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Macroscale drivers of Atlantic and Gulf Menhaden growth

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Abstract

The identification of anthropogenic and environmental drivers on length-at-age of fish stocks is important to understanding ecosystem dynamics and harvest intensity. We evaluated coastwide annual growth of n = 187,115 Atlantic Menhaden (*Brevoortia tyrannus*) and n = 299,185 Gulf Menhaden (*B. patronus*), using samples collected from the North, Mid-, and South Atlantic from 1961 to 2016 and across the Gulf of Mexico from 1977 to 2016. Using hierarchical models of age 1 growth and age 2 growth, we evaluated a suite of candidate predictors including fishery landings, easterly (U) and northerly (V) wind velocity, river discharge, juvenile abundance, and the Atlantic Multi-decadal Oscillation (AMO). We found age 2 growth rates were smaller than age 1 growth rates for both species and that Atlantic Menhaden growth rates were 3–4 times greater than Gulf Menhaden. Age 1 growth rate of Atlantic Menhaden was positively affected by landings lagged by one year, indicating a density-dependent mechanism. In addition, AMO (negative effect), and wind U (positive effect) and wind V (negative effect) in the North Atlantic region were significant factors influencing coastwide age 1 Menhaden growth. Wind V (negative effect) and AMO (positive effect) influenced age 1 Gulf Menhaden growth. No environmental factors were found to have an effect on age 2 Atlantic Menhaden growth, and AMO was the only significant predictor (weak negative effect) of age 2 Gulf Menhaden growth. Fishing pressure was the primary influence on age 1 Atlantic Menhaden growth, whereas age 1 Gulf Menhaden growth was primarily influenced by environmental conditions.

KEYWORDS
Atlantic multi-decadal oscillation, *Brevoortia patronus*, *Brevoortia tyrannus*, density dependence, environmental drivers, landings, length-at-age

1 | INTRODUCTION

Though ontogenetic growth of fish is an integrative process influenced by many factors, disentangling the relative importance of these factors can be difficult (Sinclair, Swain, & Hanson, 2002). Further complicating any understanding of the primary drivers of fish growth is that environmental conditions may operate and interact at different temporal and spatial scales. As an example of the difficulty disentangling factors, in the northern Gulf of Mexico the timing and magnitude of Mississippi River flow affects Gulf Menhaden *Brevoortia patronus* recruitment, resulting in potential annual variation that could be caused by a changing climate, short-term variations in river flow, timing of spring thaws, broadscale environmental factors, and landings (Govoni, 1997; Sanchez-Rubio & Perry, 2015; Vaughan, Govoni, & Shertzer, 2011). All of these factors could also affect growth, and the relative contribution of any one factor may be difficult to quantify.

The length that an individual fish attains at a given age is determined by endogenous and exogenous factors; for example, genetics and food availability. Several environmental factors, including temperature, wind, and ocean currents (Baudron, Needle, Rijnsdorp, & Marshall, 2014; Ohlberger & Fox, 2013; Sheridan & Bickford, 2011), are thought to influence the length-at-age of fishes. Environmental factors may act directly or indirectly to influence growth. Direct influence of the environment, such as through temperature, may alter an individual's metabolism and thus influence growth. Indirect effects of the environment may act to change ecosystem conditions by regulating prey resources (Gíslason, McLaughlin, Robinson, Cook, & Dunlop, 2018; Litz et al., 2018). Ocean conditions are also temporally and spatially variable, resulting in patterns of growth that may be integrating complex exposures to different temperatures, salinities, and other conditions. For example, Chinook Salmon *Oncorhynchus tshawytscha* in each of three different regions on the US west coast were found to have growth patterns related to ocean currents, wind fields, temperature, and upwelling (Wells, Grimes, Sneva, McPherson, & Waldvogel, 2008). Such environmentally driven growth may have implications for a stock's productivity (Thresher, Koslow, Morison, & Smith, 2007) and be of interest for population monitoring.

In addition to abiotic environmental determinants of growth, other factors influence length-at-age in fish species such as fishery harvest and sources of density-dependent mortality within a population. Harvest can result in changes in length-at-age over time and affect population-level genetics (Conover & Munch, 2002; Conover, Munch, & Arnott, 2009). Genner et al. (2010) found that the size and abundance of some stocks were related to harvest intensity. Alternatively, population density can influence growth rates (Lorenzen & Enberg, 2002) due to space limitations, food availability, and predation (Post, Parkinson, & Johnston, 1999). The influence of density on the rate of growth is a density-dependent effect within the population. Density dependence has been discussed as a plausible driver of growth for several species including forage species, flatfishes, and estuarine species (Bacheler, Buckel, Paramore, & Rochet, 2012; Martino, Houde, & Marshall, 2012; Morgan & Colbourne, 1999; Schueller & Williams, 2017).

Length-at-age in fish is often variable, and this variation is important for stock and ecosystem assessment and management. Quantitative fishery stock assessments use length-at-age data to assess growth, mortality, and productivity of a stock, which determines biological reference points and directly guides management decisions. The way in which growth is characterized can influence estimation of predicted catches, fishing mortality, biomass, and metrics for spawning stock biomass for some species (Kolody, Eveson, & Hillary, 2016; Punt, 2003; Punt, Haddon, & McGarvey, 2016; Punt, Haddon, & Tuck, 2015; SEDAR, 2015). For example, time-varying length-at-age information can inform time-varying maturity and fecundity, which are not necessarily proportional to age. Thus, changes in length-at-age can affect management directly through the computation of management reference points (Schueller & Williams, 2017). In addition to single species management, many managers are interested in moving toward managing single species while recognizing ecosystem considerations (SEDAR, 2015). Because changes in length-at-age over time influence community- and ecosystem-level interactions through shifts in resource availability and rates of digestion and foraging (Ohlberger & Fox, 2013), temporal variation in length-at-age would also affect ecosystem management. These community and ecosystem impacts can be especially important for forage species, upon which many other species rely.

Two important forage species that have exhibited changes in growth over time are Atlantic Menhaden *Brevoortia tyrannus* and Gulf Menhaden. Atlantic and Gulf Menhaden stocks provision the largest fisheries along the Atlantic Coast of the United States and in the Gulf of Mexico. Both species exhibit schooling behavior and are harvested by purse seine gear then processed into products including fish meal and fish oil. The Atlantic Menhaden population also supports a bait fishery, which lands approximately a quarter of the coastwide harvest. Length-at-age for Atlantic Menhaden has varied widely over the last six decades of sampling and has been described by a sigmoidal curve (SEDAR, 2015), with density dependence considered a determinant of growth (Reish, Deriso, Ruppert, & Carroll, 1985; Schueller & Williams, 2017). Length-at-age for Gulf Menhaden has also been variable but without a trend (SEDAR, 2013). To account for changes in growth over time, the Atlantic Menhaden stock assessment (ASMFC, 2017) has incorporated time-varying growth into the assessment model. Time-varying length-at-age in the Atlantic Menhaden assessment model is used to calculate time-varying weight-at-age, maturity-at-age, and fecundity-at-age. The time-varying weight-at-age is used to predict catches over time, while the time-varying life history information is used as an average to compute the management benchmarks. Therefore, changes in length-at-age over time, which are not proportional across age classes, can have an impact on the resultant stock status. Annually variable length-at-age estimates were used in previous stock assessment for Gulf Menhaden (Vaughan, 1987), but have not been used in recent assessments. Both species are considered critical forage species within their ecosystem (Buchheister, Miller, & Houde, 2017; Geers, Pikitch, & Frisk, 2016; SEDAR, 2015); thus, changes in their length over time could affect ecosystem dynamics.

The objective of this study was to determine whether macroscale environmental and biological factors influence length-at-age for Atlantic and Gulf Menhaden. Past studies have addressed these questions for menhaden by exploring a subset of potential mechanisms and drivers (Schueller & Williams, 2017; Turner, 2017). In this analysis, we explored a broad suite of candidate factors, including fishery landings, regional patterns in wind magnitude and direction, river discharge, juvenile abundance trends, and the Atlantic multidecadal oscillation. In addition, we focused on those age classes that are not truncated due to spatial changes in the fishery over time or purse seine fishery selectivity (SEDAR, 2013, 2015, 2018). Finally, we characterized the strength of relationships between seasonal length-at-age changes and both landings and environmental determinants for both species to determine which relationships were strong or weak over time, allowing us to examine the relative impact of multiple factors influencing length-at-age during the lifespan of the fish.

2 | METHODS

2.1 | Menhaden growth data

Length-at-age information was obtained from biostatistical sampling of the commercial fisheries for both the Atlantic and Gulf of Mexico stocks. Port samples were collected on both coasts (from 1961 to 2016 for the Atlantic and from 1977 to 2016 for the Gulf of Mexico) and consisted of individual length (fork length [FL] mm), wet weight (g), and estimated age (y). Individual observations in which 20 mm < FL (mm) > 500 mm for Atlantic Menhaden and 20 mm < FL (mm) > 450 mm for Gulf Menhaden were removed. Age estimation methodology and propriety is described in each species' stock assessments (SEDAR, 2015, 2018). Annulus formation was verified by June and Roithmayr (1960). Subsequent adjustments to the technique were introduced in the Gulf Menhaden estimation shortly after their monitoring port sampling efforts began to enhance readability and precision, primarily due to them having relatively smaller scales than Atlantic Menhaden (Nicholson & Schaaf, 1978).

We selected only age 1 and 2 individuals because both fisheries target those age classes, the majority of increase in menhaden length occurs at these ages, and to focus on the age classes that are not truncated due to spatial changes in the fishery over time or purse seine fishery selectivity. In addition, there have been spatial changes to the reduction fishery on the Atlantic Coast that affect our ability to analyze Atlantic Menhaden growth. Reduction plants historically spanned Maine to Florida but have gradually closed over time such that only one plant remains in Reedville, VA, where fish harvested from New Jersey to North Carolina are landed (Figure 1; SEDAR 40). Atlantic Menhaden stratify latitudinally by length and age with fish ages 3 and older found primarily in the northern part of their range during the fishing season (Nicholson, 1978), Thus, we concentrated our analyses only on age 1 and age 2 fish to limit the influence of spatial contraction of reduction plants on the Atlantic during our study period. We also limited our analyses to ages 1 and 2 for Gulf Menhaden because ages 3 and older are relatively rare in the Gulf of Mexico fishery. The restriction in the number of age classes also allowed us to simplify the statistical modeling approach by using linear regression techniques (growth within those two years does not violate the assumptions of a linear model; Figure 2) and avoid potential convergence issues with non-linear hierarchical models. By focusing on ages 1 and 2—age 0 fish are not selected by the fishery and thus not available as samples—we expected our growth response to be the most sensitive to changes in the environment. Although individual weight-at-age information was also available, menhaden length and weight are highly correlated (fork length-to-weight correlations for age 1 were 0.93 in Gulf of Mexico menhaden and 0.94 in Atlantic menhaden), suggesting that no new information would be gained by investigating another growth variable. Additionally, while condition factor is another size metric that might warrant investigation as a response to environmental conditions, we found extremely low variability in Fulton's Condition Factor. Preliminary efforts to model Fulton's Condition Factor were unsuccessful due to the lack of information in the condition factor values; that is, condition factor estimates had very little variability. Further support for the lack of change or variability in condition factor over the spring and summer months has also been reported in other studies (Leaf, Trushenski, Brown-Peterson, & Andres, 2018). For these reasons, our analysis focused on the evaluation of fork length-at-age as the metric of fish size.

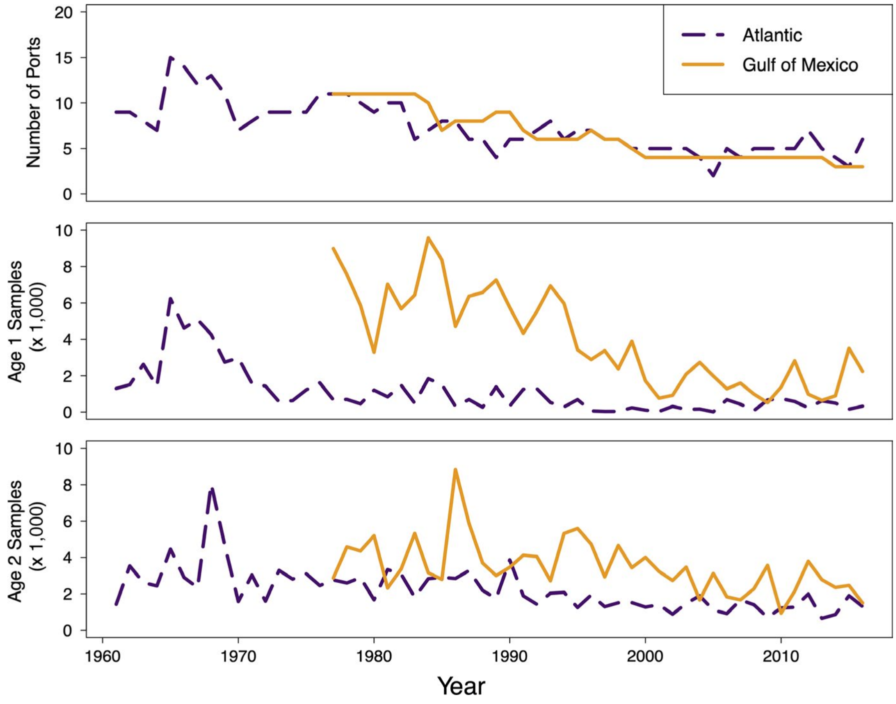

FIGURE 1 Trend in number of reduction ports sampled (top panel) and number of age 1 (middle panel) and age 2 (bottom panel) samples collected on the Atlantic, 1961–2016, and in the Gulf of Mexico, 1977–2016

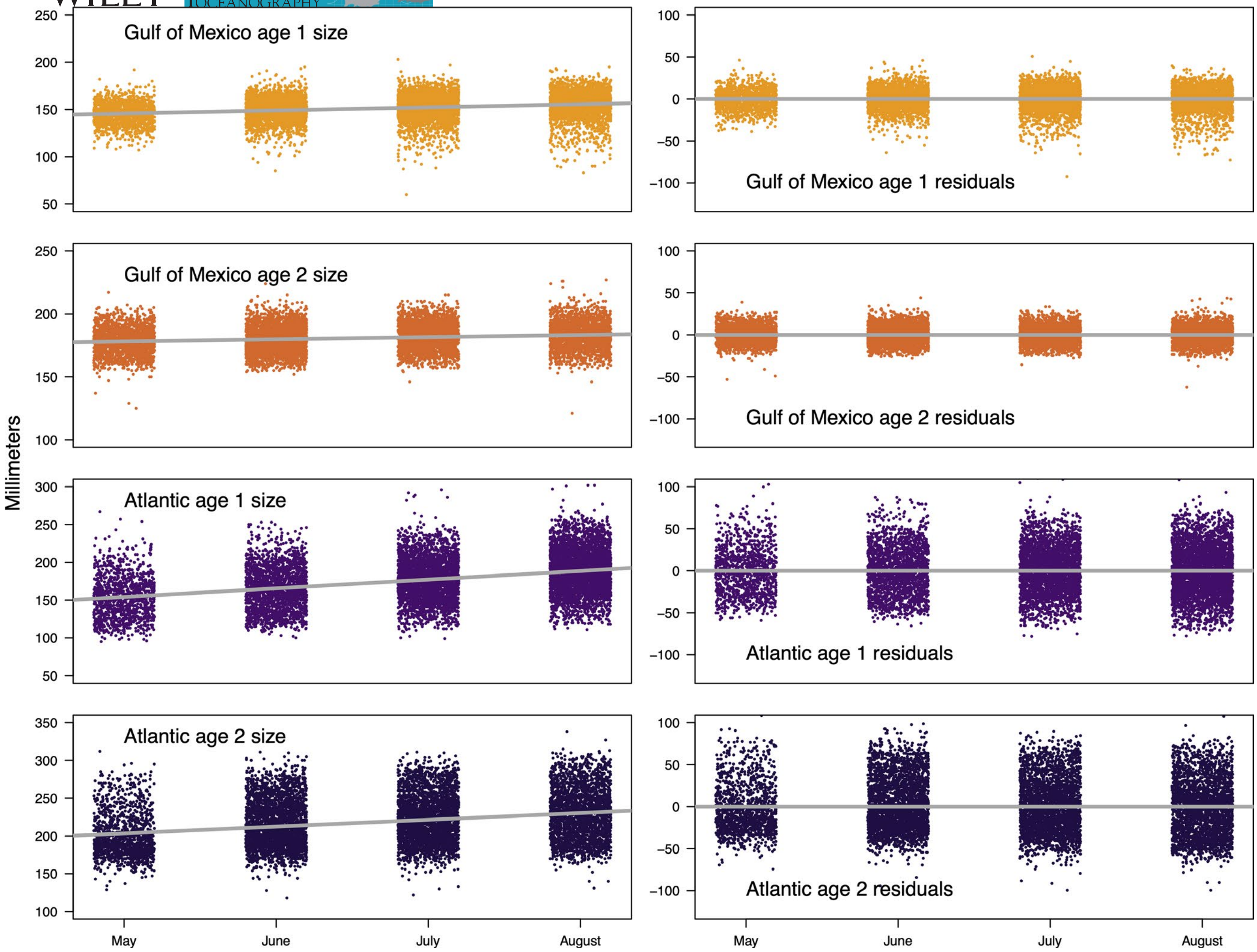

FIGURE 2 Linear model fits and diagnostics for all four age and location (species) combinations of data used. Model fits are presented in the four panels comprising the left column, and associated residuals are presented in the four panels comprising the right column (Note that for visualization purposes, each age and location combination was randomly sampled to include only *n* = 10,000 data points, which adequately represents the data, although the full data were used in the model fitting.)

2.2 | Environmental data

2.2.1 | Spatial domain

The spatial domain of our analysis of Atlantic Menhaden growth included the western North Atlantic Ocean, and the spatial domain of our analysis of Gulf Menhaden growth included the northern Gulf of Mexico. We summarized environmental predictors in the Atlantic across three regions: the US South Atlantic, the US Mid-Atlantic and the US North Atlantic (Figure 3). The three Atlantic regions were selected because they are similar to divisions used in the Atlantic Menhaden stock assessment (SEDAR, 2015) and because they represent boundaries between major marine ecoregions along the Atlantic Coast of the United States (Spalding et al., 2007). When combined, these three regions represent the latitudinal extent of the majority of Atlantic Menhaden recorded catches, which span the Canada–US border in the north to Dade County, Florida, USA, in the south. In the Gulf of Mexico, the extraction region for environmental predictors was coincident with harvest of the Gulf Menhaden stock and included a region bounded by latitude 27.67°N to 30.68°N and longitude 86.50°E to 96.50°E, a domain coincident, but with a reduced easterly extent, with the expected distribution of Gulf Menhaden reported by other authors (Geers et al., 2016).

2.2.2 | Predictors

We explored a variety of macroscale environmental variables as hypothesized predictors for growth and arrived at six potential macroscale predictors, which will be described further below. Four predictors were available for both species: *Wind U-vector*, *Wind V-vector*, the Atlantic Multi-decadal Oscillation (*AMO*), and *Landings*. Atlantic Menhaden growth models had the additional predictor of a coastwide *Juvenile Abundance Index* (*JAI*). Mississippi River discharge has been shown to influence Gulf Menhaden recruitment dynamics and could have broad impacts on growth given delivery of nutrients from the river discharge, and thus, *River Discharge* was included as a predictor in the Gulf region.

FIGURE 3 Map of the four spatial regions included in the present study. The Gulf of Mexico was considered one region, while the Atlantic Ocean was divided into three regions at Cape Cod, MA, and Cape Hatteras, NC

For each of the four study regions, we derived spatially specific extractions of remotely sensed and modeled environmental predictors (wind and sea surface temperature) to understand potential bottom-up processes that influence growth of Atlantic and Gulf Menhaden. Each of the spatially explicit data was extracted using a polygon that represented the probable or observed range of the Menhaden stock, which extended from the coast to approximately 50–80 miles offshore on the Atlantic and 30–100 miles offshore in the Gulf of Mexico. Following spatial extraction, the weighted mean (weighted by area) of each of the extracted spatially explicit environmental data was determined. Using the extraction regions, we determined the average monthly zonal wind velocity (*Wind U-vector*, easterly; *Wind V-vector*, northerly) using NOAA's Earth Systems Research Laboratory[1] data at 2.5° resolution.

Predictors representing coastwide influences on growth included *AMO*, *Landings*, *JAI*, and *River Discharge*. We used an unsmoothed index of AMO that was generated based on Kaplan sea surface temperatures in the North Atlantic.[2] AMO index values were averaged across February to April, which represent spring climate conditions that would most directly affect growth during the primary growing season. Annual coastwide *Landings* were derived from daily vessel offloads directly reported to the Beaufort Laboratory. Total annual bait landings reported by the Atlantic states were added to annual Atlantic reduction landings. We used the previous year's total landings as a predictor; thus, *Landings* in the model are lagged by one year. For our *JAI* predictor, we used the juvenile abundance index derived for the assessment of Atlantic Menhaden (SEDAR, 2015), which is comprised of 16 survey data sets (seine, trawl, and electrofishing surveys) from individual states using the methods in Conn (2010). For the Atlantic, two adult abundance indices were available, but were excluded due to lack of temporal coverage (SEDAR, 2015). In the Gulf of Mexico, both a juvenile and adult index of abundance were excluded as predictors due to the limited number of years available. We derived a time series of river discharge (*River Discharge*) for the Gulf of Mexico using annual discharge rates based on the Mississippi and Atchafalaya River flows during the winter months as described in Govoni (1997) and Vaughan et al. (2011). Daily discharge was obtained from the Tarbert Landing gauge located at river mile 306.3[3] and the Simmesport gauge at river mile 4.9.

2.2.3 | Excluded predictors

Prior to modeling, we evaluated a larger suite of candidate predictor variables. Predictors were investigated and excluded when data series were too sparse spatially, too short, or incomplete temporally, or whether if the predictor was strongly correlated with another predictor that was included in the model. Some of the predictors that were considered and excluded were regional sea surface temperature (NOAA Optimum Interpolation Sea Surface Temperature [OISST][4]) due to lack of temporal range, particularly in the Gulf of Mexico; the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) due to correlation with AMO; plankton (food availability; SEAMAP and MARMAP/ECOMON ichthyoplankton surveys) due to limited spatial (southern) and temporal coverage in the Atlantic and limited temporal range and sparsity of spring samples in the Gulf.

2.3 | Statistical analysis

We used a two-level hierarchical modeling approach to describe contrasts in annual coastwide changes in age-specific menhaden growth rates against macroscale predictors for each region. The first level of each model was a simple linear regression that estimated annual growth rates. Fork lengths (mm) for age 1 and age 2 were modeled separately as a function of month (as an integer), which ranged from May to August—the primary growing season for Menhaden and when the fishery is active in both regions. A random effect for year was included such that a growth rate for each year in the model was estimated. Growth rates were estimated as the slope coefficient for the linear model in level 1. Although a linear regression slope is not a traditional growth model, the increase in annual length for Menhaden of age 1 and age 2 from May to August is linear; thus, we used a linear model to describe growth for both species in this age range. The annual growth rates (i.e., slope coefficients) and the associated uncertainty were then carried forth directly into level 2 of the model, where annual growth coefficients were regressed in a multiple linear regression that

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[1] www.esrl.noaa.gov

[2] https://www.esrl.noaa.gov/psd/data/timeseries/AMO

[3] www.mvn.usace.army.mil

[4] http://www.ncdc.noaa.gov/sst

included five macroscale predictors that varied based on the spatial area, although four predictors were common to all regions. We evaluated a total of eight models—two models (age 1 and age 2) for each of four regions.

The first level of the model is expressed as

$$y_i \sim N\left(\alpha_{j[i]} + \beta_{j[i]} x_i, \sigma_y^2\right), \text{for } i = 1 \dots n,$$

where y_i is the fork length (mm) of an individual Menhaden i, captured at time (month) x_i. $\alpha_{j[i]}$ is the intercept for annual growth and $\beta_{j[i]}$ is the slope for annual growth, where j indexes year (and in which i is nested). σ_y^2 is the residual variance for level 1. The second level of the model is expressed as

$$\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim MVN\left(\begin{pmatrix} \gamma_0^{\alpha} \\ \gamma_0^{\beta} + \gamma_Z^{\beta} \cdot Z^{\beta} \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_\beta \\ \rho\sigma_\alpha\sigma_\beta & \sigma_\beta^2 \end{pmatrix} \right), \text{for } j = 1 \dots J,$$

where α_j and β_j are assumed to come from a multivariate normal (MVN) distribution. γ_0^{α} is the mean (intercept) for all α_j. Although annual intercepts were allowed to vary to improve model realism, they were not parameters of interest and were not further modeled in level 2. γ_0^{β} and γ_Z^{β} are the intercept and slope estimates for β_j values, where Z represents a vector of five region-specific macroscale predictors (and therefore γ_Z^{β} represents a vector of the five slope coefficients on those predictors). The variances σ_α^2 and σ_β^2 are the conditional variances of the intercepts and slopes, respectively, and $\rho\sigma_\alpha\sigma_\beta$ describes the covariance between α_j and β_j, with ρ describing the correlation between α_j and β_j.

We used Bayesian estimation to fit the models. All intercept and slope parameters were given diffuse normal priors, variances were given uniform priors, and we modeled the variance–covariance matrix using the scaled inverse-Wishart distribution (Gelman & Hill, 2006). Three parallel Markov chains were run, beginning each chain with different values. From a total of 5,000 samples for each chain, the first 2,000 samples of each chain were discarded. We then thinned to retain every third sample for a total of 1,000 samples from each chain. Combining chains resulted in 3,000 estimates used to characterize the posterior distributions. For all parameters, we assessed convergence both visually (trace plots and plots of posterior distributions), as well as with the Brooks-Gelman-Rubin statistic, $\hat{R}$, with values <1.1 indicating convergence. Analyses were run using JAGS (Plummer, 2016) in the *R2jags* package (Su & Yajima, 2015) from within R version 3.2.4 (R Core Development Team, 2018).

We examined the level-2 macroscale predictor effects at three levels of credibility: 80% (weak significance), 90% (moderate significance), and 95% (strong significance), where significance is defined as the specific interval not overlapping with 0. We adopted multiple levels of credibility due to the high amount of uncertainty possible in regressing growth against macroscale predictors, and the fact that levels of significance below a traditional 95% threshold may still be important and of interest. Credibility at all levels was determined by the corresponding percentiles of the posterior distribution overlapping (not credibly different) or not overlapping (credibly different) 0. Not only do three levels of credibility help us avoid a limited, binary interpretation (e.g., significant or not significant), but it may help to detect effects at large scales, where effects may be present but not singular or overwhelmingly strong. For example, a 90% credible effect of AMO on Menhaden growth rates might conventionally be called non-significant; however, we wanted our analysis to not exclude the possibility that something with a 90% chance of having an effect is not absent from the discussion. Furthermore, the Bayesian framework allowed us to easily integrate this probabilistic framework and evaluate any level(s) of credibility.

As a final statistical evaluation, we took the estimated growth rates from level-1 of the model and ran Spearman correlations. We correlated annual growth rates between the two ages within a given species to examine whether the magnitude of annual growth was related for both ages. We also correlated annual growth estimates for the same age between Atlantic and Gulf Menhaden, to evaluate whether similar magnitude of growth within a given year was experienced across ocean basins for the same age. Correlations between annual growth rates of Atlantic and Gulf Menhaden might indicate similarities in macroscale drivers of growth.

3 | RESULTS

3.1 | Annual growth estimates

We modeled annual growth from n = 187,115 Atlantic Menhaden (62,180 age 1 and 124,935 age 2 captured in the Atlantic Ocean from 1961 to 2016) and n = 299,185 Gulf Menhaden (159,245 age 1 and 139,940 age 2 captured in the Gulf of Mexico from 1977 to 2016) and all eight hierarchical models converged. Mean annual growth rates of Atlantic Menhaden, for both age 1 and age 2, were 3 to 4 times greater than Gulf Menhaden growth rates (Table 1, Figures 4 and 5). For both

TABLE 1 Annual growth metrics (mm/mo) for Gulf and Atlantic Menhaden

	Gulf of Mexico		Atlantic Ocean	
Statistic	Age 1	Age 2	Age 1	Age 2
Mean growth	3.30	1.77	10.40	8.28
Maximum	6.21	4.52	20.20	22.53
Minimum	−0.78	−0.52	0.25	−2.73
Mean annual change	1.90	1.09	4.80	4.50

Note: Mean growth represents the average monthly change in length per month (from May to August) over all years in the data. The maximum and minimum are the extremes in growth rates that were estimated across all years. The mean annual change is the average of the absolute value of the consecutive annual differences, which represents the expected amount of year-to-year variability in growth.

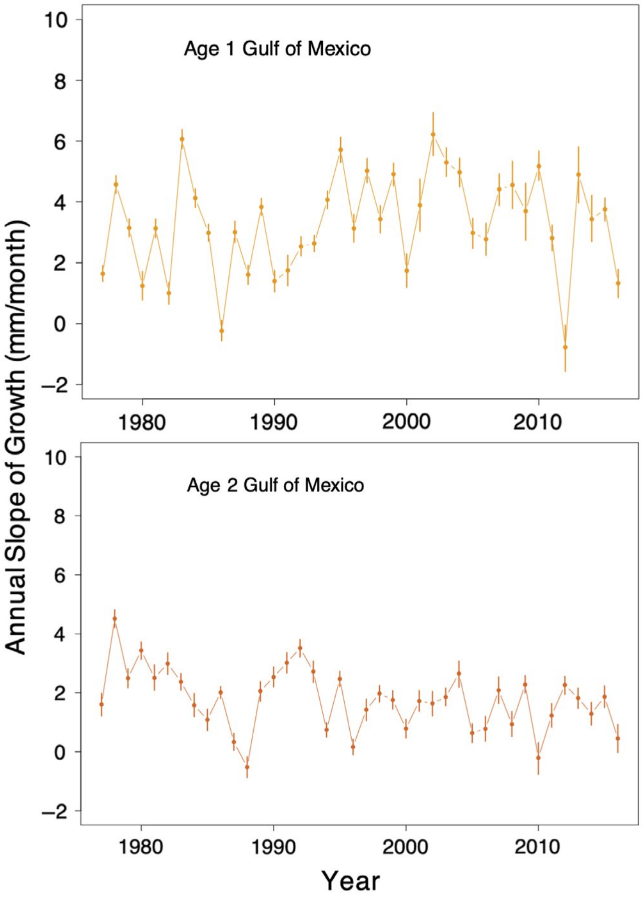

FIGURE 4 Annual growth estimates (mm per month from May to August) estimated by a hierarchical model for age 1 (top panel) and age 2 (bottom panel) Gulf Menhaden from 1977 to 2016. Points represent the mean from the posterior distribution of estimates for each year, with the vertical lines indicating the 95% credible intervals. Line segments connecting sequential years are only included for visual purposes and do not represent any model or any missing data

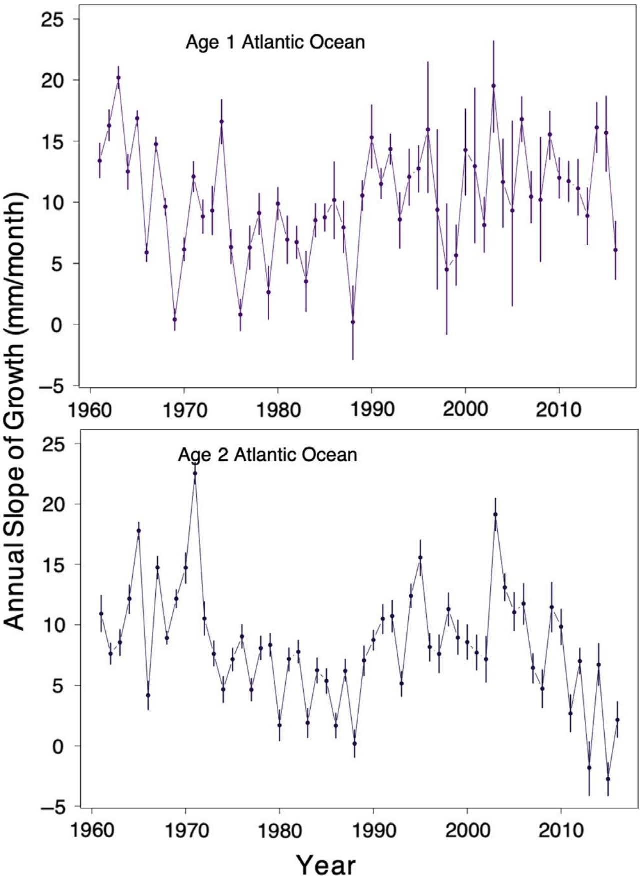

FIGURE 5 Annual growth estimates (mm per month from May to August) estimated by a hierarchical model for age 1 (top panel) and age 2 (bottom panel) Atlantic Menhaden from 1961 to 2016. Points represent the mean from the posterior distribution of estimates for each year, with the vertical lines indicating the 95% credible intervals. Line segments connecting sequential years are only included for visual purposes and do not represent any model or any missing data

species, the age 2 growth rate was smaller than the age 1 growth rate (Table 1). Both species experienced rare instances of negative annual growth. We also calculated the average absolute difference between year-to-year growth rates—representing the change in growth rates from 1 year to the next—which was 4.80 mm per month for age 1 Atlantic Menhaden and 1.90 mm per month for age 1 Gulf Menhaden. Similarly, mean annual changes in age 2 growth rates (1.09 mm per month) were about half of the age 1 estimate for Gulf Menhaden, but relatively large (4.50 mm per month) for age 2 Atlantic Menhaden. Correlations of annual growth rates between ages and species were overall weak or non-existent. The strongest correlation we detected, $\rho = 0.28$, was between age 1 and age 2 Atlantic Menhaden. Correlations between the growth of two ages of Gulf Menhaden ($\rho = -0.03$) and between the same age groups for both species ($\rho = 0.05$ for age 1 and $\rho = 0.12$ for age 2) were all weak or negligible.

3.2 | Macroscale environmental predictors

We found a total of nine significant predictors among the eight models evaluated (out of 40 total predictors in all models; Figure 6). Eight of the nine significant predictors were in models for age 1 fish (Table 2), while only one weakly significant predictor—a negative effect of AMO—was found in the model for age 2 Gulf Menhaden (Table 3). No significant effects were found for any models of age 2 growth for Atlantic Menhaden. Across age 1 models, landings for the previous year had a strongly significant positive effect on Atlantic Menhaden growth in the Atlantic Ocean, with regional wind U (positive effect) and wind V (negative effect) from the northern Atlantic Ocean region also being strongly significant. In the Gulf of Mexico, wind V had a moderately significant negative effect and AMO had a strongly significant positive effect on Gulf Menhaden growth.

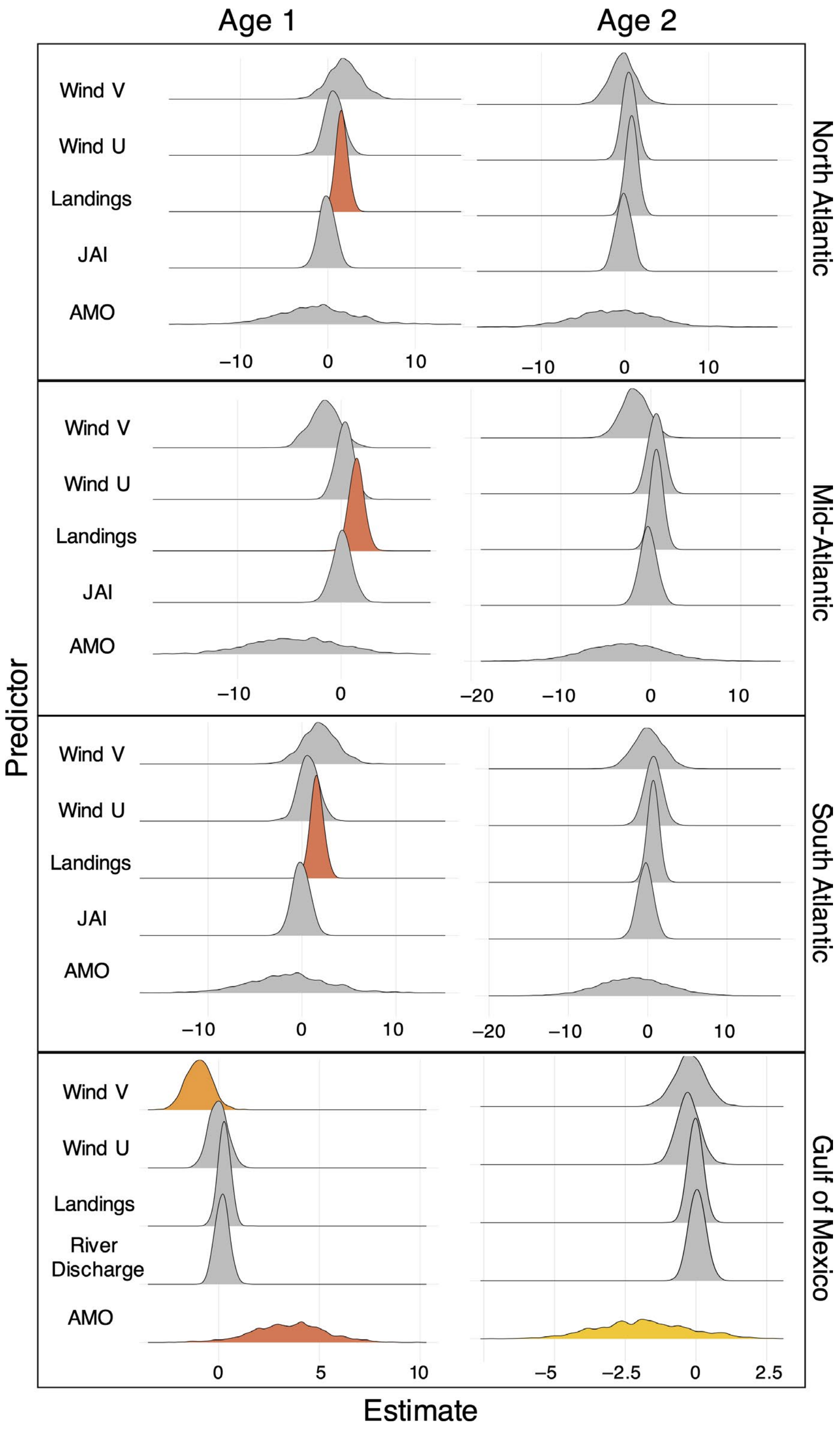

FIGURE 6 Posterior distributions for all 40 macroscale predictors evaluated in eight hierarchical models included in the present study. Distributions in red indicate effects that are strongly significant (i.e., 95% credibly different from 0). Distributions in orange indicate effects that are moderately significant (i.e., 90% credibly different from 0). Distributions in yellow indicate effects that are weakly significant (i.e., 80% credibly different from 0). Gray distributions indicate those predictors that had estimated effects not credibly different from 0

4 | DISCUSSION

4.1 | Growth

Across the Atlantic subregions, we observed much greater growth rates for both age 1 and age 2 fish compared to fish in the Gulf of Mexico. Atlantic and Gulf Menhaden, though taxonomically similar, have differing life histories, and their differences in growth are likely attributable to differing maximum sizes. Atlantic Menhaden reach larger sizes of over 400 mm fork length (Smith & O'Bier, 1996), while Gulf Menhaden reach smaller sizes of approximately 250 mm fork length (SEDAR, 2018). Thus, monthly growth would be expected to be smaller for Gulf Menhaden then Atlantic Menhaden. Both species occur in habitats that can be very different, creating an opportunity for drawing inference on large-scale environmental drivers of growth. Gulf Menhaden are mostly found in coastal areas between

TABLE 2 Model predictors for age 1 models

Level 2 predictor (*Z*)	Gulf of Mexico	US South Atlantic	US Mid-Atlantic	US North Atlantic
Landings	0.18	1.58***	1.50***	1.52***
River discharge	0.27	Not included	Not included	Not included
AMO	3.51***	−1.47	−4.71	−5.75*
Wind (U)	−0.04	0.77	0.36	1.33***
Wind (V)	−1.00**	1.93	−1.57	−3.19***
Juvenile abundance	Not included	−0.13	0.08	0.17

Note: *Indicates weak significance (i.e., 80% credible interval not overlapping 0), ** Indicates moderate significance (i.e., 90% credible interval not overlapping 0), and *** Indicates strong significance (i.e., 95% credible interval not overlapping 0).

TABLE 3 Model predictors for age 2 models

Level 2 predictor (*Z*)	Gulf of Mexico	US South Atlantic	US Mid-Atlantic	US North Atlantic
Landings	−0.10	0.70	−0.63	0.79
River discharge	−0.01	Not included	Not included	Not included
AMO	−1.90*	−1.75	−2.99	−1.15
Wind (U)	−0.15	0.70	0.59	−0.47
Wind (V)	−0.17	0.08	−1.77	−0.31
Juvenile abundance	Not included	−0.30	−0.29	−0.17

Note: *Indicates weak significance, **Indicates moderate significance, and ***Indicates strong significance.

the Yucatan Peninsula, Mexico, and Tampa Bay, Florida (Christmas, Etzold, & Simpson, 1983), which is more southerly and latitudinally compressed relative to the range of Atlantic Menhaden that are found from Canada to Florida (Ahrenholz, 1991). The more equatorial location of the Gulf of Mexico, along with its relative isolation from nearby water bodies, results in conditions that are warmer and less prone to seasonal variability than that of the Atlantic Ocean. The Atlantic Ocean, on the other hand, has few barriers constraining water or organism flow from the equator to the Arctic Ocean, allowing access to a larger variety of habitats than those available to Gulf Menhaden. Atlantic Menhaden captured farther north would be more likely to be subject to a shorter growing season, which could result in the timing of capture potentially occurring during a shortened, more rapid growth phase. This spatial variability could serve to alter the rate or timing of growth over portions of our study area, increasing spatial variability of the signals we are trying to detect in the Atlantic.

Both species of Menhaden had negative growth in some years of the analysis (although these instances were rare; Figures 4 and 5). The observations of negative growth for some years could be an artifact of sampling because the same individuals are not being sampled month after month within the same year. In addition, the protracted spawning seasons for both species (Brown-Peterson, Leaf, Schueller, & Andres, 2017; Lewis, Ahrenholz, & Epperly, 1987) could also result in negative growth for some years because harvesting individuals that were spawned at the beginning of the reproductive season could yield larger individuals than harvesting individuals that were spawned later in the season. In the Atlantic, an alternative explanation is that age-specific migration may introduce smaller individuals into the fishery area as individuals from the southern edge of the range migrate north in the fall (Liljestrand, Wilberg, & Schueller, 2019).

4.2 | Macroscale drivers of growth

Macroscale drivers of growth for age 1 Atlantic Menhaden included landings in all models, AMO, and both wind vectors for the North Atlantic region, whereas none of the macroscale drivers were significant predictors of age 2 growth in any Atlantic region. Spatial differences in predictors indicate inconsistencies in what defines growth across the Atlantic coast for menhaden. Age 1 growth was weakly significant and negatively related to AMO; strongly, negatively related to the northerly wind vector from the North Atlantic region; and strongly, positively related to the easterly wind vector from the North Atlantic region. Lower temperatures resulting from negative AMO anomalies likely reduce growth rates. Faster growth was related to higher average wind velocity from the east, possibly due to one or more factors, including wind pushing resources toward shore, the shape of the coastline, or episodic events (ASMFC, 2017). The estimated negative effect of higher average wind velocity from the north on growth is less clear but could be the result of cold water being driven south with the Labrador current that can reach as far south as the coast of North Carolina (Winters, 1982). The Labrador current is variable in its reach, and in some years, the cold water that is driven south may dampen or negate the benefits of the nutrients brought with it. Growth was not related to any of the wind or temperature predictors in the Mid-Atlantic and South Atlantic regions. Although larval growth, recruitment, and survival have been related to AMO and wind vectors (Buchheister, Miller, Houde, Secor,

& Latour, 2016; Hettler, 1976; Simpson et al., 2016), no studies to date have related growth rates of older Atlantic Menhaden individuals to a variety of environmental predictors. Strong impacts of environmental conditions on growth of age 1 fishes have been demonstrated in other species, including Chinook Salmon *Oncorhynchus tshawytscha* and Pacific Halibut *Hippoglossus stenolepis* (Henderson, Fiechter, Huff, & Wells, 2018; Holsman, Aydin, Sullivan, Hurst, & Kruse, 2018).

For Atlantic Menhaden, faster growth of age 1 fish was related to higher landings in the previous year. A link between landings and growth may indicate a density-dependent mechanism, which has been suggested by Schueller and Williams (2017), and might be related to fishery selectivity (Stevens, 2000). Increased growth rates related to increased landings have been observed for a number of species (Rose, Cowan, Winemiller, Myers, & Hilborn, 2001; Taylor & Gallucci, 2009; Trippel, 1995). For example, compensatory density dependence has been suggested as a plausible explanation for increases in growth with decreases in abundance due to exploitation for porbeagle *Lamna nasus* (Cassoff, Campana, & Myklevoll, 2007). For Atlantic Menhaden, growth rate was not related to recruitment, which could mean that cohort size is likely set sometime between the larval stage and when recruitment indices are measured (Simpson et al., 2016). When landings reduce population size, Menhaden may experience higher growth rates resulting from decreased competition for resources. Also, higher individual predation pressure may result whether fishery-induced changes in population size and length distribution change anti-predator benefits of school size and composition (Hoare, 2000).

Growth of Gulf Menhaden was positively related to AMO for both ages 1 and 2 but was negatively related to northerly wind velocity for age 1 (Wind V). AMO is a low frequency, multi-decadal, index of climate fluctuation that is positively related to growth of Gulf Menhaden and is also positively related to recruitment strength of the Gulf Menhaden stock (Sanchez-Rubio & Perry, 2015). The AMO index is associated with contrasts in precipitation patterns in the Mississippi River watershed (Enfield, Mestas-Nuñez, & Trimble, 2001), and we hypothesize that this is the mechanism that results in increased annual growth rates. Increased precipitation and enhanced discharge of the Mississippi and Atchafalaya Rivers result in increased nitrogen input to surface waters that promote phytoplankton growth and enhance feeding conditions for Gulf Menhaden (Adams, Leaf, Wu, Hernandez, & Ojaveer, 2018). Adams et al. (2018) reported that ENSO phases that are correlated with increased precipitation result in increases in individual condition of Gulf Menhaden (Fulton's condition factor, an index of the fatness of fishes), along with the finding that wind direction and magnitude influence Gulf Menhaden condition. We found that northerly winds serve to reduce growth of Gulf Menhaden and work by Adams et al. (2018) described that, for much of the study region examined, northerly winds were associated with reduced individual condition. We hypothesize that northerly winds interact with the freshwater plume from the Mississippi and Atchafalaya Rivers and promote displacement of this water offshore. Retention of nutrient-rich river discharge waters on the continental shelf is enhanced when winds are southerly (Huang, Cai, Castelao, Wang, & Lohrenz, 2013). Our findings were that landings were not a predictor of Gulf Menhaden growth, unlike Atlantic Menhaden. This could indicate that the northern Gulf of Mexico is better able to withstand the fishing pressure experienced than the Atlantic regions. Less contrast was also observed in the landings time series such that changes in growth that might occur at lower or higher harvest levels have yet to be observed.

Turner (2017) related declines in average annual Atlantic and Gulf Menhaden length and weight over time to trends in air temperature and suggested rising ocean temperatures as a possible cause. Here, we limited analyses to ages 1 and 2 fish for which adequate samples were available across the time series despite spatial changes in the fishery (Figure 1). Our results indicate that low-frequency fluctuations in pressure as evidenced by trends in the AMO are a strong predictor of age 1 Gulf Menhaden growth. Thus, cyclic climate fluctuation, not unidirectional trends in ocean warming, is the most likely cause of time-varying growth in Gulf Menhaden. Although Turner (2017) also identified smaller size-at-age for Gulf Menhaden in periods of high fishing pressure, we found that landings did not affect Gulf Menhaden growth. However, Atlantic Menhaden growth rates were higher following high landings, indicating the presence of a density-dependent population response to fishing pressure as previously identified by Schueller and Williams (2017).

4.3 | Modeling considerations

Detection of environmental effects across macroscales of space and time can be challenging yet is needed for effective management across large areas in a changing environment (Midway, Wagner, Zydlewski, Irwin, & Paukert, 2016). For instance, our analysis sought to attribute relatively small (e.g., mm-length) changes measured from individual fish to effects that play out at the ocean-basin level and across decades of time. Although there may be no perfect model for the complexity and noise in this relationship, hierarchical models provided some advantages over other models. First, our models allowed us to focus on yearly changes in growth rates, which may be estimated well due to the generally robust sample size (Figure 1). Knowing that there will still be uncertainty in annual estimates of growth, hierarchically linking the second level of the model created a reinforced way to model both the annual growth rates while also carrying forth the uncertainty inherent to any particular year. We also provide an unconventional interpretation of statistical significance; by creating three categories of significance, we are allowing for richer interpretation of outcomes than under a traditional hypothesis testing framework. Full posterior distributions also allow individual users (e.g., managers) to use the probabilistic framework of the effects to make decisions at levels of confidence that are based on whatever criteria or threshold may be relevant to a situation. For instance, a higher threshold of significance may be relevant for an environmental predictor that cannot be manipulated, while a lower threshold of significance may be more appropriate for landings, or a predictor that can be regulated. We also see the value in our methodological approach as not being specific to Menhaden. In other words, macroscale effects on fish growth are likely ubiquitous, yet traditional models are not always able to account for the different scales of the system being modeled. Further application of hierarchical models could help establish additional and more quantifiable associations between fish and the larger environment that influences their life history.

Differences in spatial scale between growth data and some predictor variables may have affected our interpretation of model results on the Atlantic. Given lack of spatial specificity in location of harvest for Atlantic Menhaden landings prior to 1985, we were unable to model the effects of long-term climate and environmental trends on growth on a regional basis. This limitation may have influenced our ability to identify the influence on growth of wind variables, which were summarized regionally. In addition, spatial contraction and decline in magnitude of the Atlantic reduction fishery over time (Figure 1) could have influenced our results if available length data are no longer representative of coastwide growth patterns. Despite declines in sample size over time, it is unlikely these changes had a large impact on our results given sample sizes generally remained quite large and because we limited our analyses to age 1 and 2 fish. By eliminating fish ages 3 and older from our analyses, we hoped to avoid the confounding influence of fishery changes on the Atlantic given Atlantic Menhaden stratify by age and size during the fishing season such that older fish (ages 3+) are typically found farther north where the reduction fishery no longer operates (Nicholson, 1978). Also, monotonic trends in growth rate were not observed for either species or age class (Figure 5); thus, our results are unlikely to be driven by long-term downward trends in sample size and spatial extent of the location of reduction plants.

4.4 | CONCLUSION

Our study highlights important differences in individual growth rates between two species of Menhaden and the potential mechanisms driving those differences. We found that Atlantic Menhaden growth rates were much higher than that of Gulf Menhaden, suggesting that growth assumptions may not be readily transferable among closely related species. Our results also indicated that the primary driver of time-varying growth in Atlantic Menhaden is a density-dependent response to fishing pressure, whereas low-frequency fluctuations in sea surface temperature (as indicated by the AMO) are the most likely cause (that we examined) of time-varying growth in Gulf Menhaden. Species-specific differences in the magnitude and history of the fishery, life histories, and local climate and ecosystem structure likely contribute to the differences we observed in individual growth responses between Atlantic and Gulf Menhaden. Given that assumptions regarding individual fish growth affect both the population and biological reference point models used in stock assessments for these two economically and ecologically important species (Quinn & Deriso, 1999), more work is needed to identify best practices for incorporating time-varying growth. Incorporation of time-varying growth should also be considered for other species of interest. In addition, fishery-driven density-dependent growth of forage fishes like Atlantic Menhaden may have trophic consequences that are overlooked in current ecosystem and multispecies models (Buchheister et al., 2017; Garrison et al., 2010; Nesslage & Wilberg, 2019). Careful examination of the patterns and potential causes of time-varying growth for young forage fish is needed to refine our understanding of ecosystem impacts of fishing on forage species (Hilborn et al., 2017; Pikitch, 2015).

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTION

All authors contributed extensively to the work presented in this paper. All authors were equally active in designing the study, analyzing the data, interpreting the results, and writing the paper.

DATA AVAILABILITY STATEMENT

Data are available on request due to ethical/privacy restrictions. Some data are subject to third party restrictions.

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REFERENCES

Adams, G. D., Leaf, R. T., Wu, W., Hernandez, F. J., & Ojaveer, H. (2018). Environmentally driven fluctuations in condition factor of adult Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico. *ICES Journal of Marine Science*, *75*(4), 1269–1279. https://doi.org/10.1093/icesjms/fsy002

Ahrenholz, D. (1991). Population biology and life history of the North American menhadens, *Brevoortia* spp. *Marine Fisheries Review*, *53*, 3–19.

ASMFC (2017). *Atlantic Menhaden Stock Assessment Update*. Retrieved from http://www.asmfc.org/uploads/file/59832ee0MenhadenStockAssessmentUpdate_Aug2017.pdf

Bacheler, N. M., Buckel, J. A., Paramore, L. M., & Rochet, M.-J. (2012). Density-dependent habitat use and growth of an estuarine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(11), 1734–1747. https://doi.org/10.1139/f2012-098

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Marshall, C. T. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*(4), 1023–1031. https://doi.org/10.1111/gcb.12514

Brown-Peterson, N. J., Leaf, R. T., Schueller, A. M., & Andres, M. J. (2017). Reproductive dynamics of Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico: Effects on stock assessments. *Fishery Bulletin*, *115*(3), 284–299. https://doi.org/10.7755/fb.115.3.2

Buchheister, A., Miller, T. J., & Houde, E. D. (2017). Evaluating ecosystem-based reference points for Atlantic Menhaden. *Marine and*

Coastal Fisheries, *9*(1), 457–478. https://doi.org/10.1080/19425120.2017.1360420

Buchheister, A., Miller, T. J., Houde, E. D., Secor, D. H., & Latour, R. J. (2016). Spatial and temporal dynamics of Atlantic menhaden (*Brevoortia tyrannus*) recruitment in the Northwest Atlantic Ocean. *ICES Journal of Marine Science: Journal Du Conseil*, *73*(4), 1147–1159. https://doi.org/10.1093/icesjms/fsv260

Cassoff, R. M., Campana, S. E., & Myklevoll, S. (2007). Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(1), 19–29. https://doi.org/10.1139/f06-167

Christmas, J. Y., Etzold, D. J., & Simpson, L. B. (1983). *The menhaden fishery of the Gulf of Mexico United States: A regional management plan*. https://www.gsmfc.org/publications/GSMFCNumber008.PDF

Conn, P. B. (2010). Hierarchical analysis of multiple noisy abundance indices. *Canadian Journal of Fisheries and Aquatic Science*, *67*, 108–120. https://doi.org/10.1139/F09-175

Conover, D. O., & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science*, *297*(5578), 94–96. https://doi.org/10.1126/science.1074085

Conover, D. O., Munch, S. B., & Arnott, S. A. (2009). Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society of London. Series B: Biological Science*, *276*(1664), 2015–2020. https://doi.org/10.1098/rspb.2009.0003

Enfield, D. B., Mestas-Nuñez, A. M., & Trimble, P. J. (2001). The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U.S. *Geophysical Research Letters*, *28*(10), 2077–2080. https://doi.org/10.1029/2000gl012745

Garrison, L. P., Link, J. S., Kilduff, D. P., Cieri, M. D., Muffley, B., Vaughan, D. S., ... Latour, R. J. (2010). An expansion of the MSVPA approach for quantifying predator-prey interactions in exploited fish communities. *ICES Journal of Marine Science*, *67*(5), 856–870. https://doi.org/10.1093/icesjms/fsq005

Geers, T. M., Pikitch, E. K., & Frisk, M. G. (2016). An original model of the northern Gulf of Mexico using Ecopath with Ecosim and its implications for the effects of fishing on ecosystem structure and maturity. *Deep Sea Research Part II: Topical Studies in Oceanography*, *129*, 319–331. https://doi.org/10.1016/j.dsr2.2014.01.009

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., ... Hawkins, S. J. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, *16*(2), 517–527. https://doi.org/10.1111/j.1365-2486.2009.02027.x

Gíslason, D., McLaughlin, R. L., Robinson, B. W., Cook, A., & Dunlop, E. S. (2018). Rapid changes in age and size at maturity in Lake Erie yellow perch (*Perca flavescens*) are not explained by harvest. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(2), 211–223. https://doi.org/10.1139/cjfas-2016-0211

Govoni, J. J. (1997). The association of the population recruitment of gulf menhaden, *Brevoortia patronus*, with Mississippi River discharge. *Journal of Marine Systems*, *12*(1–4), 101–108. https://doi.org/10.1016/s0924-7963(96)00091-7

Henderson, M., Fiechter, J., Huff, D. D., & Wells, B. K. (2018). Spatial variability in ocean-mediated growth potential is linked to Chinook salmon survival. *Fisheries Oceanography*, *28*(3), 334–344. https://doi.org/10.1111/fog.12415

Hettler, W. F. (1976). Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. *Journal of Fish Biology*, *8*(1), 55–65. https://doi.org/10.1111/j.1095-8649.1976.tb03907.x

Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., & Walters, C. J. (2017). When does fishing forage species affect their predators? *Fisheries Research*, *191*, 211–221. https://doi.org/10.1016/j.fishres.2017.01.008

Hoare, D. J., Krause, J., Peuhkuri, N., & Godin, J.-G J. (2000). Body size and shoaling in fish. *Journal of Fish Biology*, *57*(6), 1351–1366. https://doi.org/10.1111/j.1095-8649.2000.tb02217.x

Holsman, K. K., Aydin, K., Sullivan, J., Hurst, T., & Kruse, G. H. (2018). Climate effects and bottom-up controls on growth and size-at-age of Pacific halibut (*Hippoglossus stenolepis*) in Alaska (USA). *Fisheries Oceanography*, *28*(3), 345–358. https://doi.org/10.1111/fog.12416

Huang, W.-J., Cai, W.-J., Castelao, R. M., Wang, Y., & Lohrenz, S. E. (2013). Effects of a wind-driven cross-shelf large river plume on biological production and CO2 uptake on the Gulf of Mexico during spring. *Limnology and Oceanography*, *58*(5), 1727–1735. https://doi.org/10.4319/lo.2013.58.5.1727

June, F. C., & Roithmayr, C. M. (1960). Determining age of Atlantic Menhaden from their scales. *U. S. Fish Wildlife Service Fishery Bulletin*, *60*, 323–342.

Kolody, D. S., Eveson, J. P., & Hillary, R. M. (2016). Modelling growth in tuna RFMO stock assessments: Current approaches and challenges. *Fisheries Research*, *180*, 177–193. https://doi.org/10.1016/j.fishres.2015.06.016

Leaf, R. T., Trushenski, J., Brown-Peterson, N. J., & Andres, M. J. (2018). Temporal dynamics oflipid and fatty acid characteristics of Gulf Menhaden, *Brevoortia patronus*, in thenorthern Gulf of Mexico. *Regional Studies in Marine Science*, *24*, 1–9. https://doi.org/10.1016/j.rsma.2018.06.011

Lewis, R. M., Ahrenholz, D. W., & Epperly, S. P. (1987). Fecundity of Atlantic Menhaden, *Brevoortia tyrannus*. *Estuaries*, *10*(4), 347–350. https://doi.org/10.2307/1351894

Liljestrand, E. M., Wilberg, M. J., & Schueller, A. M. (2019). Estimation of movement and mortality of Atlantic menhaden during 1966–1969 using a Bayesian multi-state mark-recovery model. *Fisheries Research*, *210*, 204–213. https://doi.org/10.1016/j.fishres.2018.10.015

Litz, M. N. C., Miller, J. A., Brodeur, R. D., Daly, E. A., Weitkamp, L. A., Hansen, A. G., & Claiborne, A. M. (2018). Energy dynamics of subyearling Chinook salmon reveal the importance of piscivory to short-term growth during early marine residence. *Fisheries Oceanography*, *28*(3), 273–290. https://doi.org/10.1111/fog.12407

Lorenzen, K., & Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: Evidence from among-population comparisons. *Proceedings of the Royal Society of London. Series B: Biological Science*, *269*(1486), 49–54. https://doi.org/10.1098/rspb.2001.1853

Martino, E. J., Houde, E. D., & Marshall, C. T. (2012). Density-dependent regulation of year-class strength in age-0 juvenile striped bass (*Morone saxatilis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 430–446. https://doi.org/10.1139/f2011-149

Midway, S. R., Wagner, T., Zydlewski, J. D., Irwin, B. J., & Paukert, C. P. (2016). Transboundary fisheries science: Meeting the challenges of inland fisheries management in the 21st century. *Fisheries*, *41*(9), 536–546. https://doi.org/10.1080/03632415.2016.1208090

Morgan, M., & Colbourne, E. B. (1999). Variation in maturity-at-age and size in three populations of American plaice. *ICES Journal of Marine Science*, *56*(5), 673–688. https://doi.org/10.1006/jmsc.1999.0487

Nesslage, G. M., & Wilberg, M. J. (2019). A performance evaluation of surplus production models with time-varying intrinsic growth in dynamic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*, 2245–2255. https://doi.org/10.1139/cjfas-2018-0292

Nicholson, W. R. (1978). Movements and population structure of Atlantic menhaden indicated by tag returns. *Estuaries*, *1*(3), 141–150.

Nicholson, W. R., & Schaaf, W. E. (1978). Aging of Gulf menhaden, *Brevoortia patronus*. *Fishery Bulletin*, *76*(2), 315–322.

Ohlberger, J., & Fox, C. (2013). Climate warming and ectotherm body size – From individual physiology to community ecology. *Functional Ecology*, *27*(4), 991–1001. https://doi.org/10.1111/1365-2435.12098

Pikitch, E. K. (2015). Stop-loss order for forage fish fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(21), 6529–6530. https://doi.org/10.1073/pnas.1505403112

Plummer, M. (2016). *rjags: Bayesian graphical models using MCMC*. Retrieved from http://mcmc-jags.sourceforge.net

Post, J. R., Parkinson, E. A., & Johnston, N. T. (1999). Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. *Ecological Monographs*, *69*(2), 155–175. https://doi.org/10.1890/0012-9615(1999)069[0155:Ddpisf]2.0.Co;2

Punt, A. E. (2003). The performance of a size-structured stock assessment method in the face of spatial heterogeneity in growth. *Fisheries Research*, *65*(1–3), 391–409. https://doi.org/10.1016/j.fishres.2003.09.028

Punt, A. E., Haddon, M., & McGarvey, R. (2016). Estimating growth within size-structured fishery stock assessments: What is the state of the art and what does the future look like? *Fisheries Research*, *180*, 147–160. https://doi.org/10.1016/j.fishres.2014.11.007

Punt, A. E., Haddon, M., & Tuck, G. N. (2015). Which assessment configurations perform best in the face of spatial heterogeneity in fishing mortality, growth and recruitment? A case study based on pink ling in Australia. *Fisheries Research*, *168*, 85–99. https://doi.org/10.1016/j.fishres.2015.04.002

Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. New York, NY: Oxford University Press.

R Core Development Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reish, R. L., Deriso, R. B., Ruppert, D., & Carroll, R. J. (1985). An Investigation of the Population Dynamics of Atlantic Menhaden (*Brevoortia tyrannus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(S1), s147–s157. https://doi.org/10.1139/f85-270

Rose, K. A., Cowan, J. H., Winemiller, K. O., Myers, R. A., & Hilborn, R. (2001). Compensatory density dependence in fish populations: Importance, controversy, understanding and prognosis. *Fish and Fisheries*, *2*(4), 293–327. https://doi.org/10.1046/j.1467-2960.2001.00056.x

Sanchez-Rubio, G., & Perry, H. (2015). Climate-related meteorological and hydrological regimes and their influence on recruitment of Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico. *Fishery Bulletin*, *113*(4), 391–406. https://doi.org/10.7755/fb.113.4.3

Schueller, A. M., & Williams, E. H. (2017). Density-dependent growth in Atlantic Menhaden: Impacts on current management. *North American Journal of Fisheries Management*, *37*(2), 294–301. https://doi.org/10.1080/02755947.2016.1264511

SEDAR (2013). *SEDAR 32A – Gulf of Mexico Menhaden stock assessment report*. Retrieved from http://www.sefsc.noaa.gov/sedar/Sedar_Workshops.jsp?WorkshopNum=32A

SEDAR (2015). *SEDAR 40 – Atlantic Menhaden stock assessment report*. Retrieved from http://www.sefsc.noaa.gov/sedar/Sedar_Workshops.jsp?WorkshopNum=40

SEDAR (2018). *SEDAR 63 – Gulf Menhaden stock assessment report*. SEDAR, North Charleston SC. 352 p. Retrieved from http://sedarweb.org/sedar-63

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Simpson, C. A., Wilberg, M. J., Bi, H., Schueller, A. M., Nesslage, G. M., & Walsh, H. J. (2016). Trends in relative abundance and early life survival of Atlantic Menhaden during 1977–2013 from long-term ichthyoplankton programs. *Transactions of the American Fisheries Society*, *145*(5), 1139–1151. https://doi.org/10.1080/00028487.2016.1201004

Sinclair, A. F., Swain, D. P., & Hanson, J. M. (2002). Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(2), 372–382. https://doi.org/10.1139/f02-014

Smith, J. W., & O'Bier, W. B. (1996). An exceptionally large Atlantic menhaden, *Brevoortia tyrannus*, from Chesapeake Bay, VA. *The Journal of the Elisha Mitchell Scientific Society*, *112*(3), 121–123.

Spalding, M., Fox, H., Allen, G., Davidson, N., Ferdaña, Z., Finlayson, M., … Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, *57*, 573–583. https://doi.org/10.1641/B570707

Stevens, J. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, *57*(3), 476–494. https://doi.org/10.1006/jmsc.2000.0724

Su, Y.-S., & Yajima, M. (2015). R2jags: Using R to Run 'JAGS'. R package version 0.5-7. https://CRAN.R-project.org/package=R2jags

Taylor, I. G., & Gallucci, V. F. (2009). Unconfounding the effects of climate and density dependence using 60 years of data on spiny dogfish (*Squalus acanthias*). *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(3), 351–366. https://doi.org/10.1139/f08-211

Thresher, R. E., Koslow, J. A., Morison, A. K., & Smith, D. C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(18), 7461–7465. https://doi.org/10.1073/pnas.0610546104

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience*, *45*(11), 759–771. https://doi.org/10.2307/1312628

Turner, R. E. (2017). Smaller size-at-age menhaden with coastal warming and fishing intensity. *Geo: Geography and Environment*, *4*(2), e00044. https://doi.org/10.1002/geo2.44

Vaughan, D. S. (1987). *Stock assessment of the Gulf menhaden, Brevoortia patronus, fishery* (NOAA Technical Report, Vol. 58). US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Vaughan, D. S., Govoni, J. J., & Shertzer, K. W. (2011). Relationship between Gulf Menhaden recruitment and Mississippi River flow: Model development and potential application for management. *Marine and Coastal Fisheries*, *3*(1), 344–352. https://doi.org/10.1080/19425120.2011.620908

Wells, B. K., Grimes, C. B., Sneva, J. G., McPherson, S., & Waldvogel, J. B. (2008). Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska, USA. *Fisheries Oceanography*, *17*(2), 101–125. https://doi.org/10.1111/j.1365-2419.2008.00467.x

Winters, G. H. (1982). Life history and geographical patterns of growth in Capelin, *Mallotus villosus*, of the Labrador and Newfoundland areas. *Journal of Northwest Atlantic Fishery Science*, *3*, 105–114.

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