Environmental Influences on American Plaice Stock Dynamics

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BACKGROUND

Over the last 40 years, the waters of the northwest Atlantic have warmed at a rate more than three times the global average and the recent decadal warming in this region is among the fastest in the world (Pershing et al. 2015, 2018, NEFSC 2022b). 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). American plaice is a cold-water demersal flatfish species native to the North Atlantic and Arctic oceans (NEFMC 1985). Changes in ocean conditions have been documented to affect key life history processes, including recruitment, distribution, and growth of American plaice (see detailed description in ToR 1 section of WG report).

The goal of this work was to conduct exploratory modeling to examine the relationship between key aspects of American plaice 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. Time series of relevant environmental variables included sea surface (SST) and bottom temperature anomalies, Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), and the Gulf Stream Index (GSI) and were related to time series of stock variables using generalized additive models (GAMs). These analyses were used to inform the environmental covariates considered in performance testing of climate-integrated stock assessment modeling of American plaice (see ToR 4 section of WG report).

METHODS

Data Sources

American Plaice Data

We estimated recruitment success using indices of abundance at age from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey (spring and fall surveys, see tables 9a and 9b from https://apps-nefsc.fisheries.noaa.gov/saw/sasi/uploads/2019_PLA_UNIT_TAB_OA2017_DATA_RESULTS_TABLES.pdf). These data represent the standardized stratified mean number per tow of American plaice, by age, in offshore strata 13-30 and 36-40 of the Gulf of Maine and Georges Bank areas. We utilized data from 1980-2019 from the spring bottom trawl survey and 1980-2018 from the fall survey. Spawning stock biomass (SSB) data were estimated using spring and fall NEFSC bottom trawl survey numbers at age for American plaice. The aggregate biomass for these indices was calculated for each year (1980-2019) and for each season, in Albatross calibrated units (kg/tow). Recruits per spawners was used as a metric of recruitment success (Perretti et al. 2017) and calculated as recruit = index of abundance at age one in year t per SSB in year t-x , where x =1, (R_t/SSB_{t-x}). Seasonal American plaice spawning stock aggregate biomass data were also used as independent variables in the distribution and growth analyses.

Distribution analyses used American plaice mean depth and mean latitude (center of gravity) timeseries as response variables which were sourced from the NOAA Fisheries Distribution Mapping and Analysis Portal (https://apps-st.fisheries.noaa.gov/dismap/DisMAP.html). These seasonal data are derived from the NEFSC bottom trawl survey and are calculated as biomass-weighted averages of depth and latitude, weighted by the interpolated biomass at each depth or latitude for each year (1974-2019) of the survey (DisMAP Technical Report 2022).

Growth analyses relied on American plaice 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 NEFSC trawl survey from 1992-2019 (2022 State of the Ecosystem New England report). American plaice WAA anomaly data were calculated from WAA data from the NEFSC Bottom Trawl survey for year classes 1-11+ from 1992-2019. Due to the limited timespan of these data, the full timeseries (1992-2019) were used as the baseperiod for anomaly estimates.

Environmental Data

Bottom water temperature and SST data were sourced from the Finite-Volume Community Ocean Model (FVCOM, Chen et al. 2006). The FVCOM has demonstrated correspondence with bottom temperatures taken by the NEFSC bottom trawl survey (Turner et al. 2017), making it appropriate for use in this exploration. Temperature anomalies were calculated from monthly averaged FVCOM data between the years 1978-2019 using 1981-2010 as a reference baseline period for comparison.

North Atlantic Oscillation (NAO) data were obtained from the NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov/teleconnections/nao/). These data are monthly anomalies of the surface sea level pressure difference (hPa) calculated from the 1950-2000 climatological daily mean and standard deviation base period. These data span from January 1950 to present and are calculated over 0-90 °N latitude.

Atlantic Multidecadal Oscillation (AMO) index data were available from the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/data/timeseries/AMO/). This timeseries spans from 1948-present and is calculated from the Kaplan SST dataset, which represent gridded global SST anomalies. The AMO index is recorded at a monthly time interval, the unsmoothed dataset was used in this study.

The Gulf Stream Index (GSI) dataset was sourced through direct communication with Dr. Zhuomin Chen at Woods Hole Oceanographic Institute where data were derived following the methods of Joyce et al. (2019). These data characterize a 200-m depth 15°C isotherm derived GSI and were recorded at monthly time interval for years 1954-2019. This GSI timeseries are not publicly available, however the source dataset was obtained from NOAA's National Oceanographic Data Center and represent 3-month smoothed ocean temperature values at 200m along the north wall from 75°W to 55°W at a resolution of 1° latitude/longitude (https://www.ncei.noaa.gov/access/global-ocean-heat-content/). Temperature variability of the Gulf stream is equivalent to a 50-100 km north-south shift (Joyce et al. 2019) and thus the Gulf Stream Index is recorded in terms of the Gulf Stream position anomaly (degrees latitude). More information about the analytical methods used to derive this dataset can be found in Joyce et al. (2019).

Each of these environmental variables were aggregated into annual and 6-month means, which represented the 12-month and 6-month period before the start of each seasonal trawl survey. The NEFSC spring trawl survey runs from February-April, while the fall survey runs from September-October of each year. Thus, the 12-month mean for each environmental variable spans from $\text{March}_{(year-1)}$ – $\text{February}_{(year)}$ for spring data, and $\text{October}_{(year-1)}$ – $\text{September}_{(year)}$ for fall data. Likewise, the 6-month mean for each environmental variable spans from $\text{September}_{(year-1)}$ – $\text{February}_{(year)}$ for spring data, and $\text{April}_{(year)}$ – $\text{September}_{(year)}$ for fall data. This time period selection method was used in Fredston-

Hermann 2020 and ensures that only environmental data prior to the survey were considered as potentially influential on aspects of plaice dynamics.

Generalized Additive Model Fitting

Pearson correlation coefficient tests were conducted prior to model development to test for variable independence. There was a high correlation between GSI and all temperature variables (bottom temperature and SST), as well as between AMO and NAO variables. Subsequently, if both variables were significant in the model ($p < 0.05$), the significant variable that resulted in the lowest model Akaike Information Criterion (AIC; Akaike 1974) was kept in the model, and the other removed. Similarly, variables summarized at different time-steps (e.g. SST at 6-month vs. 1 year) were filtered from final models such that each potential covariate was tested in each model but only unique, significant variables that explained the most variance were kept in the final model to avoid effects of multicollinearity.

Each of the dependent variables were modeled independently using GAMs (Hastie and Tibshirani 1986). GAMs are an extension of a generalized linear model (GLM), with a smoothing function added. GAMs estimate relationships between independent and dependent variables by use of spline functions, allowing them flexibility to model relationships beyond the parametric forms common to GLMs (Wood 2017; Yee and Mitchell 1991). Often, nonlinear relationships are observed between species population dynamics and environmental drivers. In this study, GAMs were used to evaluate the relationships between American plaice population dynamics (i.e., recruitment, distribution, and growth) and environmental variables. A backward fitting technique based upon covariate significance ($p < 0.05$) and AIC were used in tandem to build and select the best fitting model for each population dynamic × season group. AIC is a method which tests the goodness of fit of a model (i.e., smaller is better) while also including considerations of model complexity (Zuur et al. 2009). 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:

$$\begin{aligned} Recruits/SSB = {} & s(GSI6) + s(GSI12) + s(AMO6) + s(AMO12) + s(NAO6) + s(NAO12) \\ & + s(NAO2) + s(Bt) + s(Bt6) + s(SST4) \end{aligned}$$

where *s* is a spline smoother, and *GSI, AMO, NAO, NAO2, Bt, Bt6*, and *SST4* are the independent variables representing the Gulf Stream Index (6- and 12-month), the Atlantic Multidecadal Oscillation (6- and 12-month), the North Atlantic Oscillation (6-month, 12-month, and lagged an additional year), 12-month mean bottom temperature anomalies, 6-month mean bottom temperature anomalies, and 4-month mean SST anomalies, respectively. Similar GAM equations were constructed for the distribution and growth analyses based upon these methods.

Recruitment Analysis Model Development

Explanatory variables tested for associations with recruits per spawner include averaged bottom temperature anomalies, SST anomalies, AMO, NAO, and the Gulf Stream Indices. Each of these explanatory variables were aggregated into annual and 6-month means with two exceptions: a 6-month post-spawning average bottom temperature variable and a 4-month averaged SST anomaly variable. The 6-month bottom temperature anomaly represented a mean March-August period which characterizes the thermal environment in first 6 months of life, starting from the beginning of the spawning season (i.e., March in the GOM, Johnson 2004). The 4-month SST average anomalies spanned from March-June to correspond with post spawning period during which plaice eggs typically float at or near surface waters for 4 months before descending towards the bottom (Huntsman 1918; Johnson 2004).

NAO was included with both a one- and two-year lag in the recruitment model. Brodziak and O'Brien (2005) found that NAO lagged by 2 years explained the most deviance in recruits per spawner anomalies amongst 12 New England groundfish stocks. In addition, there is generally a two-year lag between changes in the NAO and changes in the position of the Gulf Stream's northern boundary (Taylor and Stephens 1998). A full list of environmental variables and associated time-lags tested can be found in Table 1.

Distribution Analysis Model Development

Environmental variables considered for the distribution analysis include AMO, NAO, GSI, and bottom temperature anomaly, as well as SSB. The timeseries used in the distribution analysis spanned from 1980-2019 for both depth and latitude models. Our analysis of depth change of plaice focused on data from the fall survey (i.e., non-spawning period as plaice are known to move inshore during spawning) and latitude data from both fall and spring surveys. A full list of environmental variables tested for each model can be found in Table 1.

Growth Analysis Model Development

Analyses of growth were conducted using condition and weight at age anomaly data. Environmental variables considered for the growth analyses include AMO, NAO, GSI, bottom temperature anomaly, and SSB. The timeseries used in the growth analyses spanned from 1992-2019 (spring and fall). Condition index analysis included one model (i.e., fall data), and WAA models included a model for each age-class and season (i.e., 11 age-classes × 2 seasons). A full list of environmental variables included in each model can be found in Table 1.

Table 1: Environmental Variables Tested in Each Model. Unless specifically noted otherwise, variables denoted with "(6-month mean)" represent the mean of the 6-months prior to the start of the corresponding seasonal survey used in each model. Likewise, variables denoted with "(annual mean)" represent the mean of the 12-months prior to the start of the corresponding seasonal survey used in each model, unless specified otherwise. "Bt" denotes bottom temperature.

Recruitment	Distribution	Growth
GSI (6-month mean) GSI (annual mean)	GSI (6-month mean) GSI (annual mean)	GSI (6-month mean) GSI (annual mean)
AMO (6-month mean) AMO (annual mean)	AMO (6-month mean) AMO (annual mean)	AMO (6-month mean) AMO (annual mean)
NAO (6-month mean) NAO (annual mean, lagged 1 and 2 yrs.)	NAO (6-month mean) NAO (annual mean)	NAO (6-month mean) NAO (annual mean)
Bt Anomaly (6-month post-spawning mean) Annual Bt Anomaly SST (4-month mean: March-June)	Bt Anomaly (6-month mean) Annual Bt Anomaly	Bt Anomaly (6-month mean) Annual Bt Anomaly
	SSB (annual mean: Jan-Dec)	SSB (annual mean: Jan-Dec)

RESULTS

Recruitment Analysis Results

American plaice recruits per spawner exhibited a variable and general increasing trend over the timeseries in fall, but showed very relatively little change over time based on spring data (Figure 1). AMO was significant and explained the most deviance in both fall and spring models. GSI was also significant, but only in the fall model and did not contribute much deviance explained. Together GSI and AMO explained 33.1% deviance in recruits per spawner in the fall model and AMO alone explained 36.6% deviance in the spring model. GAM response curves were examined for each significant predictor variable. The shape of the GAM response curves varied amongst predictor variables but showed consistency within variables (Figures 2 & 3). For example, the shape of the fall model AMO response curve differs from that of the GSI response curve (Figure 2), but response curves were similar for AMO in fall and spring models. Recruits per spawner increased with increasing AMO values up to a point (+0.15-2.0℃), however, after this point recruits per spawner declined. See Table 2 for a full list of environmental variables that were included in the final models and for more details on model fit diagnostics. See Supplemental Figure 1 for model residual plots.

Table 2: Recruitment Model Result Diagnostics and Significant Variables: The abbreviation "DE" denotes deviance explained.

Model	Significant Covariates (% DE when alone in model)	Full Model DE	Full Model AIC	Reduced Model DE	Reduced Model AIC
Fall	AMO – 6-month mean (26.0%) GSI – Annual mean (1.13%)	53.7%	39.46	33.1%	43.16
Spring	AMO – 6-month mean (36.6%)	63.4%	-75.96	36.6%	-65.04

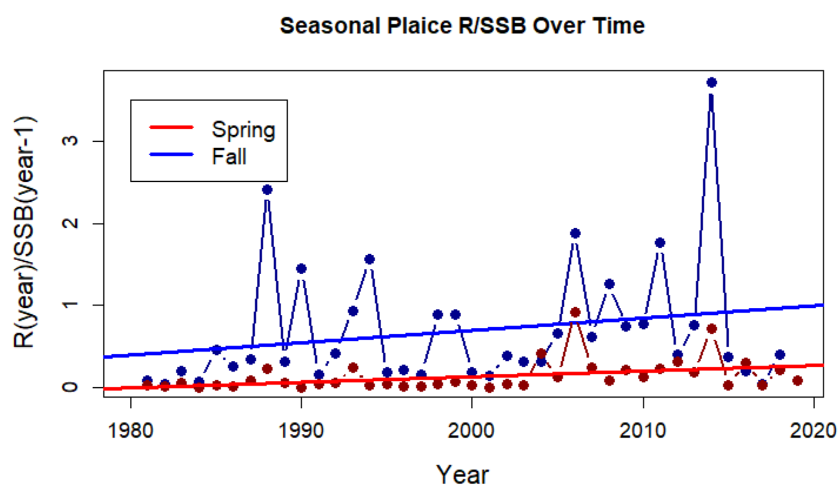


Figure 1: Survey Indices of Recruitment Rate (R/SSB).

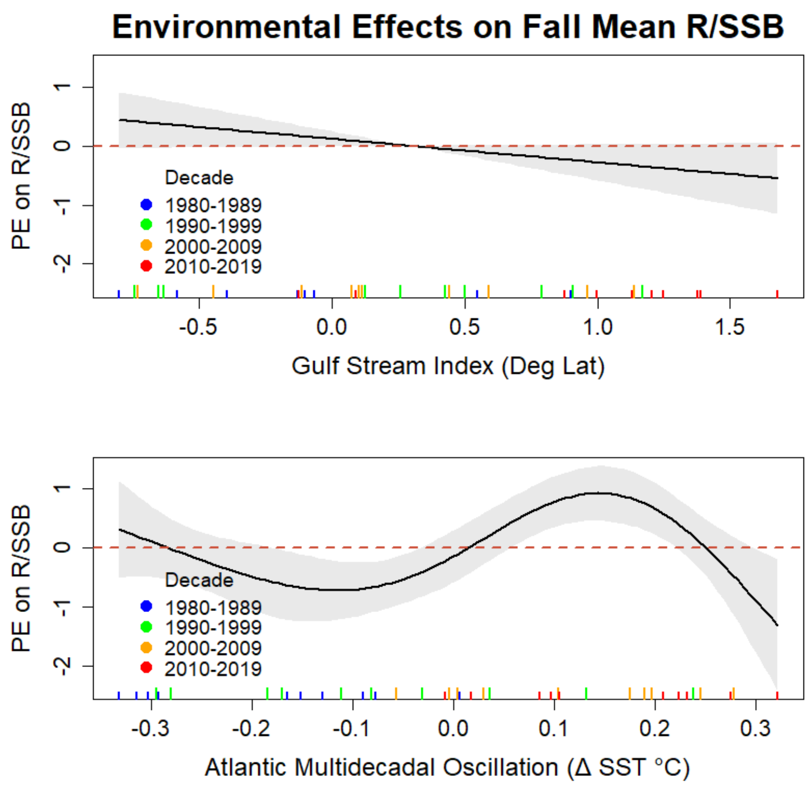


Figure 2: GAM Response Curves of Significant Covariates in Fall Recruitment Model. "PE" denotes the partial effect the independent variable has on the dependent variable, R/SSB. Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

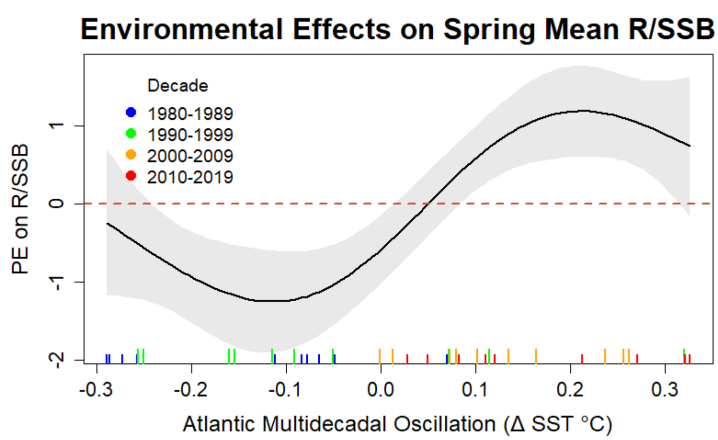


Figure 3: GAM Response Curves of Significant Covariates in Spring Recruitment Model. "PE" denotes the partial effect the independent variable has on the dependent variable, R/SSB. Rug plot lines along the x-axis of each plot indicate distribution of the AMO data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

Distribution Analysis Results

The mean depth of occurrence of plaice became shallower up to 1990 in the fall survey and subsequently shifted deeper over the rest of the timeseries (Figure 4). NAO, bottom temperature anomaly and SSB were found to have a significant influence on depth of occurrence in fall with increasing depth associated with increasing bottom temperature and SSB and the highest values of NAO in the timeseries (Figure 5). There was, however, minimal change in the mean depth of occurrence of plaice in spring over the timeseries (Figure 4) and no significant variables were identified in this model. We hypothesize this difference in response is related to the fact that plaice are known to move inshore in spring for spawning, whereas in fall they are selecting habitat based on their thermal preference.

Mean latitude has gradually shifted northward since the late 1990s and bottom temperature anomaly and SSB were found to have significant positive influence on the center of gravity of plaice in both fall and spring models (Figure 4, 6, and 7). Tweedie, gaussian, and gamma family distributions were tested for each model. Although all three family types resulted in similar fit diagnostics, tweedie distributions were chosen due to a combination of best looking residual plots and AIC scores.

See Table 3 for a full list of environmental variables that were included in each finalized model and for more details on model fit diagnostics. Additionally, model residual plots were generated and can be found in Supplemental Figure 2.

Table 3: Distribution Model Result Diagnostics and Significant Variables: The abbreviation "DE" denotes deviance explained.

Model	Significant Covariates (% DE when alone in model)	Full Model DE	Full Model AIC	Reduced Model DE	Reduced Model AIC
Fall Depth	NAO – Annual (16.9%) 6-Month Bt Anomaly (7.4%) SSB (5.99%)	55.6%	264.2	53.3%	262.43
Spring Depth	No Variables Returned Significant	N/A	N/A	N/A	N/A
Fall Latitude	AMO – 6-Month Mean (3.74%) Annual Bt Anomaly (24.8%) SSB (14.1%)	70.5%	-77.39	60.6%	-75.87
Spring Latitude	NAO – 6-Month Mean (9.39%) Annual Bt Anomaly (33.9%) SSB (14.1%)	73.9%	-101.22	69.5%	-101.40

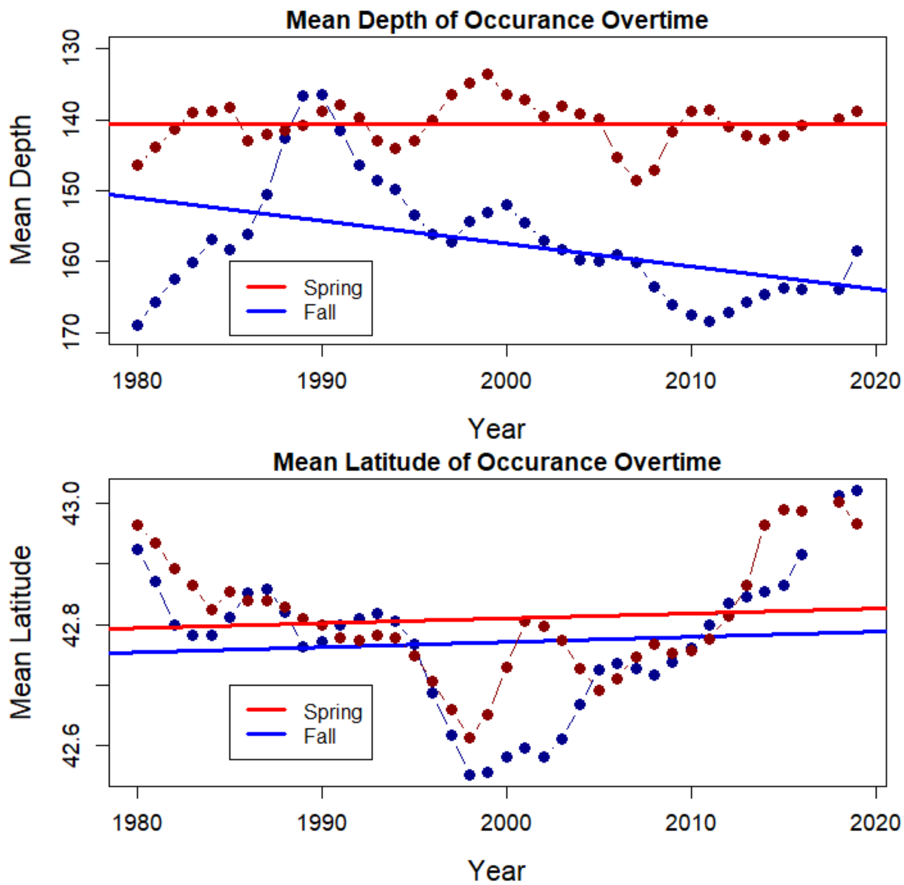


Figure 4: Mean Depth and Latitude of catches from NEFSC spring and fall bottom trawl surveys.

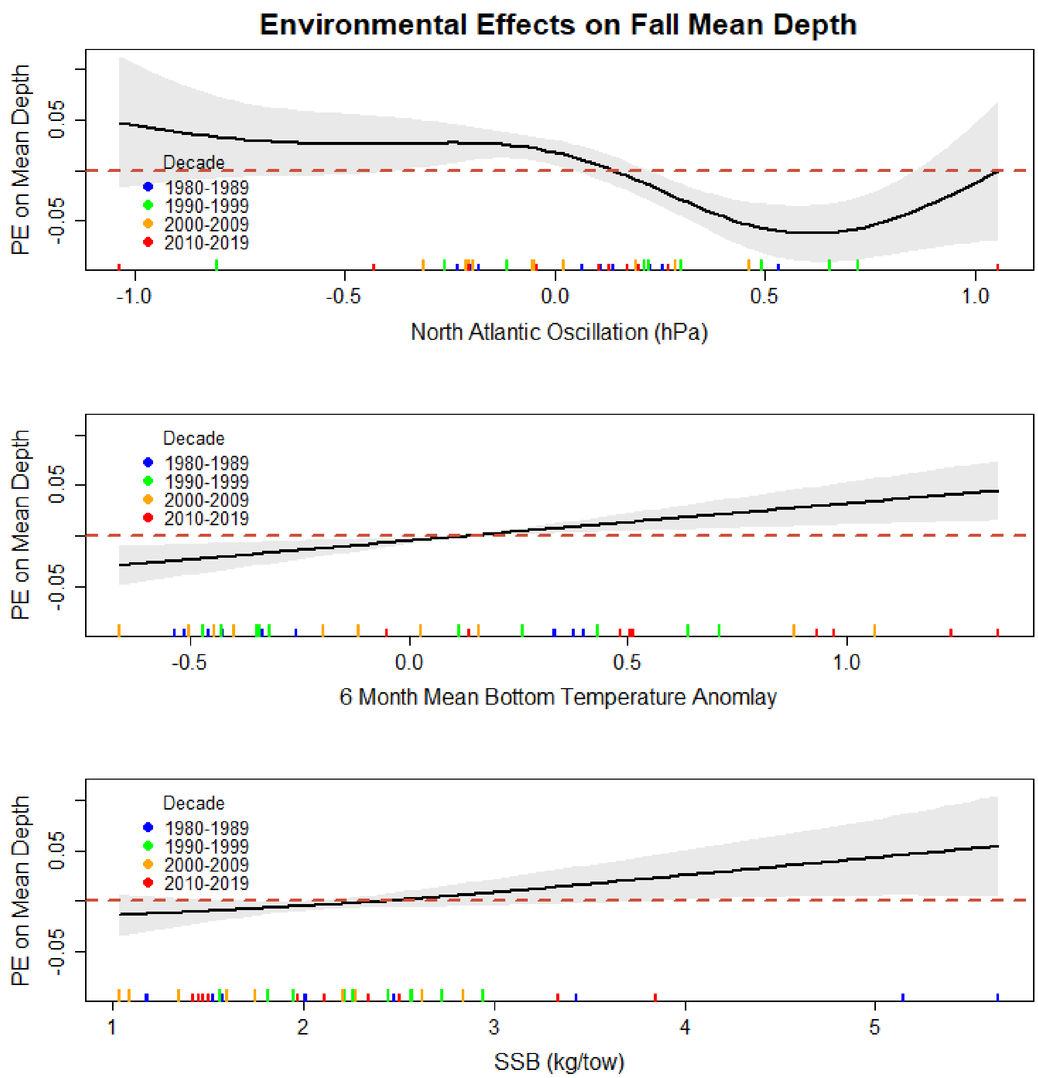


Figure 5: GAM Response Curves of Significant Covariates in Fall Distribution Model (Fall Depth). "PE" denotes the partial effect the independent variable has on the dependent variable, mean depth of occurrence (m). Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

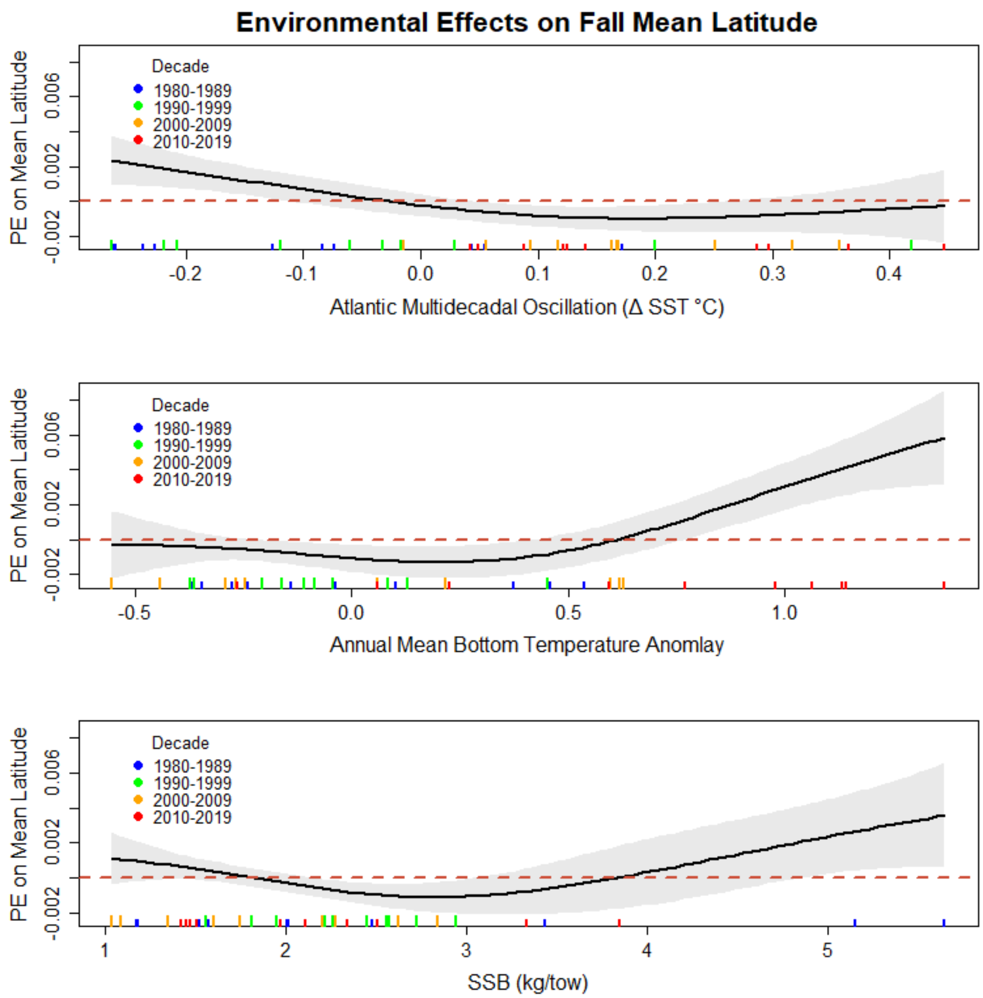


Figure 6: GAM Response Curves of Significant Covariates in Fall Recruitment Model (Fall Latitude). "PE" denotes the partial effect the independent variable has on the dependent variable, mean depth of occurrence (m). Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

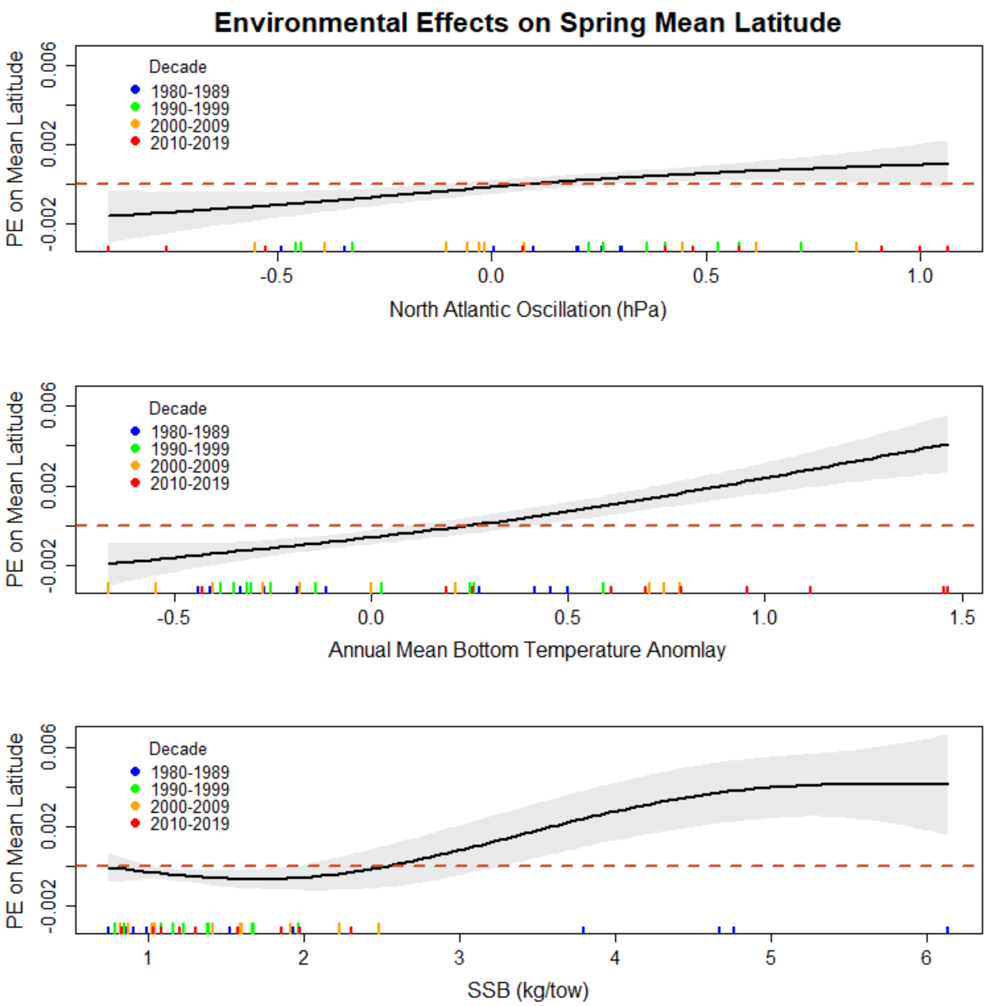


Figure 7: GAM Response Curves of Significant Covariates in Recruitment Model (Spring Latitude). "PE" denotes the partial effect the independent variable has on the dependent variable, mean depth of occurrence (m). Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

Growth Analysis Results

Plaice condition decreased through the mid-2000s, increased through the 2010s, and exhibited a decline in the most recent years of the timeseries (Figure 10). SSB had the most significant influence on mean condition, followed by annual bottom temperature anomaly, and a 6-month mean AMO variable. Plaice condition increased with increasing SSB and bottom temperature, but exhibited a curvilinear response to AMO (Figure 11). This model explained 57.5% of variation, and the model fit diagnostics and residual plots can be found in Supplemental figures.

Table 4: Model Result Diagnostics and Significant Variables for Growth Analyses (Fall Condition Index): The abbreviation "DE" denotes deviance explained.

Model	Significant Covariates (% DE when alone in model)	Full Model DE	Full Model AIC	Reduced Model DE	Reduced Model AIC

Fall Condition Index	AMO – 6-month mean (10.2%) Annual Bt Anomaly (12.1%) SSB (25.5%)	58.3%	107.28	57.5%	-111.255

Trends in WAA of the youngest ages (age 1-3) were relatively stable over time whereas age 4 and 5 fish exhibited a decline in WAA during the early 2000s, increased during the 2010s, and declined again in recent years (Figure 12). WAA of older ages showed a consistent declining trend since the early 2000s (Figure 12). For the WAA analysis, a unique model was run for each year class (1-11+) and each season and model results are summarized in Table 5, 6, and 7. Model residual plots were generated for each of the weight at age anomaly models that had significant environmental variables (See Supplemental figures).

AMO was the most consistent significant variable across the age classes with a tendency for more variance explained in deviance of WAA at older ages and a negative relationship with increasing AMO. GSI explained more deviance in WAA trends at younger ages and tended to exhibit a positive relationship on WAA in these models (Figure 13 and 14). Bottom temperature exhibited a significant, positive relationship on WAA of plaice at age one (fall model), however, there was a negative relationship between WAA and bottom temperature at older ages when significant. There was a positive relationship between WAA and SSB for ages 3-6 up to point but this declined at greater SSB values (Figure 13 and 14). Plaice condition response curves displayed overall agreement in trends with the WAA anomaly response curves, with the exception of the bottom temperature anomaly variable, which displayed a positive trend with fall mean condition rather than negative.

CONCLUSIONS

- **Recruitment:** Recruits per spawner increased with increasing AMO values up to a point, but then declined.
- **Distribution:** Bottom temperature anomaly and SSB were both significant factors influencing plaice shift to deeper and more northward distribution.
- **Growth:** AMO was the most prevalent significant variable between both the condition index and WAA analyses.
    - Significant variables in the condition index model also included bottom temperature anomaly and SSB.
    - Significant variables in the WAA anomaly models also included GSI, SSB, and bottom temperature anomaly.

Table 5: Model Result Diagnostics and Significant Variables for Growth Analyses (Fall Weight at Age): The abbreviation "DE" denotes deviance explained.

Age	Significant Covariates (% DE when alone in model)	Full Model DE	Full Model AIC	Reduced Model DE	Reduced Model AIC
1	Annual Bt Anomaly (35.6%)	46.9%	-310.40	35.6%	-311.30
2	GSI – Annual (25.5%) AMO – Annual (1.76%)	73%	-260.85	34.5%	-239.58

3	GSI – Annual (25.7%) AMO – Annual (2.59%) SSB (36%)	73.1	-192.99	55.6%	-181.29
4	GSI – Annual (20.3%) AMO – Annual (2.77%) SSB (28.4%)	64.3%	-141.56	45.4%	-135.01
5	AMO – Annual (14.2%) SSB (21.7%)	36.4%	-91.18	32.4%	-94.02
6	AMO – Annual (24.6%)	45.8%	-65.17	24.6%	-62.69
7	AMO – Annual (21.1%)	46.9%	-18.50	21.1%	-15.23
8	Nothing Significant	N/A	N/A	N/A	N/A
9	AMO – 6 Month Mean (18.4%) 6 Month Mean Bt (14.9%)	42.6%	22.96	33.7%	20.31
10	AMO – Annual (21.1%)	57.0%	18.49	21.1%	25.88
11+	AMO – Annual (7.05%)	18.0%	51.51	7.05%	48.54

Table 6: Model Result Diagnostics and Significant Variables for Growth Analyses (Spring Weight at Age): The abbreviation "DE" denotes deviance explained.

Age	Significant Covariates (% DE when alone in model)	Full Model DE	Full Model AIC	Reduced Model DE	Reduced Model AIC
1	Nothing Significant	N/A	N/A	N/A	N/A
2	GSI – 6 Month mean (33.1%) AMO – 6 Month mean (2.98%)	56.3%	-302.62	49.8%	-304.67
3	GSI – Annual (14.8%) AMO – Annual (11.4%)	57.1%	-210.11	33.7%	-205.16
4	GSI – 6 Month Mean (47.8%) AMO – Annual (7.39%)	67.1%	-182.03	62.8%	-138.25
5	GSI – Annual (18.3%) AMO – 6 Month Mean (7.79%) SSB (19.8%)	78.4%	-158.62	48.9%	-136.02
6	GSI – Annual (3.7%) AMO – 6 Month Mean (19.4%) SSB (8.87%)	56.3%	-97.07	45.7%	-93.43
7	AMO – Annual (28.0%)	56.8%	-52.78	28.0%	-47.13
8	AMO – 6 Month Mean (16.0%)	27.5%	-6.46	16.0%	-9.14
9	AMO – 6 Month Mean (15.8%)	36.7%	18.85	15.8%	20.63
10	AMO – 6 Month Mean (17.5%) Annual Mean Bt Anomaly (9.04%)	34.6%	20.40	22.5%	18.85
11+	AMO – Annual (17.4%)	29.2%	31.67	26.8%	27.01

	Annual Mean Bt Anomaly (14.6%)				

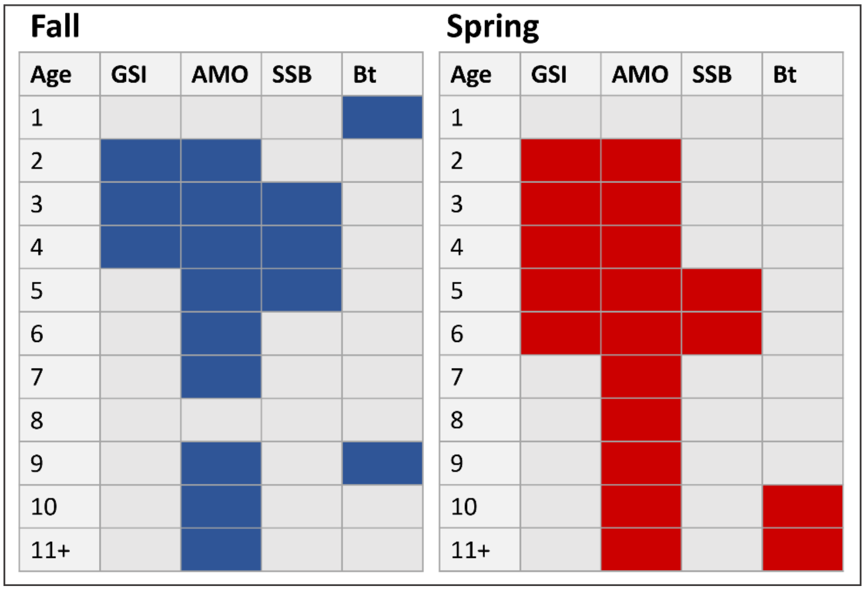


Table 7: Visualizing Significant WAA Anomaly Variables by Year Class. "Bt" denotes the bottom temperature anomaly variable. Each shaded cell signifies the corresponding environmental variable (column) and year class (row) displayed significance in the model.

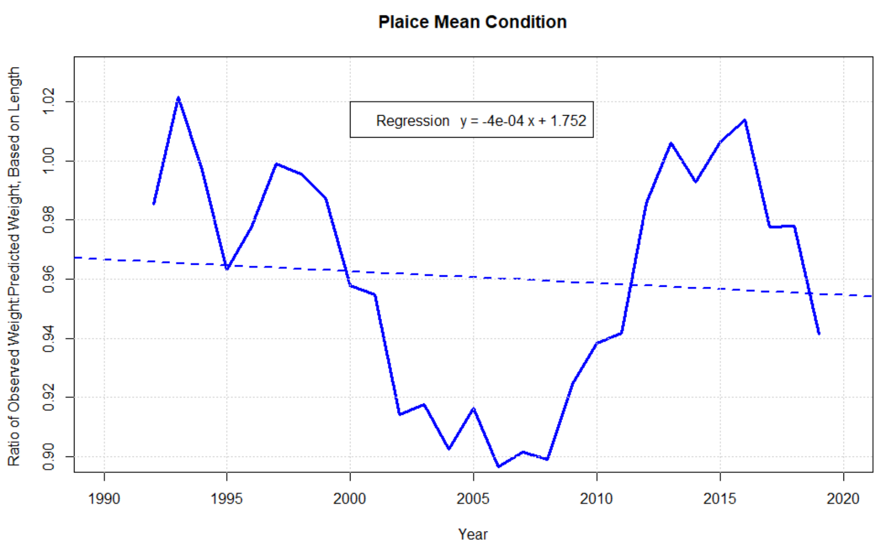


Figure 10: Mean Condition Factor from the Fall NEFSC Bottom Trawl Survey.

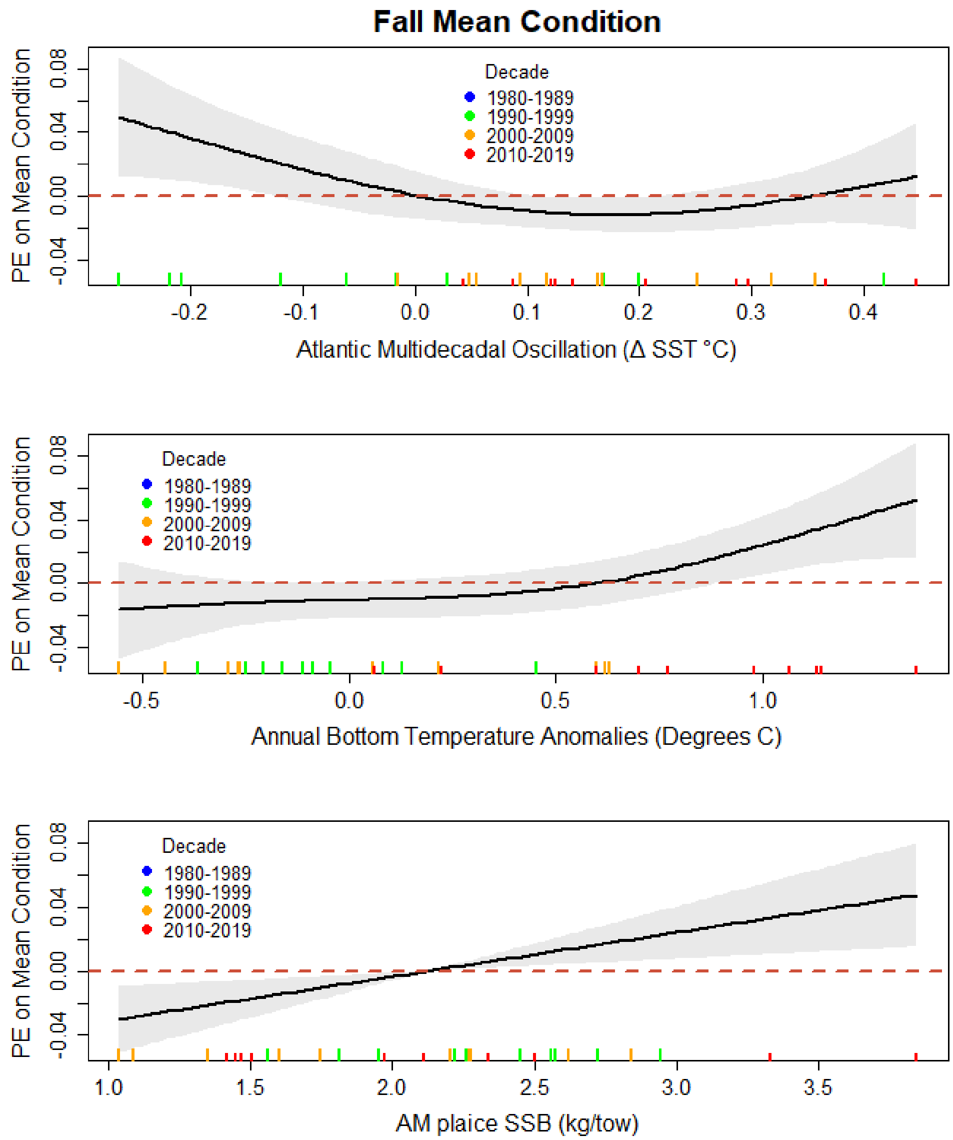


Figure 11: GAM Response Curves of Significant Covariates in Fall Growth Model (Condition Index). "PE" denotes the partial effect the independent variable has on the dependent variable, mean relative condition. Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade of occurrence, as shown in the legend. Shaded regions indicate the standard error confidence intervals.

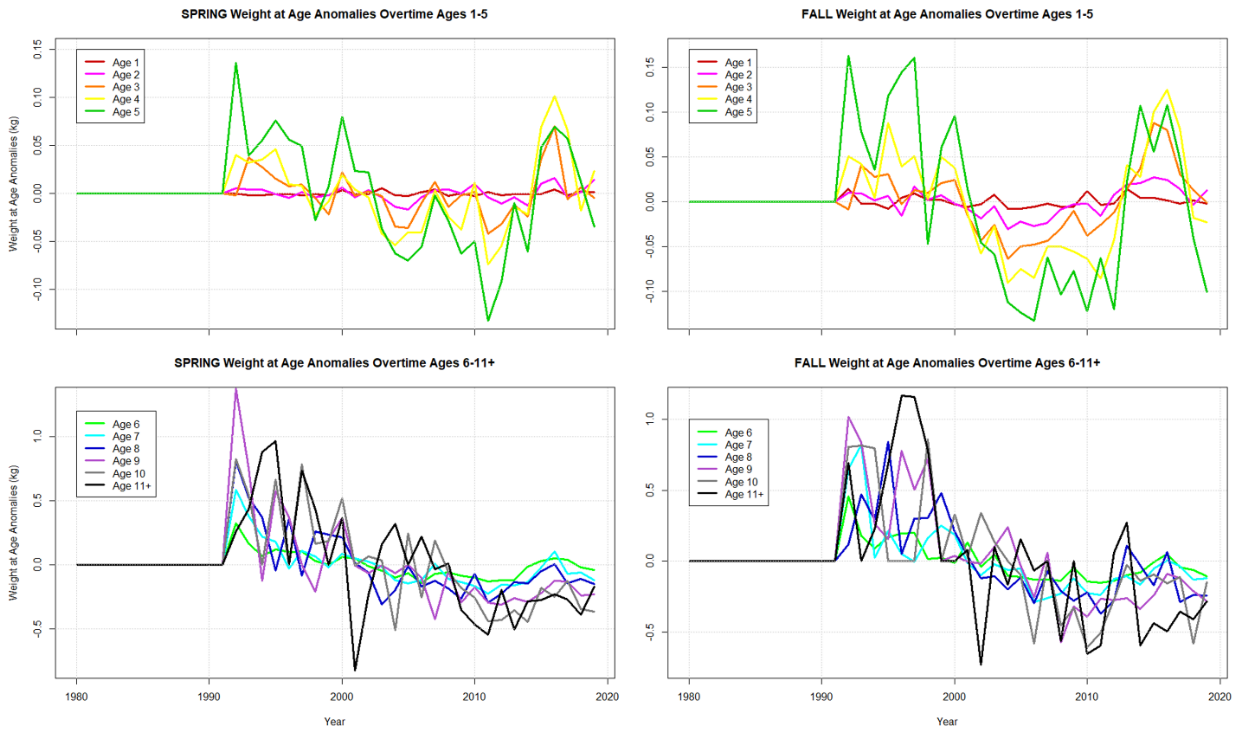


Figure 12: Weight at Age Anomalies from Spring and Fall Surveys.

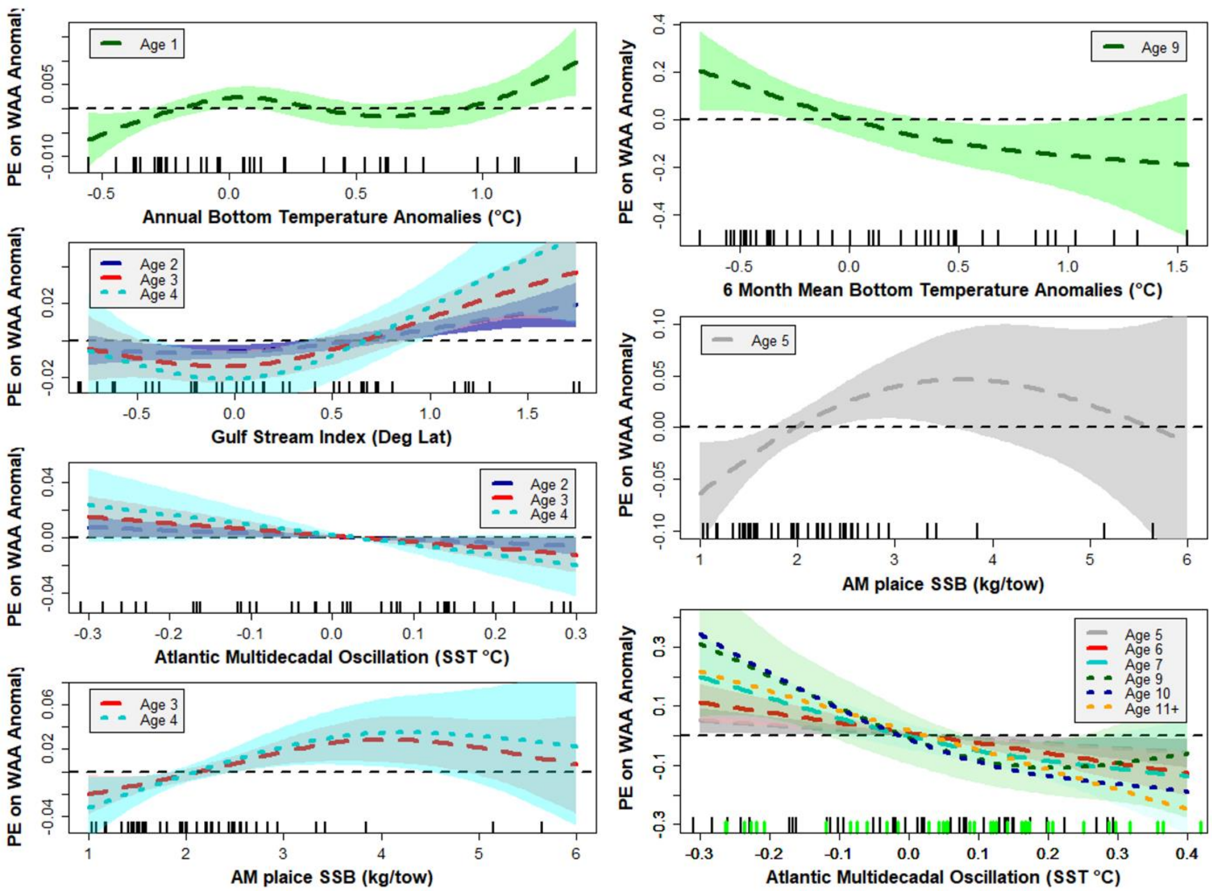


Figure 13: GAM Response Curves of Significant Covariates in Growth Model (Fall WAA Anomaly). Fall year-classes 1-4 are on the left and year classes 5-11+ are on the right. "PE" denotes the partial effect the independent variable has on the dependent variable, mean WAA anomaly. Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by year-class, where black represents all year classes and any other color shown corresponds with the year-class of the same color listed in the legend. A maximum of two colors could be displayed in the rug plots to distinguish between 6-month mean and annual mean rug plot lines. Shaded regions indicate the standard error confidence intervals.

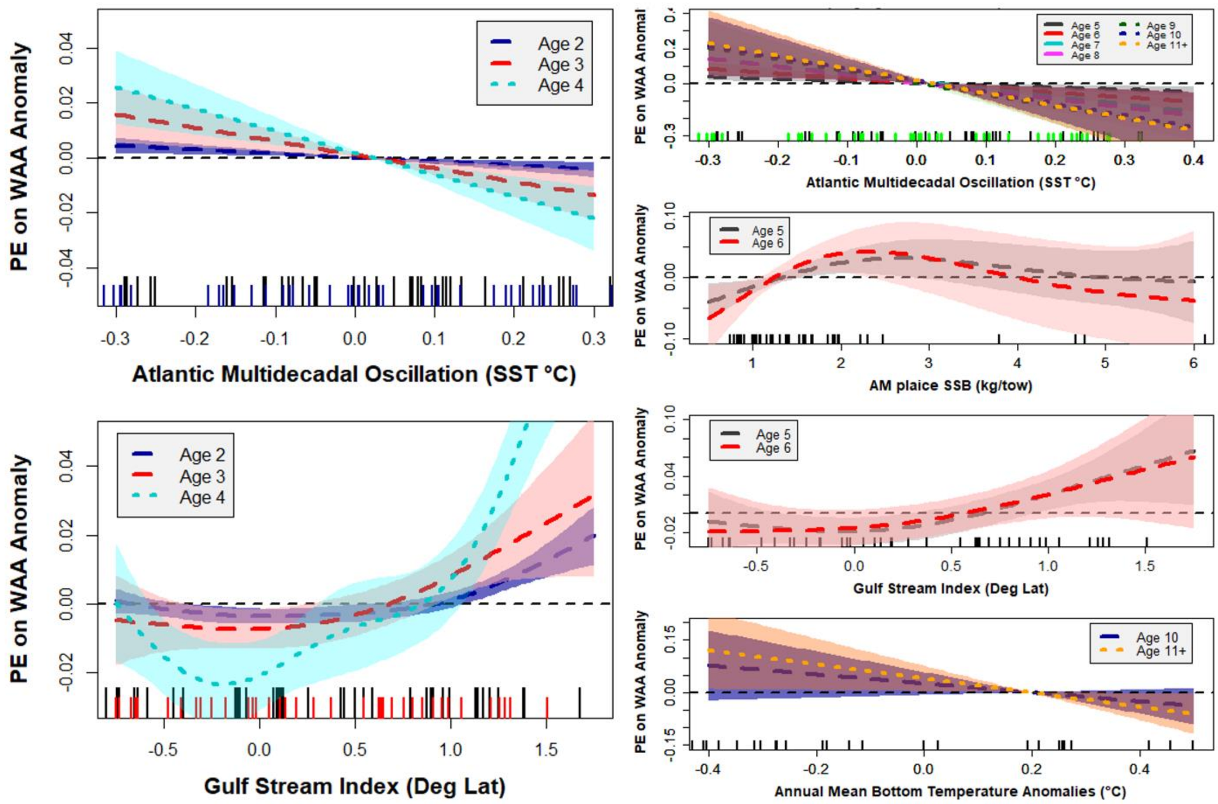
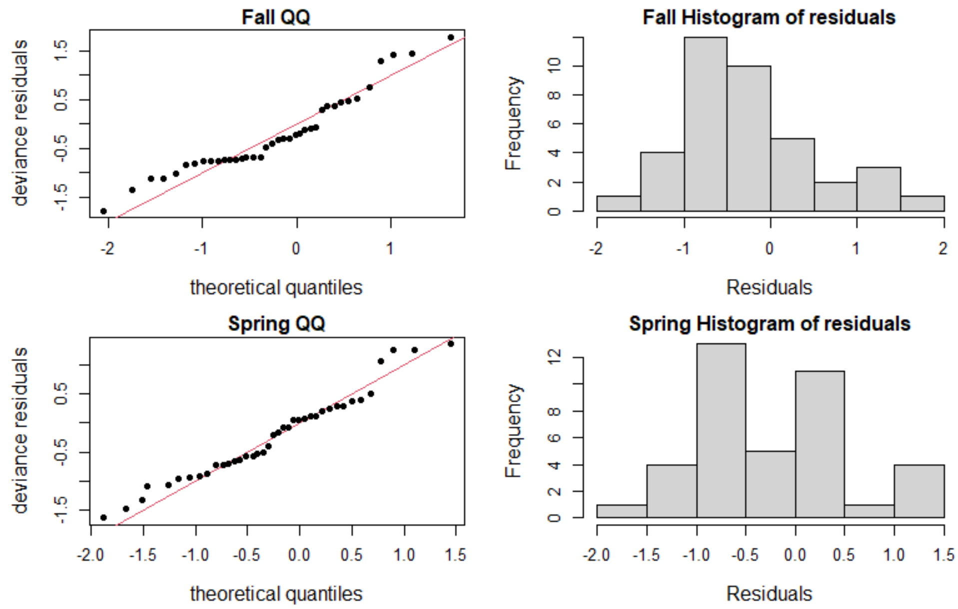
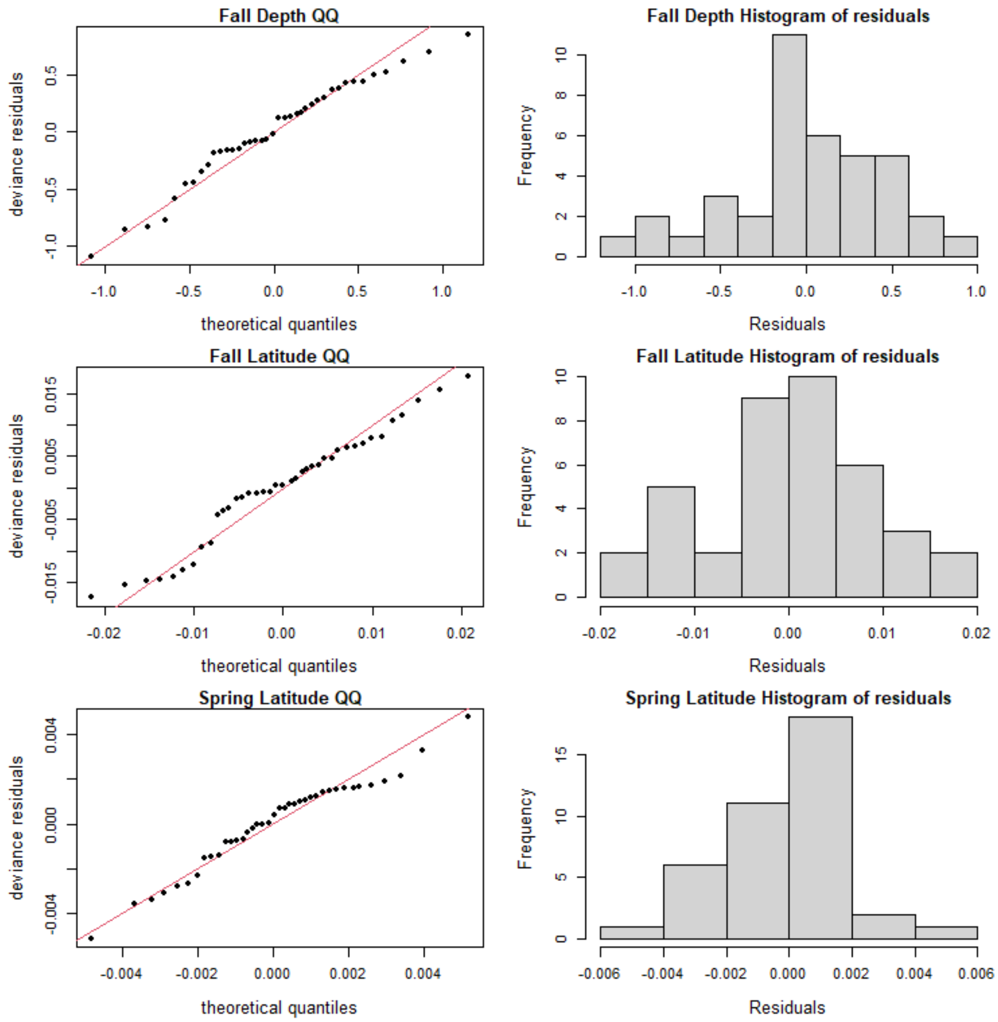


Figure 14: GAM Response Curves of Significant Covariates in Growth Model (Spring WAA Anomaly). Spring year-classes 2-4 are on the left and year classes 5-11+ are on the right. See Figure 12 for figure details.

SUPPLEMENTAL FIGURES



Supplemental Figure 1: Recruitment Model Residual Diagnostic Plots for both Fall (top row) and Spring (bottom row).



Supplemental Figure 2: Distribution Model Residual Diagnostic Plots for both fall depth (top row), fall latitude (middle row), and Spring latitude (bottom row).

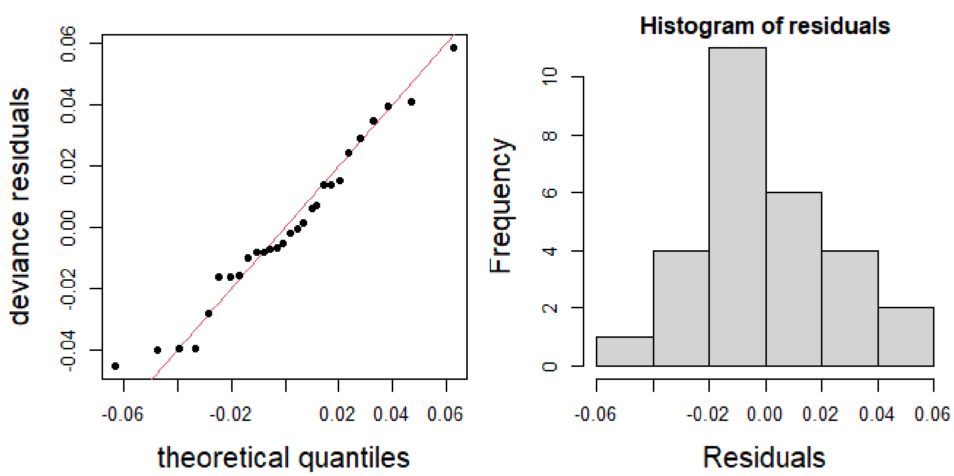
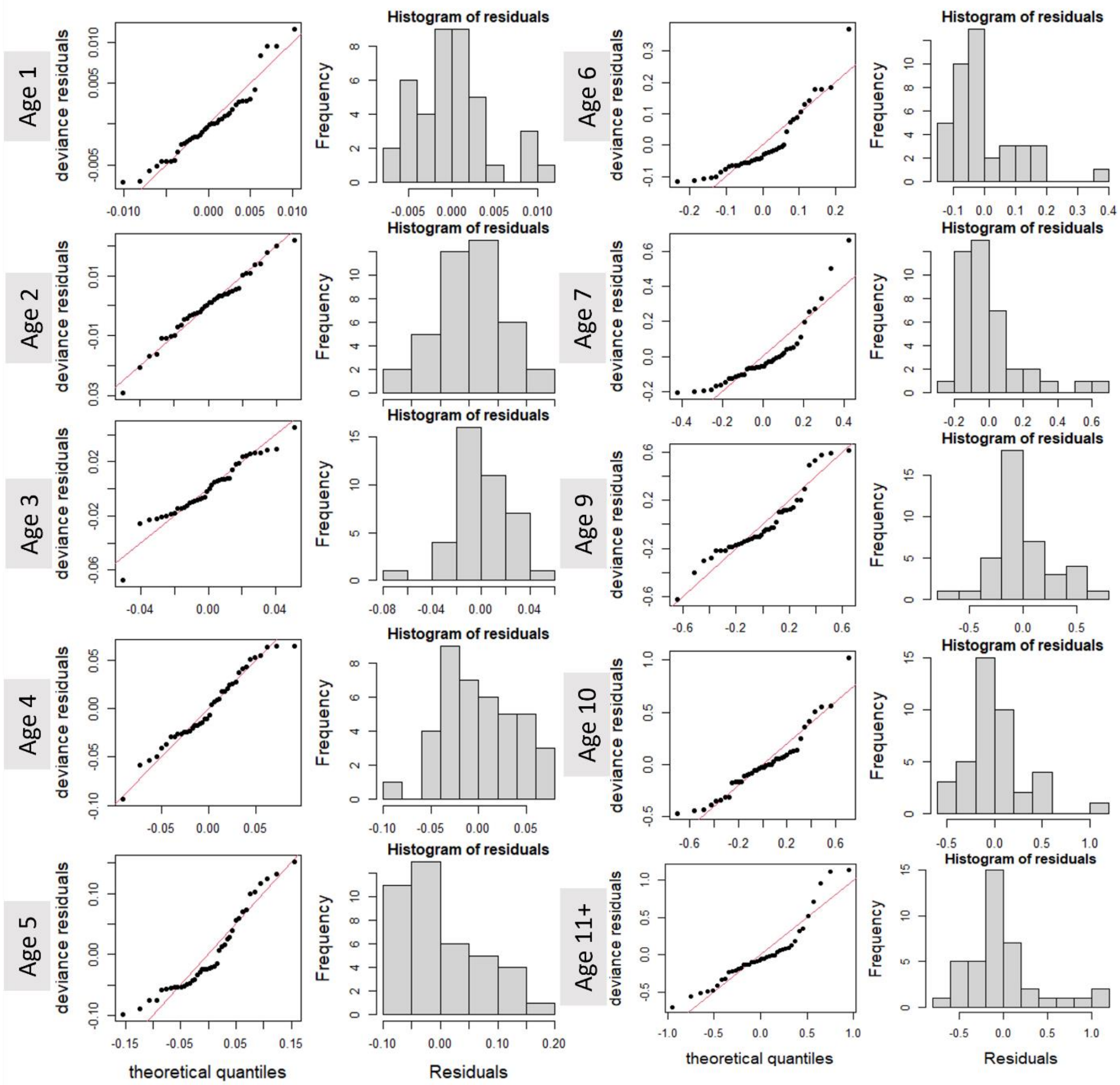
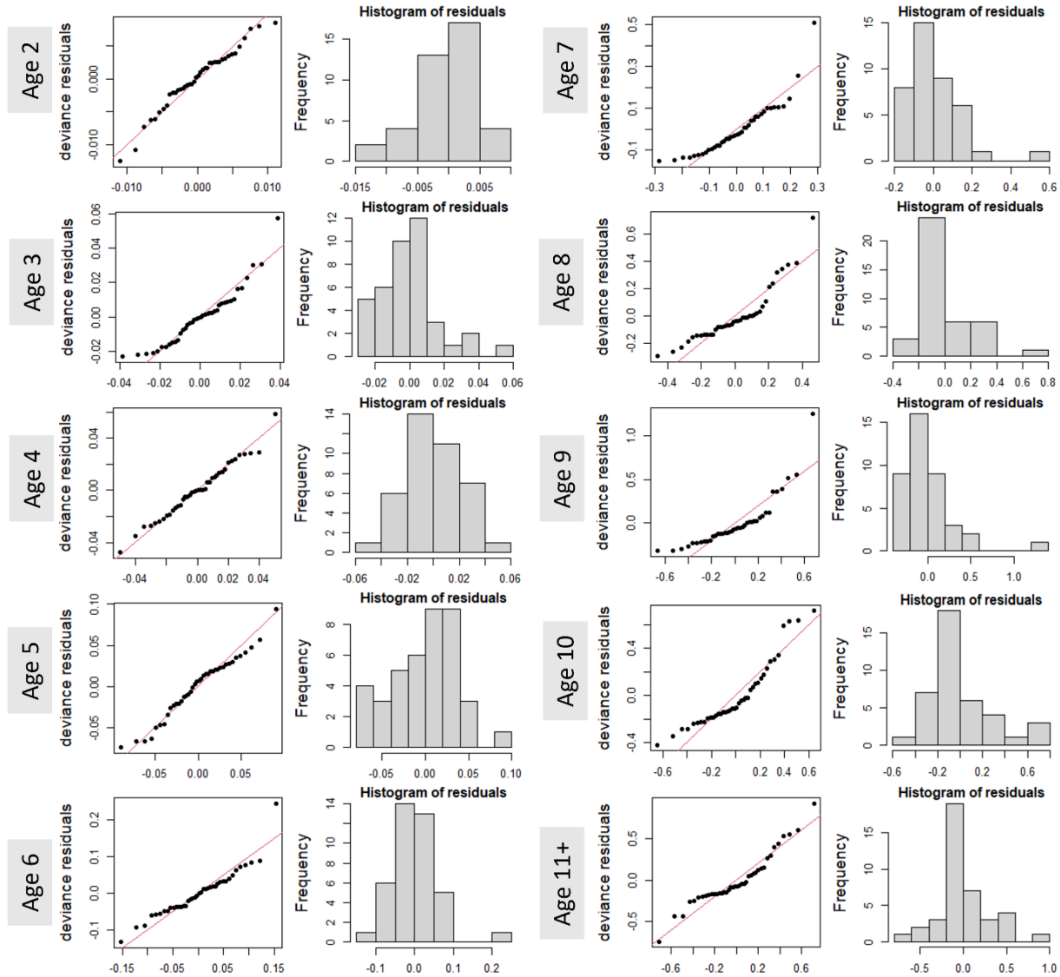


Figure 3: Growth Model (Fall Condition Index) Residual Diagnostic Plots.



Supplemental Figure 3: Growth Model (Fall WAA Anomaly) Residual Diagnostic Plots.



Supplemental Figure 4: Growth Model (Spring WAA Anomaly) Residual Diagnostic Plots.

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