Importance of the spring transition in the northern Gulf of Mexico as inferred from marine fish biochronologies

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ABSTRACT: Linkages between climate variability and the productivity and functioning of Gulf of Mexico marine ecosystems remain poorly described, largely due to a lack of time series sufficiently long to establish robust bio-physical relationships. To address this issue, multidecadal biochronologies were generated from otolith growth-increment widths of red snapper *Lutjanus campechanus*, gray snapper *L. griseus*, black drum *Pogonia cromis*, and king mackerel *Scombero-morus cavalla* in the Gulf of Mexico. Synchronous growth patterns were evident among red snapper, gray snapper, and black drum, which all significantly ($p < 0.05$) correlated to one other, but not with king mackerel. Positive growth anomalies in the snapper and drum chronologies were associated with anomalously warm sea surface temperatures, southeast wind stress, and high sea level pressure in the western Atlantic during the early spring months, suggesting that an early transition from a winter to a summer climate pattern is favorable for growth. In contrast, the king mackerel chronology was dominated by decadal-scale patterns and significantly ($p < 0.01$) and negatively correlated to the Atlantic Multidecadal Oscillation. Overall, these results show the importance of the spring transition for resident species in the northern Gulf of Mexico, that growth among individuals in a migratory species can be synchronous, and that differences in life history and geography are reflected in climate–biology relationships.

KEY WORDS: Otolith · Growth · Chronology · Gulf of Mexico · Climate variation · Atlantic Multidecadal Oscillation · Fisheries

INTRODUCTION

The Gulf of Mexico is the ninth largest body of water in the world, supports one-third of the fisheries production in the continental United States, and accounts for more than one billion dollars in seafood annually (Karnauskas et al. 2013). However, fisheries catch and production vary considerably over annual to decadal time scales; the causes of which remain poorly understood (Karnauskas et al. 2013, 2015) but may be influenced by climate variability, climate change, human activity, and their interactions (Shepard et al. 2010, Cowan et al. 2011, Karnauskas et al. 2013).

In the most comprehensive integration of physical and biological datasets, Karnauskas et al. (2013) identified the Atlantic Multidecadal Oscillation (AMO) as a key climate driver of Gulf of Mexico ecosystems. The AMO index is the leading empirical orthogonal function of sea surface temperature (SST) anomalies from 0 to 60° N in the Atlantic basin, cycles between warm and cool phases approximately every 30 to 40 yr, and is linked to Gulf of Mexico water temperature, depth of the mixed layer, and hurricane activity, as well as to precipitation in the Mississippi River basin (Schlesinger & Ramankutty 1994, Karnauskas et al. 2015). These climate factors help gov-

ern stratification, plankton production, eutrophication, and development of hypoxia in the Gulf of Mexico with indirect effects on upper trophic levels, and ultimately, the economies of coastal communities (Karnauskas et al. 2015). However, the greatest obstacle to assessing climate–biology relationships in the Gulf of Mexico is the absence of annually resolved time series that are sufficiently long to capture extreme events, regime shifts, or multiple cycles of decadal-scale variability (Legendre & Legendre 1998). Existing biological datasets start at the earliest in the 1980s and largely involve fisheries catch data (Karnauskas et al. 2013) that can be biased by fishing regulations and fleet effort (Rochet & Trenkel 2003, de Mutsert et al. 2008).

In an attempt to better connect biology to climate, a dendrochronology (tree-ring analysis) approach has been increasingly applied to growth-increment widths in fish otoliths (Rountrey et al. 2014, Stocks et al. 2014, Doubleday et al. 2015, Ong et al. 2015). These biochronologies have annual resolution, are exactly dated, can span multiple decades (Black et al. 2005), and reflect population-wide fish condition, measured in one example as mean anomaly in the population-level length–weight relationship (Black et al. 2013). Given their exact placement in time, otolith chronologies can be readily integrated with instrumental records to quantify growth responses to climate or other observational environmental indicators (Morrongiello et al. 2012). Target fish species for this approach include long-lived species or those with archival otolith collections, which ensures that chronologies are sufficiently long to capture as much of the historical range of variability as possible, including low-frequency variability and extreme events (Black et al. 2005).

In the northern Gulf of Mexico, otolith biochronologies have been developed for red snapper *Lutjanus campechanus* caught off the Louisiana coast, and gray snapper *L. griseus* from the Florida coast (Black et al. 2011a, our Fig. 1). The 2 chronologies span 30 yr and significantly correlate with one another as well as springtime (March/April) SST, wind speed and direction (Black et al. 2011a). Indeed, the climate of the Gulf of Mexico has been categorized into distinct winter and summer patterns (Morey et al. 2003a). During the boreal summer, the Intertropical Convergence Zone (ITCZ) is at its most northern extent and coincides with persistently high atmospheric pressure in the western Atlantic (Bermuda High), resulting in predominantly southeasterly winds across the Gulf of Mexico and the Caribbean (Morey et al. 2003a, Poore et al. 2003). In contrast, winter winds are variable but

dominated by north and northwesterly flows coinciding with the passage of cold fronts (Morey et al. 2003a). An early (late) transition to this summer pattern appears to be associated with favorable (unfavorable) growth, as indexed by these chronologies (Black et al. 2011a). Such a strong seasonal shift would be expected to influence growth in upper-trophic indicators given that temperatures and wind-driven currents affect growth and metabolic rates of consumers (Hoff & Fuiman 1993, Neer et al. 2007, Black et al. 2011a), as well as the location and extent of primary production (Chen et al. 2000, Russell & Montagna 2007, Muller-Karger et al. 2015) and hypoxia (Feng et al. 2012, Rabalais et al. 2002). In the California Current along the west coast of North America, the timing of the spring transition has been widely shown to affect ecosystem functioning, and a similar phenomenon may be occurring in the Gulf of Mexico (Huyer et al. 1975, 1979, Bograd et al. 2009, Holt & Mantua 2009).

Here, we quantify a Gulf of Mexico spring transition and examine its importance to fish in the northern Gulf of Mexico using otolith chronologies of red snapper, gray snapper, king mackerel *Scomberomorus cavalla*, and black drum *Pogonias cromis*. Study species were chosen due to their longevity, availability of otoliths, and clarity of growth-increment boundaries, as well as the wide range of life histories, habitats, and geography they represent. Additionally, each species is economically important, supporting commercial and recreational fisheries with a combined take of over 6000 metric tonnes yr^{-1} (National Marine Fisheries Service landings query). Given its recognized importance to Gulf of Mexico ecosystem functioning, relationships to the AMO (Karnauskas et al. 2015) are also examined. Ultimately, the multidecadal, annually-resolved, exactly dated otolith chronologies facilitate direct comparisons across species and instrumental climate records, enabling an ecosystem-level assessment of biophysical coupling from the perspective of these upper-trophic indicators.

MATERIALS AND METHODS

Study species and sample collection

Adult red and gray snapper co-occur, exhibit little movement away from reef habitat, and feed primarily on crustaceans and benthic fish (Moran 1988, Wells et al. 2008, Flaherty et al. 2014). Juvenile red snapper inhabit shallow reef and rocky substrate,

while juvenile gray snapper inhabit mangrove channels and seagrass beds. Juveniles of both species feed on zooplankton and mysid shrimp (Moran 1988, Hettler 1989, Flaherty et al. 2014). Black drum are demersal, estuarine fish that have limited inter-estuary movement and consume primarily crustaceans, mollusks, and shrimp (Osburn & Matlock 1984, Sutter et al. 1986). King mackerel are generally found over the continental shelf and seasonally migrate between Texas/Louisiana and the Florida Keys/southeast Florida or the Yucatan Peninsula (Fable et al. 1987, Finucane et al. 1990, Wall et al. 2009). King mackerel are principally piscivorous throughout their life and are often associated with baitfish that aggregate along ocean fronts (Finucane et al. 1990, Wall et al. 2009). Red snapper and black drum can live more than 40 yr, while gray snapper and king mackerel can attain ages into the upper 20s (Murphy & Taylor 1989, Baker & Wilson 2001, Fischer et al. 2005, Shepard et al. 2010).

Otoliths used in this study were obtained from archival collections from a variety of sources. The NOAA National Marine Fisheries Service Panama City Laboratory (Panama City, FL) provided red snapper otoliths collected from the Texas coast (TX red snapper) and king mackerel otoliths collected within the northern Gulf of Mexico. The Louisiana Department of Wildlife and Fisheries (Baton Rouge, LA, via the NOAA Southeast Fisheries Science Center) provided black drum otoliths from the Louisiana coast. A total of 500 black drum otoliths (collected between 1994 and 2009), 43 TX red snapper otoliths (collected from 2010 to 2013), and 80 king mackerel otoliths (collected between 1990 and 2011) were available for chronology development. Ninety black drum otoliths were selected for chronology development based on otolith age and collection year. One red snapper chronology and one gray snapper chronology were previously developed by Black et al. (2011a) from samples collected from the Louisiana coast and Florida coast, respectively, and are subsequently referred to as LA red snapper and FL gray snapper (see Fig. 1).

Chronology development

All sagittal otoliths were embedded in epoxy and then thin-sectioned to 0.4 mm through the transverse plane. Red and gray snapper otoliths were sectioned on a high-speed saw following the methods of Cowan et al. (1995), whereas black drum and king mackerel were sectioned on a Buehler Isomet low-speed saw.

Sections were mounted on a slide using Crystalbond then polished using 12 and 8 µm lapping film. Only those otoliths that had well-defined growth-increment boundaries and that were sufficiently long-lived were retained. Due to differences in maximum age among species, otoliths aged >19 yr (black drum and red snapper), >14 yr (gray snapper), and >8 yr (king mackerel) were retained. Each otolith was photographed with a Leica DFC295 3.1 megapixel digital camera attached to a Leica M125 dissecting microscope. Black drum, TX red snapper, and king mackerel otoliths were photographed with transmitted light at 40, 50, and 50× magnification, respectively. All otolith growth-increment analyses were performed on the dorsal side of the sulcal groove.

To ensure that the correct calendar was assigned to each otolith growth increment, all individuals were visually crossdated. Crossdating works under the assumption that some aspect of climate influences growth, and as it varies over time it induces a synchronous pattern or 'bar code' in the otolith increment-widths of individuals from a given region or species (Douglass 1941, Fritts 1976). If one increment was accidentally missed or falsely added, the growth pattern would be offset by 1 yr in that individual relative to the others, indicating that an error had occurred (Fritts 1976). Note that these growth patterns were never 'forced' on these samples. If a pattern appeared to be offset in an individual, a correction was made only if the error could be confirmed upon visual inspection of the otolith.

After visual crossdating, growth-increment widths were measured continuously along a transect perpendicular to the axis of growth, starting at the marginal increment and ending as close to the core as possible, using ImagePro Premier v.7.4 (Media Cybernetics). One year of growth was measured starting at the distal side of the previous year's opaque zone to the distal side of the current year's opaque zone.

Crossdating was statistically corroborated using the program COFECHA (Holmes 1983, Grissino-Mayer 2001), which has been used in a variety of marine fish and bivalve species (Black et al. 2005, Matta et al. 2010, Gillanders et al. 2012). First, each set of measurements was fit with a cubic spline that had a 50% frequency response of 15 yr. Then each measurement was divided by the value predicted by the spline, thereby removing low-frequency variability and isolating high-frequency, year-to-year variability. Each detrended measurement time series was correlated with the mean of all others, and any samples for which the correlation was not highly significant ($p < 0.01$) were visually inspected for possible

errors (Grissino-Mayer 2001). The average correlation between each individual time series and the average of all others was reported as the interseries correlation. Additionally, COFECHA calculated mean sensitivity as an index of high-frequency variability. Mean sensitivity ranges from 0 to 2, with a value of 0 indicating increments of the same width and a value of 2 indicating a pair of increments in which one has a width of zero (locally absent) (Fritts 1976).

Once crossdating was completed, the original measurement time series were detrended to remove age-related growth declines. TX red snapper increment-width time series were detrended by fitting a negative exponential curve to each measurement time series then dividing observed values by those predicted. All detrended increment measurements were subsequently averaged using a biweight robust mean to form a master chronology (Cook 1985). The same detrending technique was used to generate the LA red snapper and FL gray snapper chronologies, all using the program ARSTAN (Cook & Holmes 1986, Cook & Krusic 2005).

The king mackerel and black drum increment series were detrended by (1) grouping all increment widths by age-of-formation, (2) calculating the mean increment width for each age group, and (3) dividing each measurement by the age-specific mean. Detrended growth-increments were averaged with respect to calendar year to yield the master chronology. This method better preserved low-frequency variability for these species collected over a range of years, especially for the relatively short-lived mackerel.

The expressed population signal (EPS) statistic, calculated by ARSTAN, is a measure of how well the chronology represents the theoretical population from which it was drawn and was used to assess the quality of each chronology (Wigley et al. 1984). Although there is no significance level associated with EPS, a value >0.85 is considered adequate and only those portions of the chronologies that exceeded this value were retained (Wigley et al. 1984). This corresponded to a minimum sample depth of >15 increment measurements per year for TX red snapper and black drum. EPS could not be calculated for mackerel; their short lifespan precluded attempts to calculate correlations among measurement time series, which is part of the EPS formula. Thus, the chronology for mackerel was limited to portions with >15 measurements per calendar year.

A principal components analysis (PCA) was calculated in R v.3.2.2 ('prcomp') and was used to extract the dominant patterns of variability in growth-increment widths shared by all chronologies (PCA_{fish}).

PCA was calculated over the shared interval where all chronologies had an EPS of >0.85 or sample depth >15 for mackerel.

Climate–biology relationship

Northern Gulf of Mexico SST, wind stress, and sea level pressure (SLP) were chosen as primary climate drivers based on the results for red and gray snapper in Black et al. (2011a). Wind stress and SLP data were obtained from the NOAA-CIRES 20th Century Reanalysis V2c 2 × 2 degree dataset (www.esrl.noaa.gov/psd/data/gridded/data.20thC_ReanV2c.html), and SST data were obtained from the Hadley HadISST 1.1 1 × 1 degree dataset (http://hadobs.metoffice.gov.uk/hadisst). SST, U wind stress (west to east), and V wind stress (south to north) used for correlations with the chronologies and were averaged over the northern Gulf of Mexico, targeting the shelf region <180 m deep (26° to 32° N × 80° to 98° W, excluding 26° to 28° N × 85° to 94.5° W; see Fig. 1). SLP data spanned the region of the Bermuda High (27° to 37° N and 65° to 85° W). Mississippi River discharge at Tarbert Landing (river mile 306.3) as obtained through the US Army Corps of Engineers was also included (http://rivergages.mvr.usace.army.mil/WaterControl/stationinfo2.cfm?sid=01100Q&fid=&dt=S).

Each chronology was correlated with monthly-averaged U wind stress, V wind stress, SST, SLP, and Mississippi River discharge (60 variables total). Significant Bonferroni-corrected Pearson correlations ($p < 0.05$) between climate variables and fish chronologies were retained for further analysis. These and all other statistical analyses were performed in R v.3.2.2 (R Core Team 2015).

Seasonal climate patterns and spring transition index

We attempted to quantify the transition between the winter and summer climate patterns and whether this 'spring transition' index was detectable in fish chronologies. To accomplish this, U wind, V wind, SST, and SLP data spanning 1900 to 2011 were standardized to a mean of 0 and standard deviation of 1. Matrices of U wind stress, V wind stress, and SLP were then combined into one composite climate matrix (36 columns × 111 years) for a PCA analysis ($PCA_{climate}$). SST has higher autocorrelation than the other 3 variables due to the high specific heat capacity of water; as such, monthly-averaged SST was

entered into a separate PCA (PCA$_{SST}$). Loadings were examined for seasonal patterns.

Black et al. (2011a) identified March as a month for peak climate sensitivity for red and gray snapper. Thus, March SST, SLP, *V* wind stress, and *U* wind stress (March climate) were entered into a principal component regression with PCA$_{fish}$. Principal components regression was used to derive uncorrelated (orthogonal) variables from this suite of collinear climate variables, which better meets the assumptions of multiple linear regression. The Durbin-Watson statistic (DW; durbinWatsonTest <stats> in R v.3.2.2) was used to test for autocorrelation in the regression residuals.

Mean values of gridded SST, winds, and SLP were calculated for the highest quartile and then the lowest quartile for values of PC1$_{fish}$. Differences between mean climate values for high and low growth years were tested using a Student's *t*-test. Lastly, each chronology was correlated with monthly and mean annual AMO index obtained from the NOAA Earth System Research Laboratory (www.esrl.noaa.gov/psd/data/climateindices).

RESULTS

Chronology development

Black drum and king mackerel otolith increments had boundaries that were more clearly defined than those in TX red snapper. Of the 43 TX red snapper otoliths of sufficient age, 26 were used to develop the final chronology aged 15 to 35 yr. Seventy-five out of 80 king mackerel otoliths aged 9 to 18, and 78 out of 90 black drum otoliths aged 16 to 46 were used for chronology development. Otoliths were discarded if they had distorted or diffuse increments, or if they could not be visually crossdated. However, of all otoliths across all species, only 4 black drum otoliths were discarded due to lack of crossdating.

Among otoliths measured, growth was synchronous within each species, as reflected by high interseries correlations (Fig. 1b, Table 1). There was also synchrony among species; chronologies were particularly well correlated among the coastal/reef species (red snapper, gray snapper, and black drum) (Table 2). In contrast, the king mackerel chronology
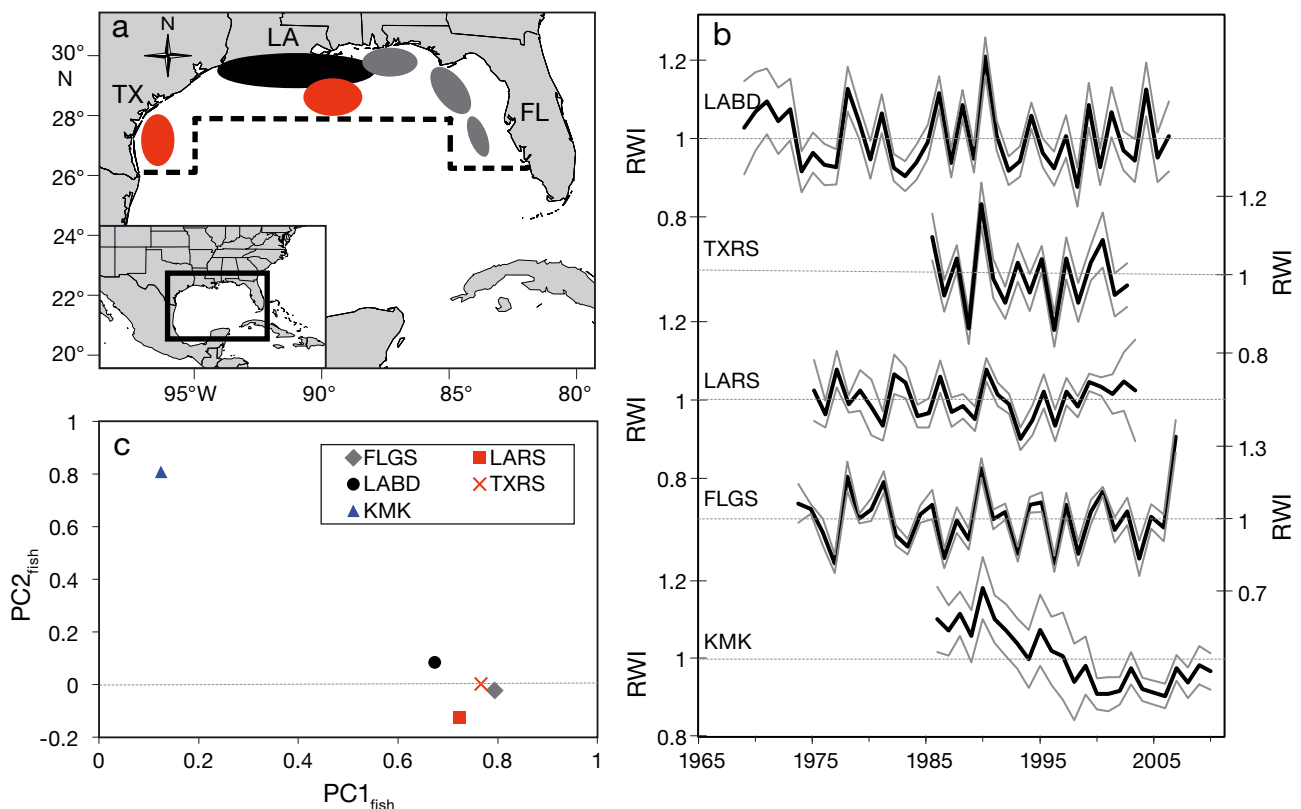

Fig. 1. (a) Collection locations of species used in chronology development. Colors coincide with species codes in (c). Climate data were extracted from the area contained by the dashed lines extending from Texas (TX) to Florida (FL). Note: capture locations were unavailable for king mackerel. (b) Ring-width index (RWI; black line) and 95% confidence intervals (gray lines) for Louisiana (LA) black drum (LABD), TX red snapper (TXRS), LA red snapper (LARS), FL gray snapper (FLGS), and king mackerel (KMK). (c) Principal component loadings for biochronologies of the 5 Gulf of Mexico fish species

Table 1. Interseries correlation and mean sensitivity for LA black drum, TX red snapper, and king mackerel chronologies. LA red snapper and FL gray snapper values taken from Black et al. (2011a)

Species	Interseries correlation	Mean sensitivity
LA black drum	0.54	0.18
TX red snapper	0.54	0.18
King mackerel	0.43	0.17
LA red snapper	0.54	0.13
FL gray snapper	0.76	0.18

was not significantly correlated with any of the other chronologies (Table 2). However, when the low-frequency signal was removed using a 15 yr 50% frequency response spline, the mackerel chronology did significantly ($p < 0.05$) correlate with the black drum and TX red snapper chronologies (Table 2).

Increment-width values for the years 1986 to 2002 were used in PCA_{fish}, as all chronologies had sufficient sample depth and EPS > 0.85 over this time span. $PC1_{fish}$ explained 61.9% of the variability, and the resident coastal/reef species had the strongest loadings (Fig. 1c, Table S1 in the Supplement at www.int-res.com/articles/suppl/m565p149_supp.pdf). $PC2_{fish}$ explained 21.2% of the variability and had highest loadings for king mackerel (Fig. 1c). Scores on $PC2_{fish}$ were linearly related to the king mackerel growth chronology ($R^2 = 0.81$, $p < 0.001$; Table S2 in the Supplement). In order to simplify interpretation of the data, the king mackerel chronology was used in place of $PC2_{fish}$ for the remaining analyses.

Climate–biology relationship

March SST, August U wind stress, and March V wind stress were positively correlated with $PC1_{fish}$, while March U wind stress was negatively correlated with $PC1_{fish}$ ($p < 0.05$; Fig. 2). Thus, years with overall high growth were associated with warm SST and
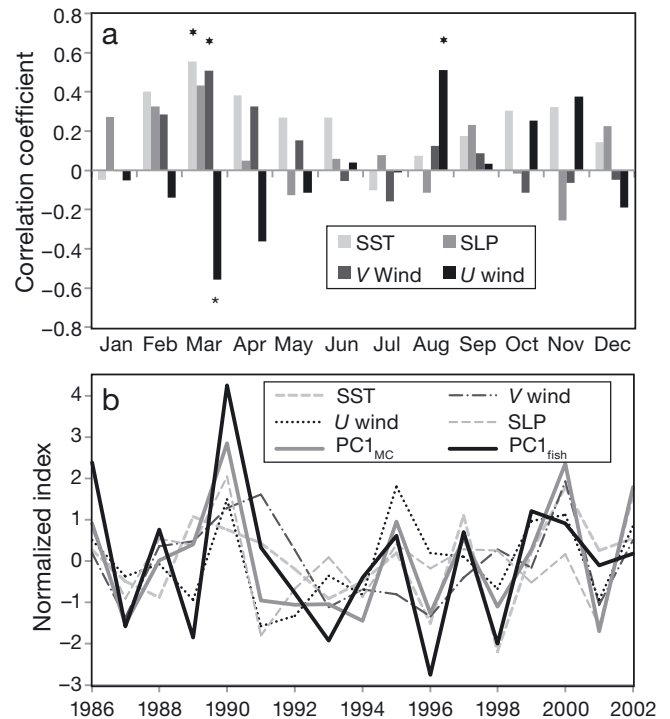

Fig. 2. (a) Correlation coefficients between $PC1_{fish}$ and mean monthly sea surface temperature (SST), sea level pressure (SLP), U wind stress (west to east) and V wind stress (south to north), data. *$p < 0.05$. (b) $PC1_{MC}$, $PC1_{fish}$, and mean monthly SST, SLP, U wind stress and V wind stress, data for the month of March. All data in (b) were standardized (mean = 0 and SD = 1). MC = March climate

winds from the south and east during March, while poor growth years were associated with cool SST in March and winds from the north and west. In addition, the strength of winds from the north in August seemed to contribute to higher overall annual fish growth (Fig. 2). SST was most strongly correlated with $PC1_{fish}$, generally within 2° of the coast in the northern Gulf of Mexico (Fig. 3a). U and V wind stress had a broader area of high correlation that spanned most of the northern Gulf of Mexico and extended onto land (Fig. 3b–d). Mississippi River discharge was not significantly correlated with any of the chronologies (see Fig. S1 in the Supplement).

March SST, V wind, and U wind were more strongly correlated with $PC1_{fish}$ ($p < 0.05$) than any other months of the year (Fig. 2). March SLP was also most strongly correlated with $PC1_{fish}$, although this relationship was not significant ($r = 0.43$, $p = 0.081$; Fig. 2). Thus, these 4 March variables were entered into a princi-
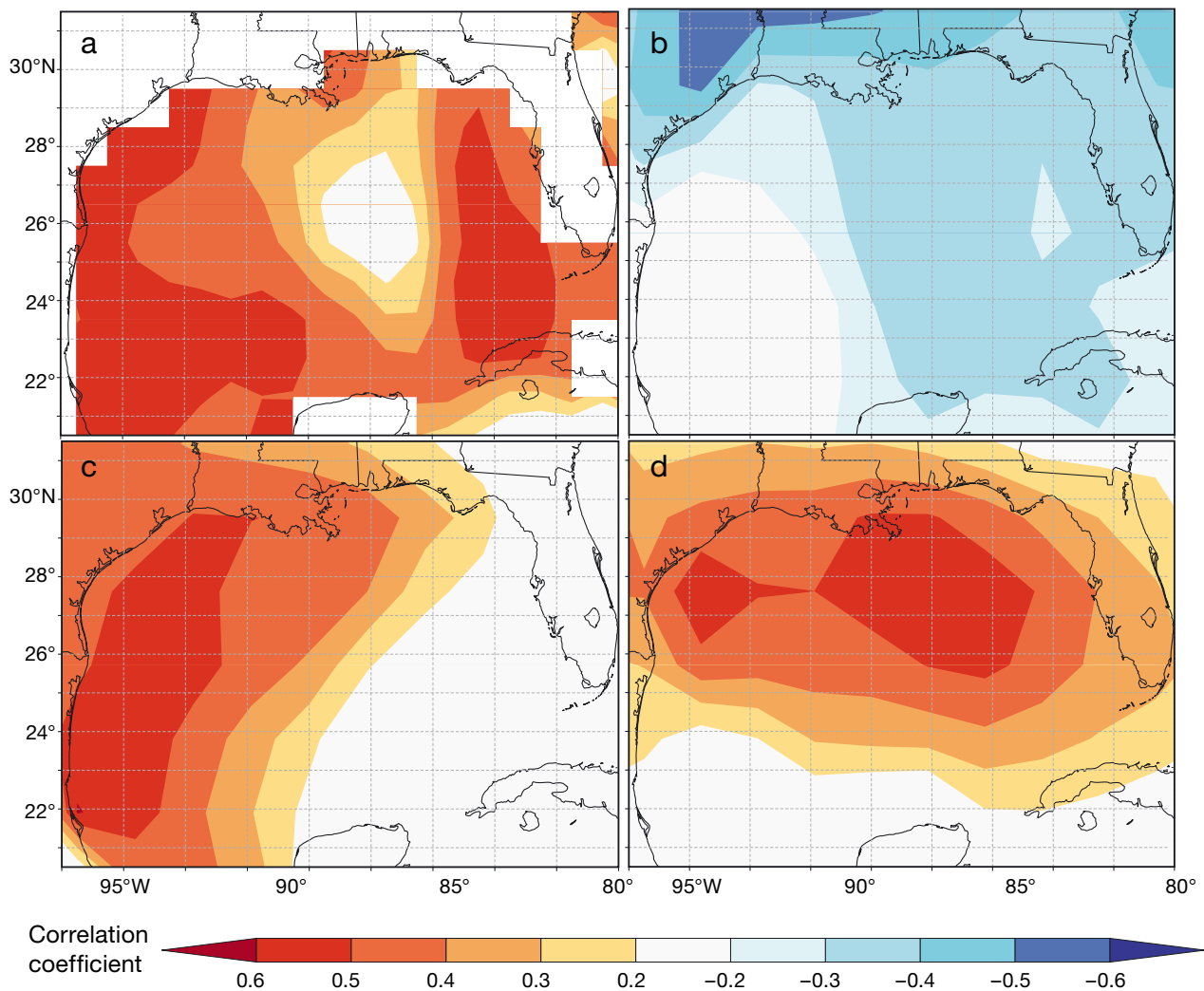
Table 2. Pearson correlation coefficients between all of the chronologies developed in the Gulf of Mexico. King mackerel (high freq.) contains only interannual variability, all long-term trends removed (*) indicates significant ($p < 0.05$, Bonferonni corrected) correlation

	LA red snapper	LA black drum	TX red snapper	King mackerel	King mackerel (high freq.)
FL gray snapper	0.76*	0.62*	0.72*	0.20	0.48
LA red snapper		0.55*	0.73*	0.04	0.52
LA black drum			0.63*	0.43	0.56*
TX red snapper				0.19	0.57*

Fig. 3. Correlation of PC1$_{fish}$ and gridded (a) March sea surface temperature, (b) March U wind stress (west to east), (c) March V wind stress (south to north), and (d) August U wind stress

pal components regression with PC1$_{fish}$ to identify the relationship between March climate and growth (Table S1 in the Supplement). The first and second PC of March climate (PC1$_{MC}$, PC2$_{MC}$) explained 50.1 and 29.0% of the variability in the physical datasets, respectively. Only PC1$_{MC}$ was significant in a regression with PC1$_{fish}$ with an R^2 of 0.51 (p = 0.001; DW = 1.9, p = 0.6) (Fig. 2, Table S2).

The king mackerel chronology negatively correlated with SST in the north central Gulf of Mexico (25° to 30° N × 93° to 85° W) from February through May and in December, with peak correlation in April (Fig. 4a). The king mackerel chronology also significantly correlated with all monthly means of the AMO index as well as the annual mean (R^2 = 0.42, p < 0.002; Fig. 3c, Table S2). The mean annual AMO index significantly correlated with SST in the

southeastern Gulf of Mexico and western Caribbean Sea from May to September, with the strongest correlations in August (Fig. 3b). The high-frequency component of the king mackerel was not significantly correlated with any climate variable or the AMO.

Lastly, March wind stress, SST, and SLP were averaged over quartiles with the highest (1986, 1990, 1999, 2000) and lowest (1989, 1993, 1996, 1998) values of PC1$_{fish}$ (Fig. 5). March in years of good growth (high PC1$_{fish}$ values) was characterized by higher SLP in the area of the Bermuda High, winds from the southeast and east-southeast, and 1.2°C (t-test, p = 0.082) warmer SST relative to low growth years (Fig. 5a,c). Conversely, cool SST and winds from the north and northwest characterized years of poor growth (low PC1$_{fish}$ values) (Fig. 5b,d).
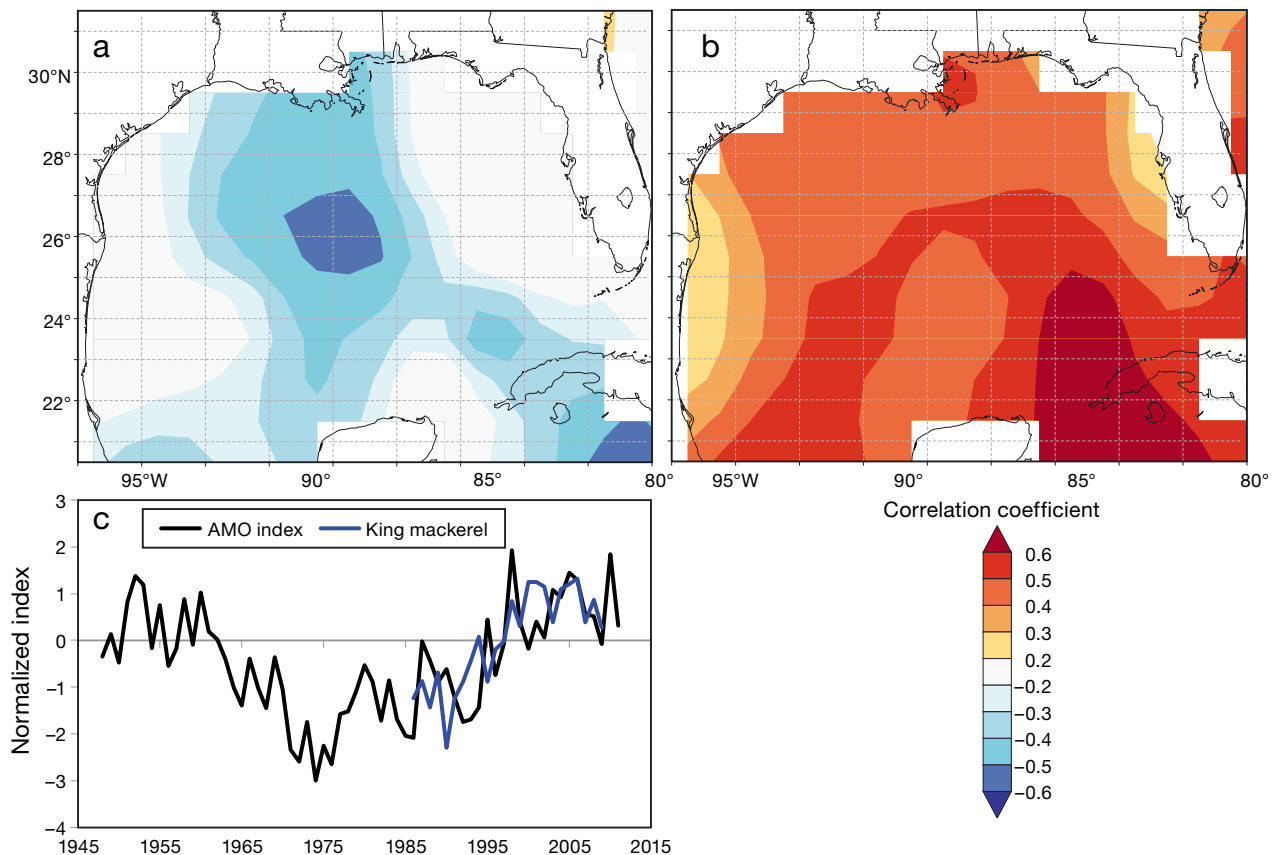
Fig. 4. Correlation of (a) king mackerel and gridded April sea surface temperature (SST) and (b) mean annual Atlantic Multi-decadal Oscillation (AMO) index and gridded August SST. (c) Time series of the AMO index and king mackerel chronology. Both are standardized (mean = 0, SD = 1) and king mackerel data are inverted to show synchrony

Seasonal climate patterns: the spring transition

In order to quantify a spring transition in the climate data, principal components analysis was performed on 111 yr of SLP, U wind, and V wind data from the northern Gulf of Mexico. The first 12 principal components of $PCA_{climate}$ had eigenvalues >1. Each was examined for seasonal patterns and correlations with $PC1_{fish}$ and king mackerel. $PC1_{climate}$ explained 10.2% of the variability in the climate data, with highest loadings to March (Fig. 6). $PC1_{climate}$ also explained ($R^2 = 35.8\%$; p = 0.011) of the variability in $PC1_{fish}$ in a linear regression, but was not correlated with king mackerel (Table 3, Table S2). Neither $PC1_{fish}$ nor king mackerel were significantly correlated with any other components, so those components were excluded from further analysis.

Given its high levels of autocorrelation, a separate principal components analysis was performed with SST data in order to identify the presence of a spring transition. The first 4 principal components of PCA_{SST}

had eigenvalues >1 and each had seasonal patterns in their loadings. $PC1_{SST}$ (26.8% of variance) had strong summer seasonality with positive peak loadings from June through September (Fig. 6b). $PC2_{SST}$ (21.2% of variance) was significantly correlated with $PC1_{climate}$ (r = 0.47, p < 0.001) and had a similar seasonality with negative peak loadings in March (Fig. 5b). However, neither $PC1_{SST}$ nor $PC2_{SST}$ were significantly related to $PC1_{fish}$ or the king mackerel chronology (Table 3).

DISCUSSION

Chronology development

Given the growth synchrony among samples, exactly dated, multidecadal chronologies could be developed for each species considered in this study. Mean interseries correlation, an index of synchrony, was relatively high and comparable to that of North Pacific fish species including rockfish *Sebastes* spp.
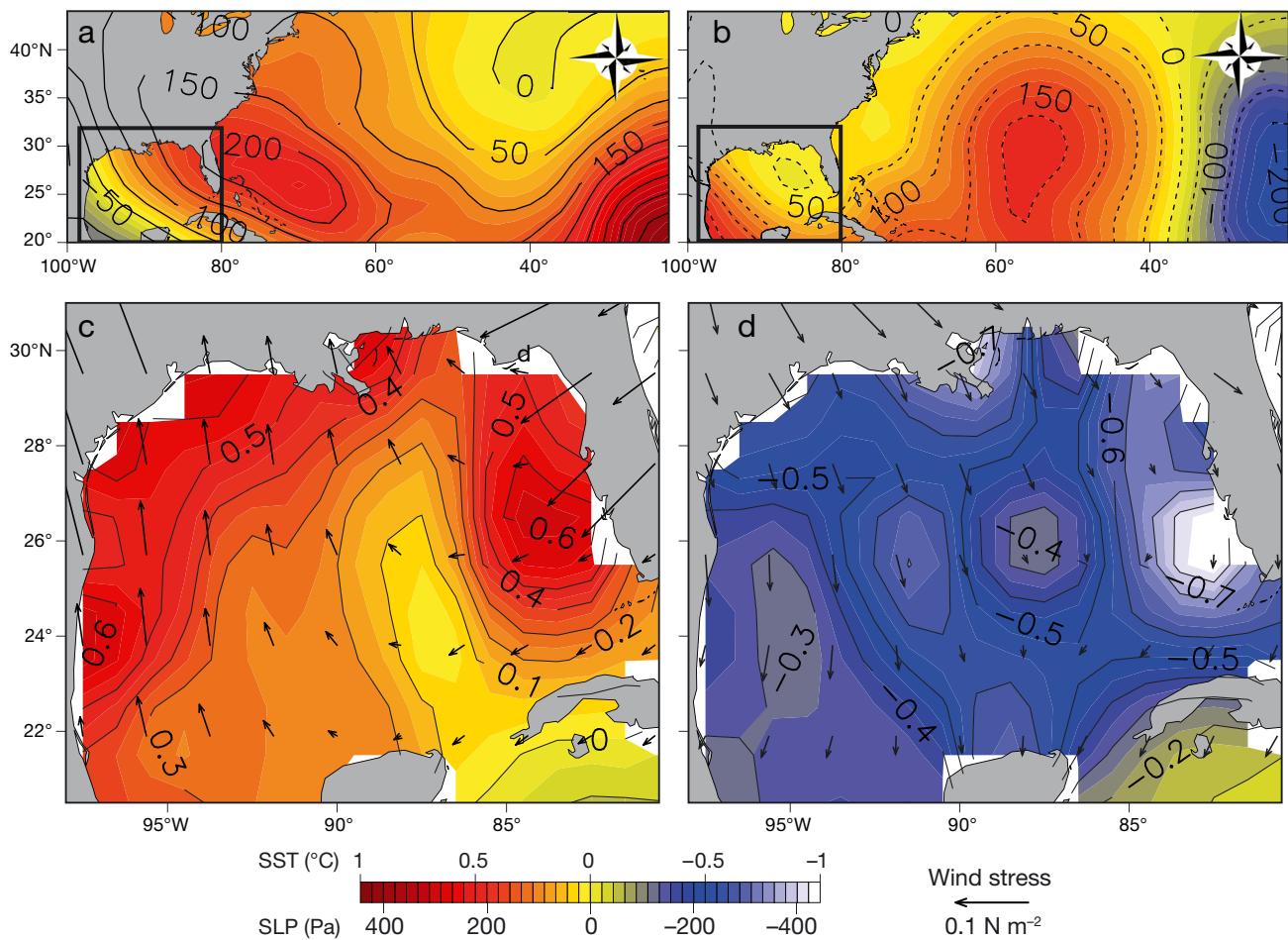
Fig. 5. Average March climate conditions of (a,c) the 4 highest years of growth and (b,d) the 4 lowest years of growth as determined by PC1$_{fish}$ expressed as (a,b) sea level pressure (SLP) anomalies and (c,d) sea surface temperature (SST) and wind stress

(0.54 to 0.65; Black 2009) and yellowfin sole *Limanda aspera* (0.66; Matta et al. 2010). Interseries correlation was lowest for the king mackerel chronology, which could be a function of such a short measurement time series (~10 yr) combined with a relatively low sample depth (15 samples) between 1994 and 1999. Moreover, large mackerel may stay in the northern Gulf throughout the year while smaller individuals migrate to the southeast near the Florida Keys or to the south to the Bay of Campeche during the winter (Fable et al. 1987, Wall et al. 2009). Such broad movement of at least some individuals across climate zones could reduce synchrony in the dataset. Notably, synchrony was still greater than has been reported for other species such as the western blue groper *Achoerodus gouldii* (0.112; Rountrey et al. 2014) and black bream *Acanthopagrus butcheriin* (0.13; Doubleday et al. 2015) in coastal Australian waters.

Two different detrending techniques were used to generate chronologies, the choice of which largely depended on the range of years over which fish were caught. The first approach (individual detrending) was to fit a separate negative exponential function to each growth-increment time series and then divide each observed increment width by the predicted value. In the second technique, detrending was performed using a single negative exponential function that best fit the average, sample-wide age-related growth decline. This 'regional curve standardization' approach can better preserve low-frequency variability, especially in situations in which samples are collected over a wide range of years, but at the cost of adding uncertainty (Briffa et al. 1992). We found that regional curve standardization preserved long-term trends in the mackerel sample set and made almost no difference to the outcome of the black drum chronology (data not shown). It did, however, add some-
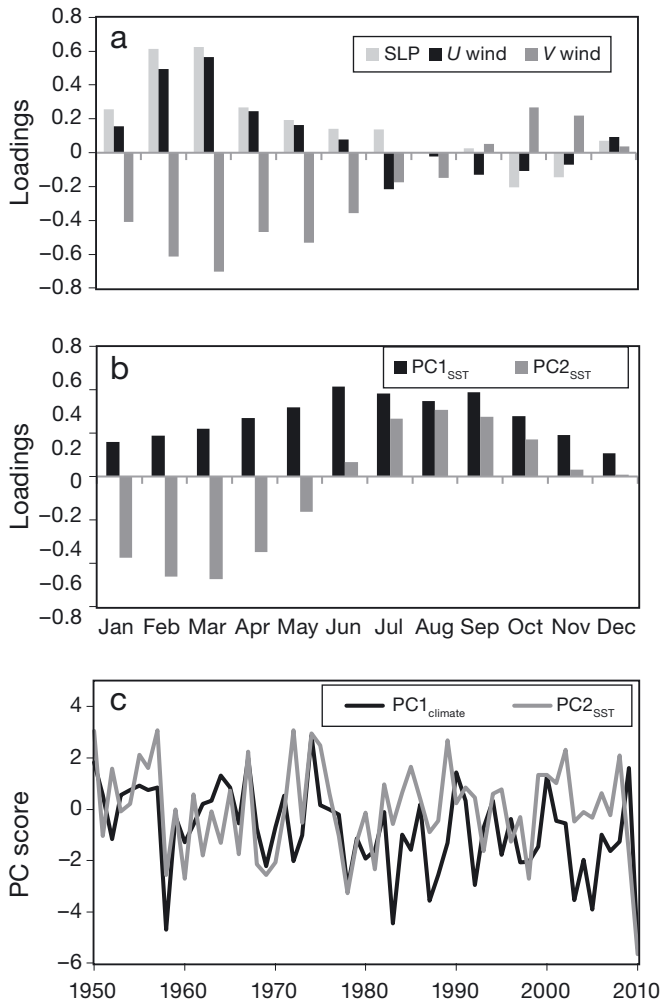
Fig. 6. Principal component (PC) loadings between (a) PC1$_{climate}$ and monthly sea level pressure (SLP), U wind stress (west to east), and V wind stress (south to north) data used to generate the principal component, and (b) PC1$_{SST}$ and PC2$_{SST}$ and the monthly sea surface temperature (SST) data used to generate the principal component. (c) Scores on PC1$_{climate}$ and PC2$_{SST}$. PC2$_{SST}$ is inverted to show synchrony

Table 3. Pearson correlation coefficients between PC1$_{climate}$, PC1$_{SST}$, PC2$_{SST}$, and all chronologies developed for the Gulf of Mexico. (*) indicates significant (p < 0.05) correlation; SST: sea surface temperature. For species definitions, see Fig. 1b

| Chronology | Correlation | | |
	PC1$_{climate}$	PC1$_{SST}$	PC2$_{SST}$
FLGS	0.61*	0.38	−0.51*
LARS	0.50*	0.53*	−0.43
LABD	0.50*	0.12	−0.27
TXRS	0.58*	0.30	−0.08
KMK	−0.097	−0.11	0.0055
PC1$_{fish}$	0.60*	0.37	−0.37

what more uncertainty to the red and gray snapper chronologies, which is why individual detrending was chosen for these species. Thus, we attempted to maximize the retention of low-frequency variability while minimizing uncertainty for each sample set. Applying these 2 detrending techniques in all species also increased confidence that long-term trends were almost certainly unique to mackerel.

Climate–biology relationship

Distinct winter and summer climate patterns have been described previously in the northern Gulf of Mexico (Morey et al. 2003a). During the summer, the Bermuda High is at its strongest, which results in persistent south and southeasterly winds across the Gulf of Mexico and Caribbean Sea (Morey et al. 2003a). Winter is dominated by the passage of cold fronts that result in north and northwesterly winds (Morey et al. 2003a). Spring is thus highly variable within and between years and is a critical transitional period between the 2 dominant seasonal climate patterns. Given their strong loadings to March, PC1$_{climate}$ and PC2$_{SST}$ can be used as indices of the spring transition, capturing whether the shift from winter to summer climate has occurred relatively late (low PC1$_{climate}$ values, high PC2$_{SST}$ values) or early (high PC1$_{climate}$ values, low PC2$_{SST}$ values) in the year. The fact that March was captured by the leading PCs also suggests that conditions during this month are highly variable from one year to the next. This is further supported by the fact that March SST and SLP have higher coefficients of variation than those of any other month of the year.

The correlation between the chronologies and climate suggests an early spring transition enhances growth. The mechanisms underlying this relationship may relate to variations in growing season length. An early start of optimal growing temperatures would presumably result in a wider annual increment (Brown et al. 2004). Alternatively, these climate–biology relationships may be indirect and mediated through prey quality or quantity. For example, rockfish *Sebastes* spp. chronologies in the California Current negatively relate to SST due to its inverse relationship to coastal upwelling and associated productivity (Black 2009, Black et al. 2011b). In the northern Gulf of Mexico, primary production is strongly influenced by riverine nutrient input, the transport of which varies with respect to season (Chen et al. 2000, Morey et al. 2003a, Karnauskas et al. 2013). During summer months, dominant winds favor a stratified

layer of low-salinity water that extends across the entire shelf (Morey et al. 2003a). By contrast, winter winds limit nutrient-rich freshwaters to the shallow coastal zone (Morey et al. 2003a). The early distribution of freshwater may stimulate primary production and ultimately enhance growth in upper-trophic level fish (Polis et al. 1997, Morey et al. 2003b). Wind-driven advection would also explain the low correlation with total Mississippi River inflow. Lastly, there may be interactions between direct and indirect linkages of climate and growth, especially if warm water stimulates lower trophic production (Sharples et al. 2006, Ouellet et al. 2011) and thereby increases prey biomass. Indeed, higher temperatures have been linked to increased prey quantity and quality across a range of ectotherms (Berrigan & Charnov 1994, Angilletta et al. 2004). However, the high-frequency synchrony among chronologies, despite a range of diets across species, suggests that environmental variability is more important than food limitations.

Low-frequency variability

The king mackerel chronology was the only chronology with a strong low-frequency signal, which could be associated with long-term changes in population density. From the 1970s to 1996 king mackerel were overfished, and reduced competition could stimulate individual growth rates (Shepard et al. 2010). Another explanation for rising trends in the chronology could be fisheries-induced pressure to quickly reach maturity (Conover & Munch 2002, Carlson et al. 2007, Shepard et al. 2010). Trends in the chronology are also consistent with climate, especially considering king mackerel's migrations to the southern Gulf of Mexico where, unlike the high-frequency pattern in northern Gulf of Mexico, SST varies at a ~60 yr cycle consistent with the AMO (Yáñez-Arancibia & Day 2004, del Monte-Luna et al. 2015). Indeed, the strongest correlations between chronology and AMO occur in the winter when king mackerel are believed to be present in the southern Gulf of Mexico (Wall et al. 2009).

Given that the king mackerel chronology spans about one-half of an AMO cycle, its relationship to such a low-frequency phenomenon cannot be firmly established. Ideally, the chronology should span multiple cycles of the AMO to establish a robust relationship (Legendre & Legendre 1998). However, the correlation is worth considering given that catch data for other mobile pelagic predators, such as bonito, permit, and jacks, show a similar negative correlation

with the AMO (Karnauskas at al. 2015). The AMO is related to SST and wind speed in the Gulf of Mexico, which are controls for primary production (Karnauskas et al. 2015, Muller-Karger et al. 2015). In the southern Gulf of Mexico, primary production peaks in the winter when the mixed layer is deepest, allowing for the greatest influx of nutrients (Muller-Karger et al. 2015). Anomalously warm winter SST and coincident weak wind fields during positive AMO phases could reduce winter upwelling, decrease primary productivity, and thus reduce mackerel growth.

Several other factors in the northern Gulf of Mexico are also consistent with the strong correlation between king mackerel and AMO. Hypoxia increases during positive phases of the AMO and restricts habitat quality for pelagic planktivorous fishes, which form a major food source for king mackerel. Warm temperatures and greater levels of eutrophication exacerbate any effects, which are also associated with positive phases of the AMO (Karnauskas et al. 2015). In combination, these factors increase mortality and reduce the physiological condition of fishes (Karnauskas et al. 2015), as has been found in bay anchovy *Anchoa mitchilli* and Gulf menhaden *Brevoortia patronus* (Zhang et al. 2014), both of which are prey of king mackerel (Godcharles & Murphy 1986). Similarly, anomalously warm temperatures over the thermal optimum could reduce growth and physiological performance of these forage species (Pörtner & Knust 2007). Moreover, king mackerel have a narrow thermal optimum (20 to 26°C) that could be more readily exceeded during positive AMO phases, compelling mackerel to move into less favorable feeding grounds or live in sub-optimal conditions (Wall et al. 2009). Indeed, 24 of 36 fish stocks examined along the US northeast coast had statistically significant poleward or depth shifts in abundance in association with the positive phase of the AMO (Nye et al. 2009).

CONCLUSIONS

The group of chronologies developed here suggest the timing of the transition from a winter climate pattern to a summer climate pattern is important to fish growth, especially resident coastal species in the northern Gulf of Mexico. However, dramatically different growth patterns and climate relationships were observed for king mackerel, suggesting life history and geography are also important factors. Especially notable is the fact that an early shift to warm conditions is favorable for the resident northern spe-

cies, while a warm phase of the AMO is associated with poor growth for the pelagic, migratory mackerel. Even within the same system, species with disparate life histories, movements, and habitats can have opposing climate–growth relationships, though there are still commonalities among more closely related species.

A number of environmental changes are underway in the Gulf and they may become increasingly important to ecosystem functioning and fish growth. The Gulf of Mexico has warmed approximately 0.6°C in the past 20 yr, and this has coincided with the range expansion of tropical fish species, including gray snapper, to the north (Fodrie et al. 2010, Gericke et al. 2014, Muller-Karger et al. 2015). In addition, eutrophication and associated dead zones as well as human exploitation of fisheries remain important pressures. It is important to note that otolith chronologies do not reflect population size, recruitment levels, or reproductive success, but are most likely associated with body condition and fat reserves (Black et al. 2013). Chronologies can therefore provide a uniquely long and annually resolved history of growth by which to evaluate environmental effects. In this case, the chronologies suggest the importance of a spring transition in the northern Gulf of Mexico, and they also support a growing body of evidence on the relevance of AMO to this region.

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