4	WAA Anomaly	Heatwave	47.4%	Negative
Spring	GBK	5	WAA Anomaly	Heatwave	47.2%	Negative
Fall	WGOM	1	WAA Anomaly	GSI	57.6%	Constant
Fall	WGOM	4	WAA Anomaly	Pseudocalanus	20.4%	Positive

Fall	WGOM	5	WAA Anomaly	Heatwave	33.0%	Negative
Fall	WGOM	6	WAA Anomaly	SST Anomaly	47.0%	Right-skewed normal
Fall	GBK	2	WAA Anomaly	SST Anomaly + Calanus	24.3%	Negative, Negative
Fall	GBK	3	WAA Anomaly	Heatwave	35.2%	Negative
Fall	GBK	4	WAA Anomaly	Calanus	28.4%	Negative

Discussion

Recruitment Analysis

Both recruitment rate and recruitment models revealed frequent significance of temperature-related variables. Amongst all (8) recruitment models where at least 1 significant environmental driver was identified (Table 1), 7 of the models included a temperature indicator. Although the specific indicators vary (bottom temperature anomaly, SST anomaly, or heatwave), all temperature variables in the recruitment results displayed a general negative relationship with increasing temperatures. These results suggest that cod recruitment decreases under warming temperatures, and these results corroborate with past literature (Drinkwater 2005; Mantzouni and MacKenzie 2010). One exception to the general negative trend in recruitment-temperature relationships was in the spring EGOM recruitment rate model, where SST anomaly was significant and displayed a curvilinear relationship (Figure 2c). This suggests the presence of thermal thresholds at both colder (<0.0 Δ°C) and warmer than average (>1.5 Δ°C) spring sea surface temperatures in EGOM, where recruitment success of cod begins to be either positively or negatively impacted as temperature increases, respectively. We speculate this relationship pattern may also be different as a result of the limited data availability in the EGOM survey region compared to better surveyed stock areas such as the WGOM region, which consistently demonstrated a clearer negative relationship pattern.

Distribution Analysis

There were 4 total models in the distribution analysis (with response variables of spring depth, spring latitude, fall depth, fall latitude). Depth models suggested cod seeking shallower waters with increasing SSB and calanus abundance. Significance of SSB in the spring depth model could suggest presence of a density dependent effect where as stock density increases, the spatial distribution could expand to less favorable areas (Brown 1984; Petitgas 1998; Anderson and Gregory; 2000), such as shallower waters. A significant relationship with calanus in the fall depth model was unexpected, especially with a negative relationship over the majority of the data, as adult cod are unlikely to consume calanus directly. We suspect this negative relationship could either be spurious, or may be reflecting the positive trend in the fall DisMAP depth data used as the dependent variable. The positive trend in the dependent data indicates a shift into shallower waters, as this negative GAM relationship does as well.

The spring and fall latitude models both suggested a northward shift in cod distribution with increasing SSB and cumulative heatwave degrees. This northward shift aligns with the northward shift in dependent spring latitude data, but not fall, which exhibited an overall southward trend in dependent data. Georges Bank Atlantic cod have demonstrated a northward shift in center of biomass, while Gulf of Maine cod have shifted deeper and further south (Nye et al. 2009). These distributional shifts are associated with a continual warming trend and changes in circulation (Atlantic Multidecadal Oscillation) across the Northeast US continental shelf (Nye et al. 2009). The dependent data used for this analysis was not separated by stock area, so it is unclear if some of these stock-area-specific trends are driving the overall results more than other regions. Considerations of spatial nonstationarity may help to clarify these results, but that is outside the scope of this work.

Growth Analysis

Eastern and Western GOM fall relative condition growth models revealed significant temperature indicators. However, the indicators differed in type and directional trend (negative bottom temperature anomaly relationship in EGOM and positive SST anomaly relationship in WGOM). The negative trend in the EGOM region suggests decreasing growth with increasing bottom temperature anomalies. The positive trend in the WGOM region with SST anomaly suggests cod condition increases with increasing sea surface temperatures. While some literature suggests that under climate change, growth is expected to increase in Gulf of Maine cod as temperatures warm (Fogarty et al. 2008; McBride and Smedbol 2022), others acknowledge that the Gulf of Maine is already nearing the southern limit of Atlantic cod's range in the Northwest Atlantic and expect the GOM's rapidly warming conditions to lead to suboptimal growth conditions for cod (Pershing et al. 2015).

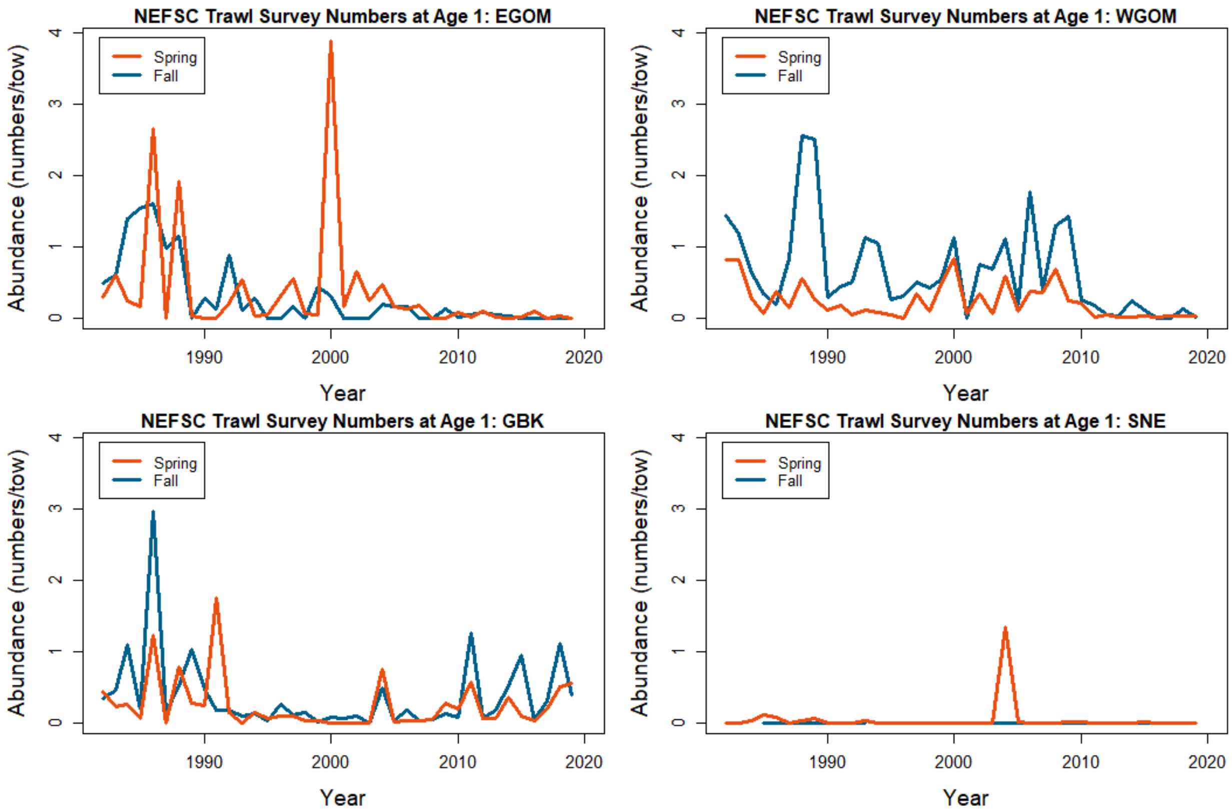
In WAA models where a temperature-related indicator was significant, the relationship between temperature and WAA was negative 9 out of 10 times (Table 4), suggesting decreased WAA under warming temperature conditions. Weight at age has declined over the past few decades (supplemental Figure 5), and the recurring negative relationships between growth and temperature indicators corroborate with literature suggesting poor cod growth under warming temperature conditions (Pershing et al. 2015). However, it is important to recognize that high fishing pressure, which is also associated with driving early maturation at smaller sizes, can confound the relationship between temperature and growth, which these exploratory analyses did not explicitly account for.

The WAA growth models also revealed a pattern in which zooplankton indicators (*Calanus finmarchicus* and *Pseudocalanus spp.* abundance anomalies) returned as commonly significant variables in WAA models for ages ≤ 4, while the heatwave indicator was commonly significant in WAA models ≥ 4. This pattern between age groups was more distinguished in the spring WAA models than for the fall, though it can be seen in both seasons (Table 4). All models where calanus abundance anomalies were significant as a covariate displayed a negative trend with WAA anomaly whereas all models where pseudocalanus was significant, including the relationship seen in the GBK relative condition model (Figure 6d), displayed a positive relationship. The positive relationship exhibited by the pseudocalanus variable was expected; although it is unlikely post-larvae stage cod would consume zooplankton of any kind (Kane 1984; Heath and Lough 2007; Jacobsen et al. 2020), there could be indirect food-web effects occurring that contribute indirectly to cod growth. Similarly, *Calanus finmarchicus* would not likely be a direct food source for cod at the ages for which they were significant (ages 2-4). However, the negative relationships observed across these models could be a reflection of the overall negative WAA anomaly dependent data trends seen across most stock areas (supplemental Figure 5). Thus we suggest the likelihood of spurious relationships or confounding effects are present, although it is unclear why these patterns recurred consistently across models and across classes < age 4.

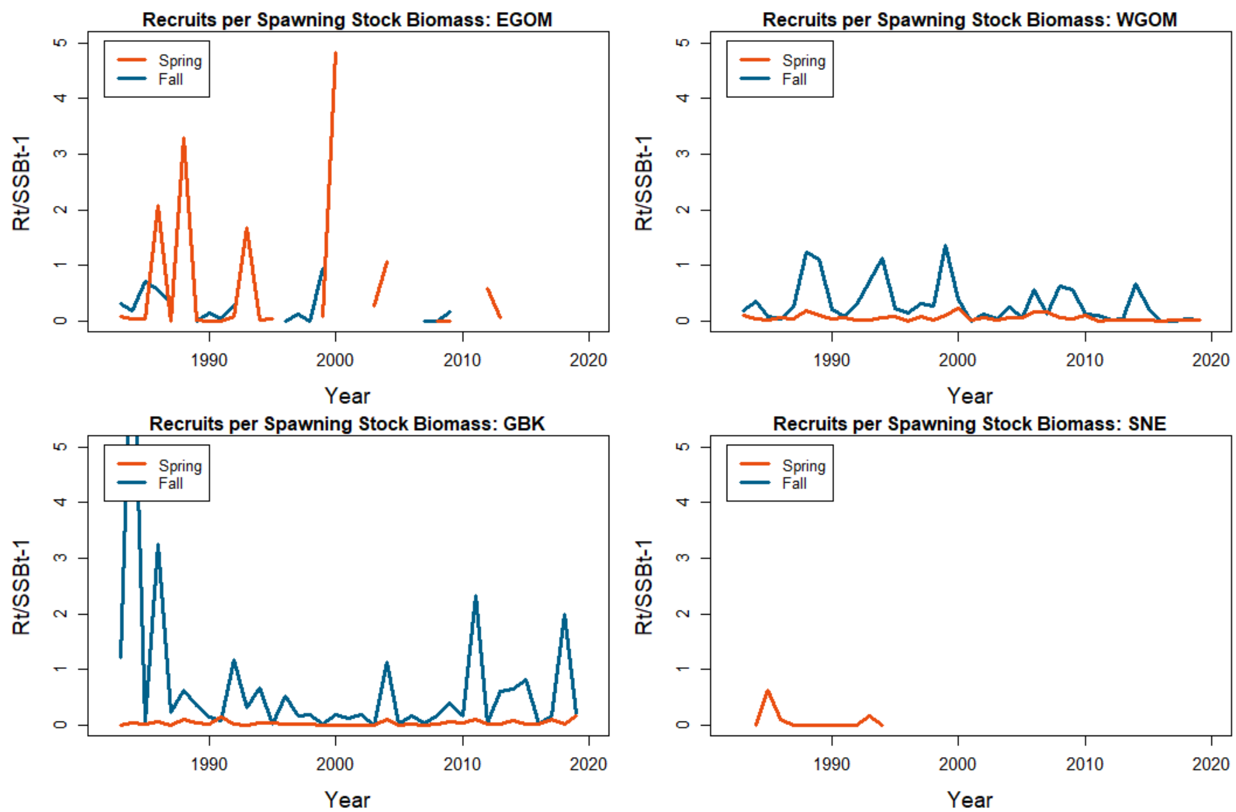
Conclusions

We used generalized additive models to explore relationships between Atlantic cod stock dynamics and ocean climate variables in the Northwest Atlantic region. Significant environmental factors varied by season and stock dynamic, and model validation and fit tests showed reasonable predictive ability. The recruitment models revealed significant relationships with all temperature-related indicators (SST anomaly, bottom temperature anomaly, and mean cumulative heatwave). Spawning stock biomass, calanus abundance, and mean cumulative heatwave were all significant in the depth and latitude distribution models. The growth models revealed a pattern in which zooplankton indicators (*Calanus finmarchicus* and *Pseudocalanus spp.* abundance anomalies) returned as commonly significant variables in weight at age growth models for ages ≤ 4, while the heatwave indicator was commonly significant in weight at age growth models for ages ≥ 4. The relationships between significant environmental indicators and cod stock dynamics overall suggest cod to be shifting northward in distribution, and suggest that cod recruitment and growth may continue to decline, especially under warming temperature conditions. These results show the potential for environmental factors to affect Atlantic cod stock dynamics and may help guide the evaluation of environmental covariates in climate-integrated stock assessment modeling for Atlantic cod as well as future assessments.

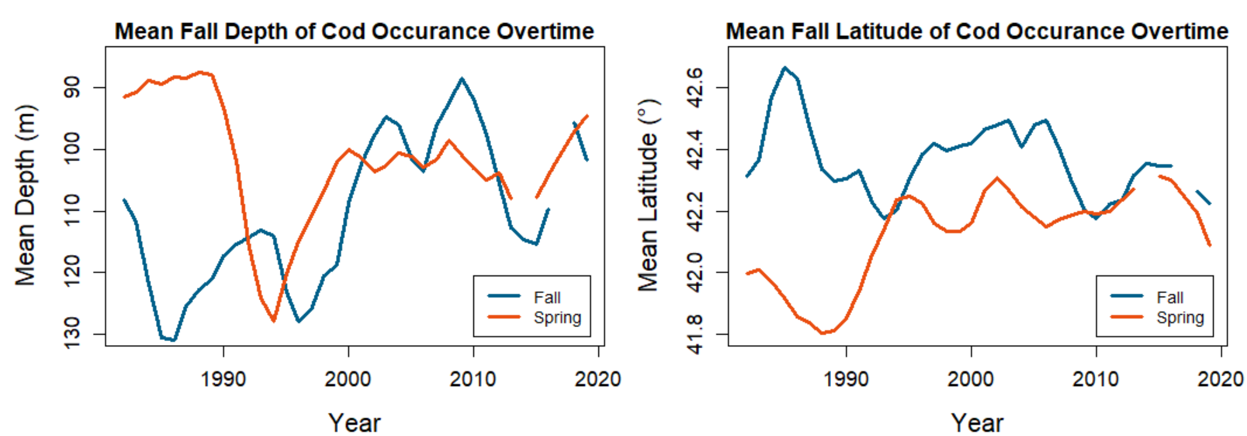
Supplemental Figures



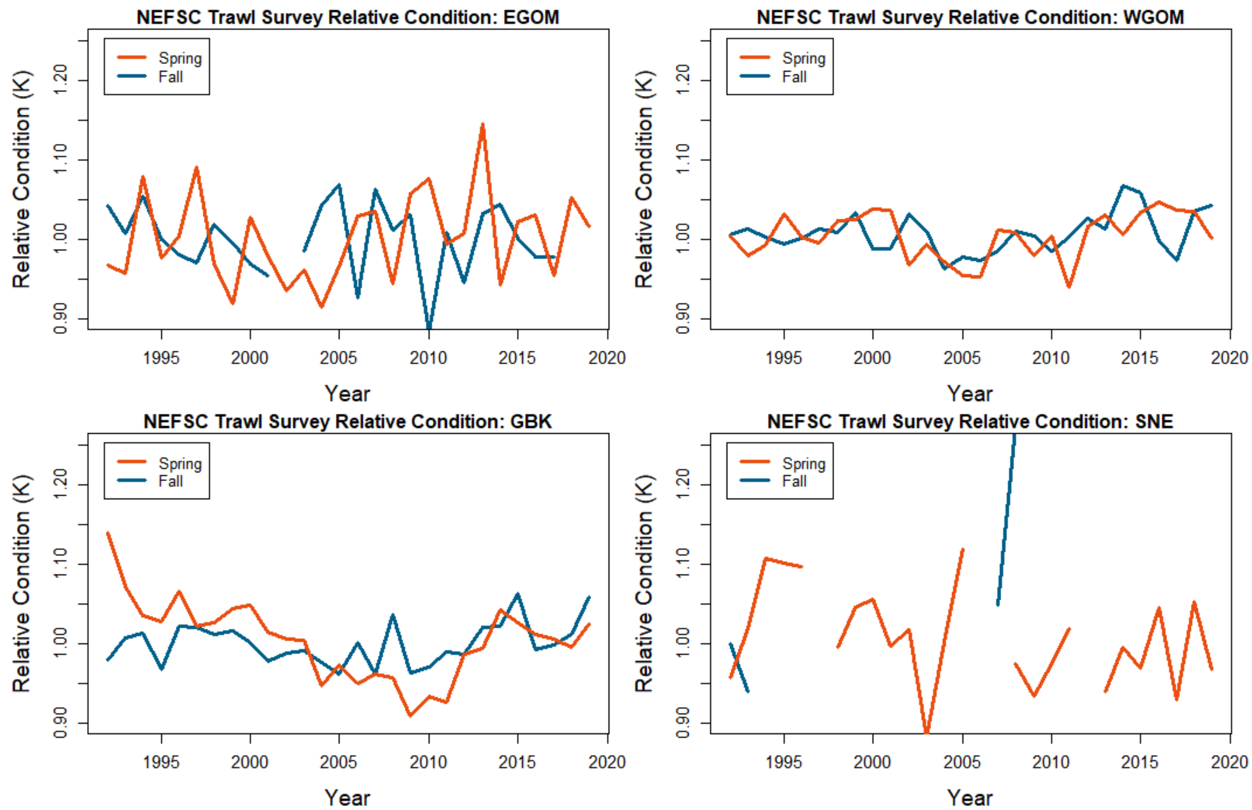
Supplemental Figure 1. Atlantic cod numbers at age 1 data by season and stock area. Numbers at age 1 data sourced from the NEFSC bottom trawl survey from years 1982-2019.



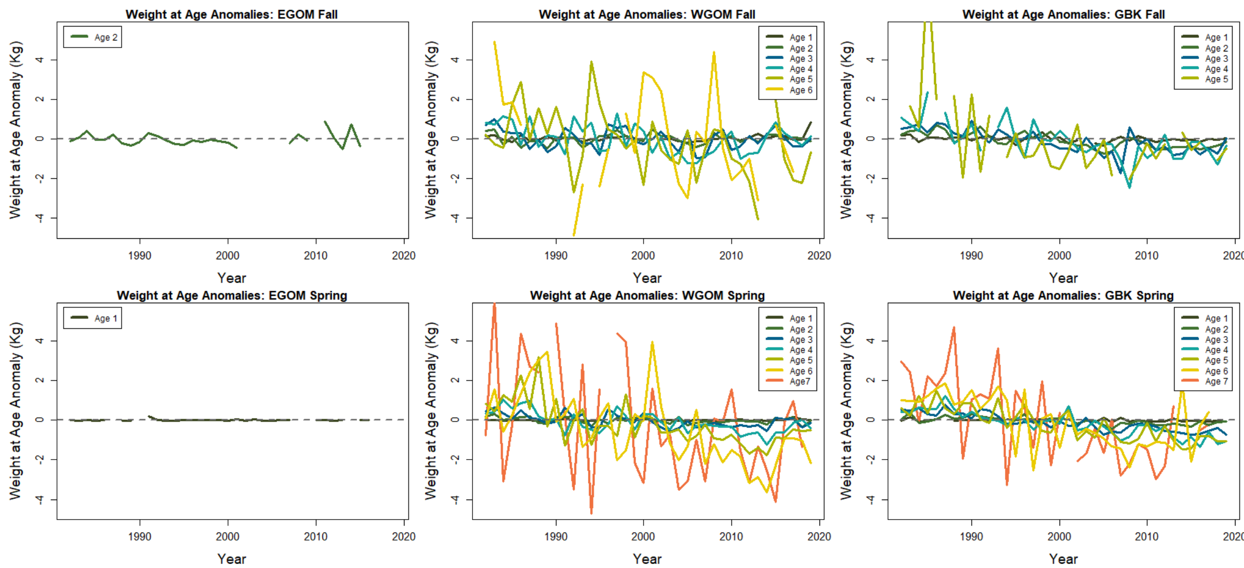
Supplemental Figure 2. Atlantic cod recruits per spawning stock biomass (R/SSB). R/SSB was calculated as recruitment = index of abundance at age 1 in year *t* per SSB in year *t-1* , e.g., R_t/SSB_{t-1}.



Supplemental Figure 3. Atlantic cod mean population depth and mean latitude of occurrence over time by season. These data were sourced from the NOAA Fisheries Distribution Mapping and Analysis Portal from years 1982-2019. These data were not separated by stock area.



Supplemental Figure 4. Atlantic cod relative condition over time by season and stock area. These data were calculated at the ratio of observed weight to predicted weight at a given length from the fall and spring NEFSC trawl surveys from 1992-2019.



Supplemental Figure 5. Atlantic cod weight at age anomalies over time by season and stock area. These data were sourced from the NEFSC trawl surveys from 1982-2019. Stock areas and ages with limited data (<30 observations per age) were excluded.

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