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**Importance of a northern Gulf of Mexico spring transition as inferred
from marine fish biochronologies**

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from marine fish biochronologies**

by

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Abstract

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

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Linkages between climate variability and productivity and functioning of marine ecosystems have thus far remained poorly described in the Gulf of Mexico, in large part due to a lack of time series that are of sufficient length to generate robust relationships. 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 (*Scomberomorus cavalla*) all collected from the Gulf of Mexico. Synchronous growth patterns were evident between red snapper, gray snapper, and black drum, which were all significantly ($p < 0.05$) correlated to each other, but not with king mackerel. The growth pattern shared by the snapper and drum species was associated with anomalously warm sea surface temperature, southeast wind stress and high sea level pressure in the western Atlantic, all during the early spring months. These data suggest that an early transition from a winter climate pattern to a summer climate

pattern is favorable to fish growth in the northern Gulf of Mexico. In contrast, king mackerel significantly ($p < 0.01$) and negatively correlated to the Atlantic Multidecadal Oscillation (AMO), consistent with a growing body of evidence as to AMOs ecological relevance in this region. Overall, the results of this study point to the importance of a spring transition for the resident coastal species in the northern Gulf of Mexico as well as the importance of life history and geography to climate-biology relationships, as underscored by the coupling of mackerel with the AMO.

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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 can vary considerably over annual to decadal time scales, and the causes of these fluctuations remain poorly understood. Yet despite its economic and ecological importance, it is among the least studied U.S. Large Marine Ecosystems with respect to biological impacts of climate variability, climate change, human activity, and their interactions (Karnauskas et al. 2013, 2015). Disentangling these effects remains a priority but is complicated by the fact that several of these fisheries have been, or currently are overfished (Shepard et al. 2010, Cowan et al. 2010, Karnauskas et al. 2013).

In the most comprehensive ecosystem-level analysis to date, which involved a synthesis of long-term time series of physical and often shorter biological datasets, Karnauskas et al. (2013) identified the Atlantic Multidecadal Oscillation (AMO) as a key climate driver in the Gulf of Mexico. The AMO index is the leading empirical orthogonal function of SST anomalies from 0° to 60°N in the Atlantic basin, and is characterized by alternations between warm and cool phases every 30 to 40 years (Delworth and Mann 2000). The AMO is linked to Gulf of Mexico water temperature, depth of the mixed layer, hurricane activity, and precipitation in the Mississippi River basin (Karnauskas et al. 2015). These climate factors help govern 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).

Perhaps the greatest obstacle to assessing climate-biology relationships in the Gulf of Mexico is the absence of long, annually resolved time series. Existing biological time series extend at most through the 1980s and largely involve fisheries catch data, which can be biased toward regulations and effort and do not capture high-frequency, interannual variability (Karnauskas et al. 2013). In an attempt to better connect biology to climate, a dendrochronology (tree-ring analysis) approach is 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). The biochronologies developed have annual resolution, are exactly dated, can span multiple decades (Black et al. 2005), and reflect population-wide fish condition, as measured in one example as mean anomaly in the length-weight relationship (Black et al. 2013, Rountrey et al. 2014). Given their exact placement in time, these chronologies can be readily integrated with instrumental climate records to quantify growth responses to climate variability and change (Morrongiello et al. 2012). Target fish species for this approach include long-lived species or those with archival collections to ensure that the resulting chronologies capture as much of the historical range of variability as possible, including 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 coast of Louisiana, and gray snapper (*Lutjanus griseus*), caught off the coast of Florida (Black et al. 2011). The growth-increment chronologies spanned 30 years and were significantly correlated with one

another, indicating that some overarching variable influences their growth (Black et al. 2011). Climate-growth analysis of these initial chronologies suggests sea surface temperature (SST) and wind speed and direction in the spring partially drive red and gray snapper growth (Black et al. 2011). Indeed, climate of the Gulf of Mexico has been categorized into distinct winter and summer patterns (Morey 2003). During the boreal summer, the Inter Tropical 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 2003, 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 2003).

The initial red and gray snapper chronologies appear to respond to the timing of this apparent transitioning from winter to summer climate pattern. We hypothesized that the timing of this climate transitioning is a general phenomenon and is important to the growth of fish over the entire northern Gulf of Mexico. Additionally, we considered the AMO in influencing fish growth, as it appears to be prominent in other indicators from the Gulf of Mexico basin. Testing this hypothesis required a more inclusive analysis across a range of fish species that captured a diversity of life histories, habitats, and locations. Red snapper (*Lutjanus campechanus*), gray snapper (*Lutjanus griseus*), king mackerel (*Scomberomorus cavalla*), and black drum (*Pogonias cromis*) were chosen as study species as they meet this criteria and have an added benefit of being commercially and recreationally important fisheries (Figure 1). The results of this study add to the

growth body of work that considers the impacts of climate of fish growth and is applicable to management strategies for these species.

Methods

STUDY SPECIES AND SAMPLE COLLECTION

Juvenile red snapper inhabit low reefs and rocky substrate, while juvenile gray snapper inhabit mangrove channels and seagrass beds (Moran 1988, Flaherty et al. 2013). Adults of both species co-occur and are often found over rocky substrates and offshore oil rigs (Moran 1988, Flaherty et al. 2013). Red snapper shift their diet from zooplankton, mysid shrimp, and squid as juveniles to benthic fish and crustaceans as adults (Wells et al. 2008). Juvenile gray snapper consume mostly small, non-decapod crustaceans in mangrove habitats then switch to larger crustaceans, in particular shrimp, and small fish after moving to reef habitats as adults (Moran 1988, Hettler 1989). Black drum are demersal, estuarine fish that rarely move between estuaries and consume primarily crustaceans, mollusks, and shrimp (Sutter et al. 1986). King mackerel are pelagic fish that migrate between the Florida Keys/ southeast Florida, Texas/ Louisiana, and Mexico (Fable Jr. et al. 1987), but have a limited environmental range of 20-26°C and 32-36 psu, generally stay in water less than 150 m deep, and are piscivorous throughout their life (Finucane et al. 1990, Wall et al. 2009). The king mackerel chronology is the first biochronology developed for a migratory species, as all previous studies have focused on species that have limited movements.

All four species have associated fisheries, and commercial landings data were obtained from the NMFS Annual Landings Query database (https://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). Red snapper continues to be one of the most fished and economically important species in the Gulf of Mexico, providing

over 2,500 metric tons in commercial landings in 2014 despite past periods of overfishing (Cowan et al. 2010). Recreational fishing pressure for gray snapper has increased (Gericke et al. 2013) due to catch restrictions on red snapper and an increase in gray snapper abundance over the past 40 years. Recreational landings are now nearly 900 metric tons per year and commercial landings are over 130 metric tons per year (NMFS personal communication). The commercial black drum fishery has remained relatively consistent over the past two decades and landings have fluctuated around 2,200 metric tons per year. Commercial king mackerel landings in the Gulf of Mexico were consistently around 500 metric tons per year over the past two decades, but spiked by 350% in 2014 (NMFS annual landings query).

Master chronologies were developed from 76 black drum otoliths (collected 1994-2009), 26 TX red snapper otoliths (collected 2010-2013), and 35 king mackerel otoliths (collected 1990-2011). 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 otoliths from red snapper collected from the Texas coast (TX red snapper) and king mackerel. Grid locations were available for red snapper but were not available for king mackerel, so exact collection locations of these specimens are unknown. The Louisiana Department of Wildlife and Fisheries (Baton Rouge, LA via NOAA Southeast Fisheries Science Center) provided black drum otoliths from the Louisiana coast. One red snapper chronology and one gray snapper chronology were previously developed by Black et al. (2011) from samples collected from the

Louisiana coast and Florida coast, respectively, and are subsequently referred to as LA red snapper and FL gray snapper (Figure 1).

CHRONOLOGY DEVELOPMENT

Sagittal otoliths were embedded in epoxy and then thin-sectioned to 0.4 mm through the transverse plane with a low speed, diamond black saw (Isomet, [manufacturer]). Sections were mounted on a slide using Crystalbond then polished using 12- and 8- μ m lapping film. In order to develop a reliable and accurate chronology, only those otoliths that had well-defined growth-increment boundaries and were sufficiently long lived were retained. Black drum, red snapper, and gray snapper otoliths aged less than 20 years old were discarded. King mackerel are not as long lived as the other species so otoliths aged 10 years old and greater 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 40x, 50x, and 50x magnification, respectively. All otolith growth-increment analyses were performed on the dorsal side of the sulcal groove.

To ensure that no otolith increments were missed or falsely identified, all individuals in were visually crossdated. The ability to crossdate individual time series depends on three conditions: 1) growth-increments are added annually, 2) increment width is correlated with some environmental variable, and 3) the climatic variable fluctuates through time (Fritts 1976). Under these conditions, environmental variability will induce a synchronous growth pattern or “bar code” among all individuals from a given region and species. Crossdating is the process of comparing these synchronous

growth patterns beginning at the marginal growth-increment formed the known year of capture, dating back to the center of each otolith (Black et al. 2005). If one increment was accidentally missed or falsely added, the growth pattern beginning at that point would be offset by one year in that individual relative to the other individuals of the same species and region, indicating the error (Black et al. 2005). 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.

Once visual crossdating was completed, growth-increment widths were measured using ImagePro Premier software (v. 7.4, Media Cybernetics, Silver Spring, MD). Growth-increment widths were measured continuously along a transect perpendicular to the axis of growth, starting at the marginal growth-increment and ending as close to the core as possible. 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 verified 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). Each set of measurements was fit with a cubic spline that had a 50% frequency response of 15 years after which each measurement was divided by the value predicted. This spline detrending removes low-frequency variability, thereby isolating high frequency, year-to-year variability, and standardizes all measurements to a time series mean. Next, each detrended set of measurements was correlated with the mean of all others, which was reported as the interseries correlation. This program does not provide precise criteria for

accepting or rejecting a crossdated time series and was used in conjunction with visual crossdating (Grissino-Mayer 2001). Additionally, COFECHA calculated mean sensitivity as an index of high frequency variability. Mean sensitivity ranges from 0 to 2, with the value 0 indicating increments of the same width and the value 1 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 and then converted to ring-width indices (RWI), such that a value >1 represented above-average growth while a value <1 represented below-average growth for a given year. This process is independent of crossdating verification in COFECHA. For the TX red snapper otolith-increment series, negative exponential curves were fit to each measurement time series and observed values were divided by predicted values to remove the age-related growth declines while preserving all variability with a frequency less the length of the measurement chronology. All detrended increment measurements were subsequently averaged using a biweight robust mean to form a master chronology (Cook 1985). This is the same detrending used to generate the LA red snapper chronology and the gray snapper chronology, and all analysis was performed using the program ARSTAN (Black et al. 2011, Cook 1985).

The king mackerel and black drum increment series were detrended using a different approach. For each species, all increment widths were grouped by age of formation, and the mean increment width was calculated for each age group. Each growth-increment width was then divided by the age-specific mean to remove age-related growth declines. Standardized (detrended) growth-increments were rearranged back into

chronological order and averaged by calendar year of formation to yield the master chronology. This method better preserved low-frequency variability for species with short life spans, especially in situations in which there were archival collections. LA red snapper and FL gray snapper chronologies were used from Black et al. (2011).

The expressed population signal (EPS) statistic was used to assess the quality of each chronology by comparing how well the sample represents the theoretical population from which it was drawn (Wigley et al. 1984). EPS is a function of correlation among individual samples and number of replicates. Although there is no level of significance associated with EPS, a value greater than 0.85 is considered adequate and only those portions of the chronologies that exceeded this value were retained (Speer 2010). This corresponded to a minimum sample depth of approximately 20 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 calculation. Thus, the chronology for Atlantic mackerel was limited to portions with 20 measurements per calendar year with the exception of 1994-1999 during which the minimum sample depth was decreased to 15 measurements per calendar year. Principal components analysis (PCA) was used to extract the dominant patterns of variability in growth-increment widths shared by all master chronologies. 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 SLP were chosen as primary climate drivers based on the initial results presented by Black et al. (2011). Wind stress and SLP data were obtained from NOAA-CIRES 20th Century Reanalysis V2c 2 x 2 degree dataset (http://www.esrl.noaa.gov/psd/data/gridded/data.20thC_ReanV2c.html), and SST data were obtained from Hadley HadISST 1.1 1 x 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 (Figure 1). SLP data spanned the region of the Bermuda High (27°N to 37°N and 85°W to 65°W). Mississippi River discharge at Tarbert Landing (river mile 306.3) as obtained through US Army Corps of Engineers was also included (<http://rivergages.mvr.usace.army.mil/WaterControl/new/layout.cfm>).

Climate during a single month can greatly influence an entire year of fish growth, so each chronology was correlated with monthly averaged climate values. Climate values from the previous year were also examined to test for any lagged relationships. Therefore, 24 variables were considered for U wind stress, V wind stress, SST, SLP, and Mississippi River discharge. Significant correlations ($P < 0.05$) between climate variables and fish chronologies were retained for further analysis.

SEASONAL CLIMATE PATTERNS: QUANTIFYING THE SPRING TRANSITION

Previous analyses indicated that Gulf of Mexico climate can be characterized by distinct summer and winter patterns (Morey 2003). We attempted to quantify, more

clearly, the transition between these two seasonal patterns and whether this “spring transition” index is detectable in fish chronologies. All climate data spanning 1900-2011 were arranged into four separate matrices (U wind, V wind, SST, SLP) of 12 months x 111 years. Each column for every matrix was standardized to a mean of 0 and standard deviation of 1. One composite matrix was created for principal components analysis, $climate_{PCA}$, which contained U wind stress, V wind stress, and SLP (3 variables; 12 months each x 111 years). SST has higher autocorrelation than the other three variables due to the high specific heat capacity of water; as such SST was entered into a separate PCA. Loadings were examined for seasonal patterns.

In a subsequent analysis, March SST, SLP, V wind stress, and U wind stress were entered into principal components regression with the first principal component of fish ($PC1_{fish}$) in order to help summarize climate-growth relationships during the month most closely associated with the spring transition (March). Principal components regression was used to derive uncorrelated (orthogonal) variables that better met the assumptions of multiple linear regression from this suite of collinear variables. The Durban-Watson (DW) statistic was used to test for autocorrelation in the regression residuals. Additionally, mean values of gridded SST, winds, and SLP were calculated for the four years with the highest, and then the years with the four lowest, values of $PC1_{fish}$. Differences between mean climate values for high and low growth years were tested using a Student’s t-test. Lastly, correlation coefficients were computed between each chronology and the monthly and mean Atlantic Multidecadal Oscillation (AMO) and multivariate El Nino-Southern Oscillation (ENSO) indices obtained from the National

Oceanic and Atmospheric Administration's Earth System Research Laboratory

(<http://www.esrl.noaa.gov/psd/data/climateindices>).

Results

CHRONOLOGY DEVELOPMENT

All species had good otolith clarity, although black drum and king mackerel had better defined increment boundaries than TX red snapper. Of the 43 TX red snapper otoliths of sufficient age only 26 were used to develop the final chronology due to the prevalence of diffuse increment boundaries or distortion in the otoliths. Fifty-five out of 83 king mackerel otoliths were used and the rest discarded due to distorted or diffuse increment boundaries. More than 800 black drum otoliths were available collected from 1994 to 2009. A random sample of 15 otoliths was taken from each collection year and 78 of these 90 otoliths were suitable for chronology development. Otoliths were discarded if they could not be visually crossdated, however less than 5 otoliths per species were discarded.

Among otoliths measured, growth was synchronous within each species as indicated by high interseries correlations (Figure 1, Table 1). There was also synchrony among species; chronologies were particularly synchronous across the coastal/reef species (snappers and black drum) collected in the northern Gulf of Mexico as shown by the high correlations coefficients (Figure 1, Table 2). In contrast, the king mackerel chronology was not significantly correlated with any of the other fish chronologies (Table 2). However, when the strong low-frequency signal (change in mean value over time shown in Figure 1f) was removed, the mackerel chronology was significantly correlated with the black drum and TX red snapper chronologies (Table 2).

PCA was used to extract the dominant pattern(s) of variation among the five fish chronologies. The 17-year interval 1986-2002 was used in the PCA, as all chronologies had sufficient sample depth and $EPS > 0.85$ over this time span. The first PC ($PC1_{fish}$) explained 61.9% of the variability, and the resident coastal/reef species (gray snapper, red snapper, and black drum) had the highest loadings (Figure 1g). $PC2_{fish}$ explained 21.2% of the variability and had highest loadings for king mackerel (Figure 1g). Scores on $PC2_{fish}$ were linearly related to the king mackerel growth chronology ($r^2 = 0.81$; $P < 0.001$). In order to simplify interpretation of the data, the king mackerel chronology was used in place of $PC2_{fish}$ for the remaining analysis.

CLIMATE-BIOLOGY RELATIONSHIP

March SST, August U wind stress, March V wind stress were positively correlated with $PC1_{fish}$, while March U wind stress was significantly negatively correlated with $PC1_{fish}$ ($P < 0.05$; Figure 2). Thus, good growth was associated with warm SST and winds from the south and east during March, while poor growth was associated with cool SST in March and winds from the north and west. In August, favorable growth is associated with winds from the north (Figure 2). SST was most highly correlated with $PC1_{fish}$ generally within 2° of the coast in the northern Gulf of Mexico (Figure 3a), and U wind stress and V wind stress had a broader area of high correlation that spanned the land and sea (data not shown). Mississippi River discharge was not significantly correlated with any of the chronologies.

The principal components analysis of March SST, V wind, U wind, and SLP included SLP because it had the highest correlation of any month with $PC1_{fish}$, even

though the correlation was not significant ($r = -0.43$, $P = 0.081$; Figure 1). The first and second PC of March climate ($PC1_{MC}$, $PC2_{MC}$) explained 50.1% and 29.0% of the variability, respectively. Scores on these two PCs were entered into a stepwise linear regression with $PC1_{fish}$. Only $PC1_{MC}$ was retained and the regression explained 51.2% of the variability in $PC1_{fish}$ ($P = 0.001$; $DW = 1.9$, $P = 0.6$) (Figure 2).

The king mackerel chronology used in place of $PC2_{fish}$ was negatively correlated with SST in the north central Gulf of Mexico ($25^{\circ}N - 30^{\circ}N \times 93^{\circ}W - 85^{\circ}W$) from February through May and in December, with peak correlation in April (Figure 3b). The high-frequency variability of king mackerel, although significantly correlated with each of the other chronologies, was not significantly correlated with any climate variables. However, the king mackerel chronology was significantly correlated with every month of the AMO monthly index, and with the annual mean ($R^2 = 0.42$; $P < 0.002$; Figure 3c). The mean annual AMO index was significantly correlated with SST in the southeastern Gulf of Mexico and western Caribbean Sea from May to September, with the strongest correlations in August (Figure 3d).

Lastly, March wind stress, SST, and SLP were averaged over the years of highest (1986, 1990, 1999, 2000) and lowest (1989, 1993, 1996, 1998) scores on $PC1_{fish}$ (Figure 4). 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 warmer than average SST in the coastal zone $1.2^{\circ}C$ (t-test, $P = 0.082$) (Figure 4 a, c). Conversely, cooler SST and winds from the north and northwest characterized years of poor growth (low $PC1_{fish}$ values) (Figure 4 b, d).

SEASONAL CLIMATE PATTERNS: THE SPRING TRANSITION

The first 12 principal components of PCA_{climate} had eigenvalues greater than one. Each component was examined for seasonal patterns and correlations with $PC1_{\text{fish}}$ and the king mackerel chronology. $PC1_{\text{climate}}$ explained 10.2% of the variability in the climate data, with highest loadings with March (Figure 5). $PC1_{\text{climate}}$ explained ($r^2 =$) 35.8% ($P = 0.011$) of the variability in $PC1_{\text{fish}}$, but was not correlated with king mackerel (Table 3). Neither $PC1_{\text{fish}}$ nor king mackerel were significantly correlated with any other components, so those components were not examined further.

The first four principal components of SST had eigenvalues greater than one. Each of these components had some seasonal patterns in their loadings. $PC1_{\text{SST}}$ (26.8% of variance) contained a somewhat seasonal pattern with high loadings in the summer and minimum loadings in the winter. $PC2_{\text{SST}}$ (21.2% of variance) was significantly correlated with $PC1_{\text{climate}}$ ($R = 0.47$, $P < 0.001$) and had a seasonal pattern similar to $PC1_{\text{climate}}$, characterized by high loadings in March (Figure 5b). Neither $PC1_{\text{SST}}$ nor $PC2_{\text{SST}}$ were significantly related to $PC1_{\text{fish}}$ or the king mackerel chronology.

Discussion

CHRONOLOGY DEVELOPMENT

Annually resolved, multidecadal chronologies could be developed for each species considered in this study. Mean interseries correlations were similar to other marine fish growth chronologies developed for Pacific species, such as rockfish (*Sebastes spp.*, 0.54-0.65; Black 2009) and yellowfin sole (*Limanda aspera*, 0.66; Matta et al. 2010), but values for each species were greater than those of chronologies developed for Australian species, such as western blue groper (*Achoerodus gouldii*, 0.112; Rountrey et al. 2014) and black bream (*Acanthopagrus butcherii*, 0.13; Doubleday et al. 2015). Each of the mean sensitivity values were low compared to yellowfin sole (0.26; Matta et al. 2010), northern rock sole (*Lepidopsetta polyxystra*, 0.23; Matta et al. 2010), and Alaska plaice (*Pleuronectes quadrituberculatus*, 0.24; Matta et al. 2010) but similar to Pacific rockfish (0.15-0.20; Black 2009). The comparatively low interseries correlation of the king mackerel chronology is likely due to the young age (~10 years old) of many of the fish that were used for chronology development combined with a relatively low sample depth between the years of 1994 and 1999. Moreover, large mackerel may stay in the northern part of the Gulf, near Louisiana and eastern Texas, 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). These migration behaviors could have produced lower levels of synchrony among individuals. Finally, the short-lived mackerel are prone to sporadic correlations (positive and

negative) with one another, which could also have reduced their overall interseries correlation. Notably, mackerel otolith increments had very well defined boundaries, so their interpretation was reliable.

Two different detrending techniques were used to generate chronologies, and these could have some effect on retention of low-frequency variability. The first approach, applied to red and gray snapper, was to fit each growth-increment time series with a separate negative exponential function and then divide each observed increment width by the predicted value. This approach removed any trends longer than the measurement time series, a phenomenon known in dendrochronology as the “segment-length curse” (Cook et al. 1995). Given that the measurement time series averaged 22 years, decadal-scale processes should be preserved. If a major low-frequency pattern comparable to that observed in mackerel were present, at least some of it should have been preserved. In contrast, king mackerel and black drum were each detrended using a single negative exponential function that best fit the average, sample-wide age-related growth decline. Had these samples been collected at the same time and been approximately the same age, the results would be similar to those using individual negative exponential curves. Instead, fish from both species had been collected across decades, which allowed us to preserve low-frequency variability even in the short-lived mackerel. The long-term trends in mackerel were almost certainly unique to this chronology given that the relatively long-lived black drum to which regional curve standardization (RCS) detrending was applied did not show low-frequency variability. Thus, the absence of long-term trends in the majority of chronologies is probably not an

artifact of detrending technique. Once the low-frequency variability was removed from the mackerel chronology, correlation with the other species improved, which corroborated dating accuracy.

CLIMATE-BIOLOGY RELATIONSHIP

Distinct winter and summer climate patterns have been described previously in the northern Gulf of Mexico. During the summer, the Bermuda High is strong, which results in persistent south and southeasterly winds across the Gulf of Mexico and the Caribbean Sea (Morey 2003). Winter is dominated by the passage of cold fronts that result in north and northwesterly winds (Morey 2003). Spring is thus highly variable within and between years and can be defined by the timing of the transition between these two dominant climate patterns. The strong loadings for March and April in $PC1_{\text{climate}}$ and $PC2_{\text{SST}}$ corroborate the observation that these months have the highest coefficients of variability. Overall, principal component scores for $PC1_{\text{climate}}$ and $PC2_{\text{SST}}$ can be considered spring transition indices, capturing whether the shift from winter to summer climate has occurred relatively late or early in the year.

The biochronology results from the present study suggest that when the spring transition occurs early (during or before March), fish growth is enhanced, and when it occurs late (after March), fish growth is reduced. The mechanisms behind why an early or late spring transition may be important to fish growth cannot be described with this dataset. However, the corresponding pattern of growth variability imprinted in the fish chronologies may be due to indirect effects on food quality or quantity and/or direct

physiological effects, extending the growing season. For example, in the North Atlantic, early stratification leads to greater phytoplankton abundance (Sharples et al. 2006) and high survival of juvenile northern shrimp (*Pandalus borealis*), an important food source for fish (Ouellet et al. 2010).

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 2003, Karnauskas et al. 2013). During summer months, dominant winds favor a stratified layer of low salinity water that extends across the entire shelf (Morey 2003). By contrast, winter winds limit nutrient-rich freshwaters to the shallow coastal zone (Morey 2003). The broader distribution of fresh water and its stimulation of primary production could partially explain enhanced growth in upper-trophic level fish such as snapper. It would also explain the low correlation with Mississippi River discharge; where total river inflow is less important to these fish than wind-driven advection.

From a physiological perspective, experiencing optimal growing temperatures for a longer period of time will increase total annual growth (Brown et al. 2004), and the effects of an early onset of summer conditions likely involve a combination of these factors. Indeed, across a range of ectotherms faster growth rates in are supported by both higher temperatures and increased food quality and quantity (Berrigan and Charnov 1994, Angilletta et al. 2004).

LOW FREQUENCY TRENDS

The king mackerel chronology was the only chronology to contain a strong low frequency signal. Why this low frequency trend was present in mackerel and not the other chronologies is unclear. A similar decrease in growth rate from historic (1986-1992) to contemporary (2006-2007) mackerel has been attributed to density-dependent response to overfishing (Shepard et al. 2010). The king mackerel fishery was considered overfished from the early 1980s to 1996 when individuals would likely be growing faster because of the absence of competition, and this could contribute to the observed patterns in the chronology (Shepard et al. 2010).

Low-frequency trends could also be due to the pelagic, migratory life history of king mackerel, which none of the other species in this study exhibit. King mackerel migrate to the southern Gulf of Mexico for the winter where SST variability is dominated by a low frequency signal with a ~60-year cycle that is consistent with the AMO (Yáñez-Arancibia and Day 2004, Monte-Luna 2015). This contrasts with the northern Gulf of Mexico, which is dominated by high frequency SST variability (Yáñez-Arancibia and Day 2004, Monte-Luna 2015). The AMO influences SST in the Gulf of Mexico through a connection with the Atlantic Meridional Overturning Circulation (AMOC) and the Loop Current (Karnauska et al. 2015, Muller-Karger et al. 2015). The present study found SST in the southern Gulf of Mexico to have the highest correlations with the mean AMO index for June through October, with particularly high correlations in August. However, SST directly south of the Yucatan Channel remains highly correlated with the AMO throughout the year. Also, king mackerel show a strong negative correlation with each of the monthly AMO indices, but the strongest correlations occur the winter, the same

months king mackerel are present in the southern Gulf of Mexico. Years in which the AMO is in a positive phase coincide with poor mackerel growth, whereas growth is high in years when the AMO is in a negative phase.

The king mackerel chronology spans about one half of an AMO cycle, so it is impossible to determine if the AMO is the main cause of low frequency variability in the chronology. However, catch data for other mobile pelagic predators, such as bonito, permit, and jacks, show a similar negative correlation with the AMO (Karnauskas et al. 2015). From a bottom up perspective, primary production in the southern Gulf of Mexico 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 or low winds in the southeastern Gulf of Mexico are associated with reduced winter upwelling, which results in decreased primary productivity (Muller-Karger et al. 2015) and may ultimately reduce mackerel growth.

Several other factors in the northern Gulf of Mexico may underlie the strong correlation between king mackerel and AMO. Hypoxia and temperature increase during positive phases of the AMO (Karnauskas et al. 2015). Hypoxia restricts habitat quality for pelagic planktivorous fishes, an effect that is exacerbated by warm temperatures and eutrophication, thus increasing mortality and reducing physiological condition (Zhang et al. 2014). Such an effect has been found for bay anchovy (*Anchoa mitchilli*) and Gulf menhaden (*Brevoortia patronus*), both of which are prey of king mackerel (Finucane et al. 1990). Anomalously warm temperatures could reduce growth and physiological performance of these forage species (Pörtner and Knust 2007). King mackerel have a

narrow thermal optimum (20°C-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. Indeed, 24 of 36 fish stocks examined along the U.S. northeast coast had statistically significant poleward or depth shifts in abundance in association with the positive phase of the AMO (Nye et al. 2009).

Conclusion

The group of chronologies developed here point to the importance to fish growth of the timing of the transition from a winter climate pattern to a summer climate pattern, especially for resident coastal species from the northern Gulf of Mexico. However, life history and geography may be important, especially given the dramatically different pattern observed for king mackerel and its apparent coupling with the AMO. Especially notable is the fact that an early shift to warm conditions is favorable for the resident northern species, while a warm phase of the AMO is associated with poor growth for the pelagic, migratory mackerel. These findings underscore the fact that mechanisms of climate forcing and imprints of response in the otolith can be highly complex.

A number of environmental changes are underway in the Gulf and they may become increasingly important. The Gulf of Mexico has warmed approximately 0.6°C in the past 20 years, corresponding to changes in community composition over the past 30 years (Fodrie et al. 2010, Muller-Karger et al. 2015). Many tropical fish species have already expanded into the north, including gray snapper, and a key question is how these species impact the local ecology and fisheries production (Gericke et al. 2013). Eutrophication and dead zones as well as continued human exploitation of fisheries are also important influences. Otolith chronologies do not reflect population size, recruitment levels, or reproductive success but are most likely associated with body condition and fat reserves (Black 2013). However, chronologies 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 support a growing body of evidence on the relevance of AMO to this region.

Tables and Figures

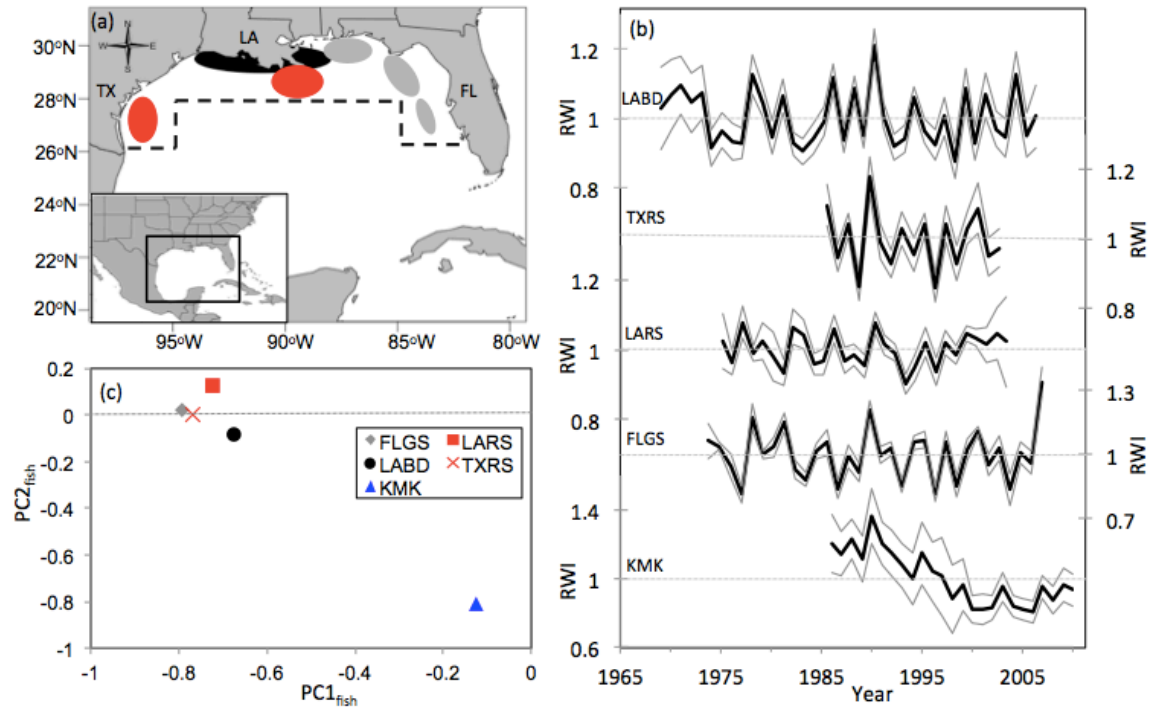


Figure 1. (a) Collection locations of species used in chronology development. Colors coincide with species codes in (c). Climate data were extracted from the northern Gulf of Mexico, the area contained above the dashed lines extending from TX to FL. Note: king mackerel were fishery-dependent collections and the exact location of capture in the northern Gulf is unknown. (b) Ring-width index (RWI; black line) and 95% confidence intervals (gray lines) for Louisiana black drum (LABD), Texas red snapper (TXRS), Louisiana red snapper (LARS), Florida gray snapper (FLGS), and king mackerel (KMK). (c) Principal component loadings for biochronologies of five 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. (2011).

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

Table 2. Pearson correlation coefficients between all of the chronologies developed in the Gulf of Mexico. Significant (Bonferonni corrected) correlations are bold.

	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

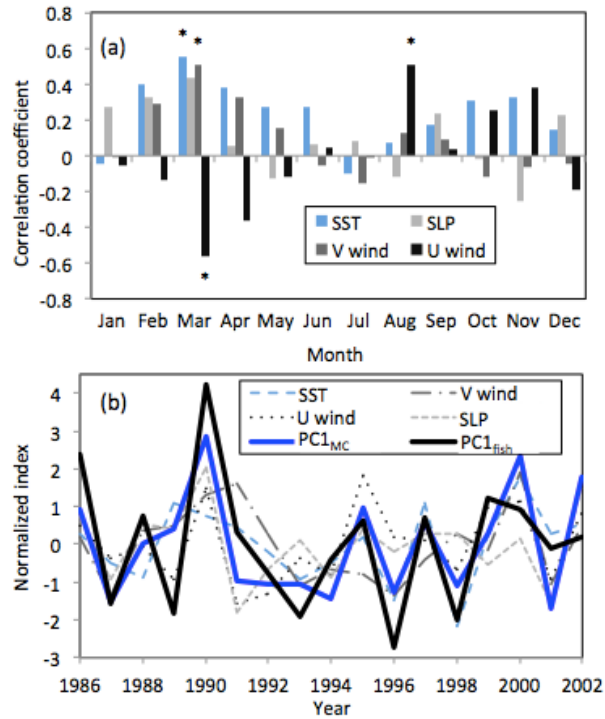


Figure 2. (a) Correlation coefficients between $PC1_{fish}$ and mean monthly SST, SLP, V wind stress, and U wind stress data. * indicates $P < 0.05$. (b) $PC1_{MC}$, $PC1_{fish}$, and mean monthly SST, SLP, V wind stress, and U wind stress data for the month of March. All data in (b) were standardized to a mean of zero and standard deviation of one.

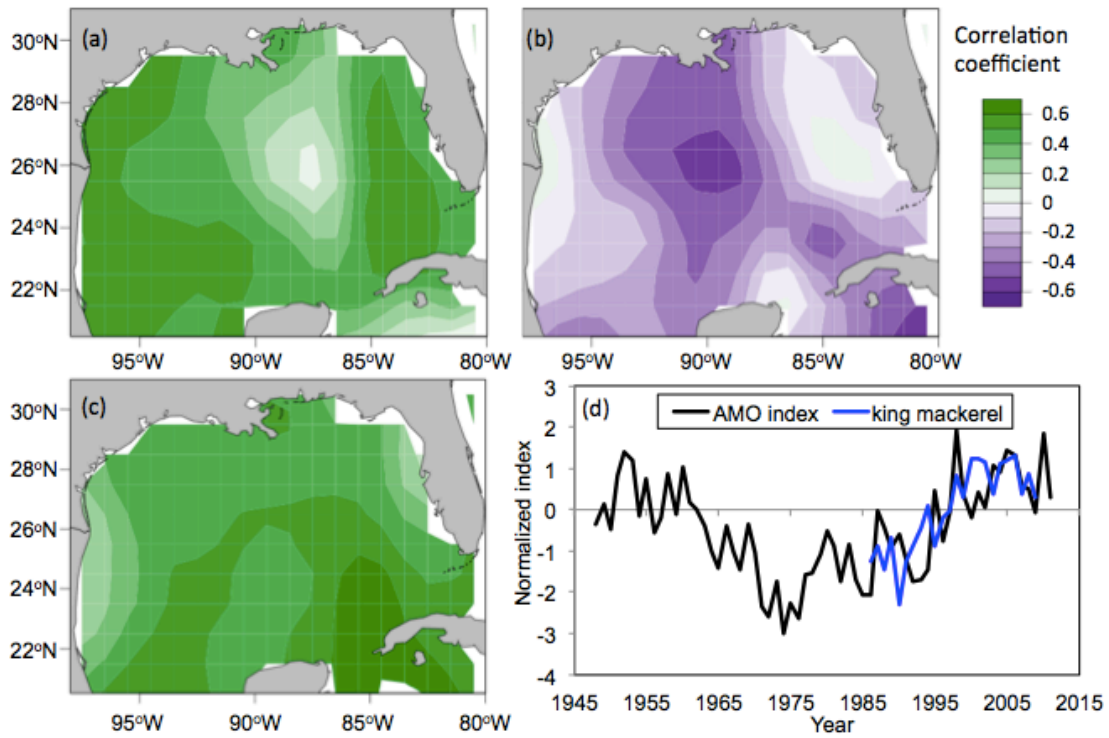


Figure 3. Correlation of (a) $PC1_{fish}$ and gridded March SST, (b) king mackerel and gridded April SST, and (c) mean annual AMO index and gridded August SST. (d) Time series of the AMO index and king mackerel chronology. Both are standardized (mean = 0, standard deviation = 1) and king mackerel data are inverted to show synchrony.

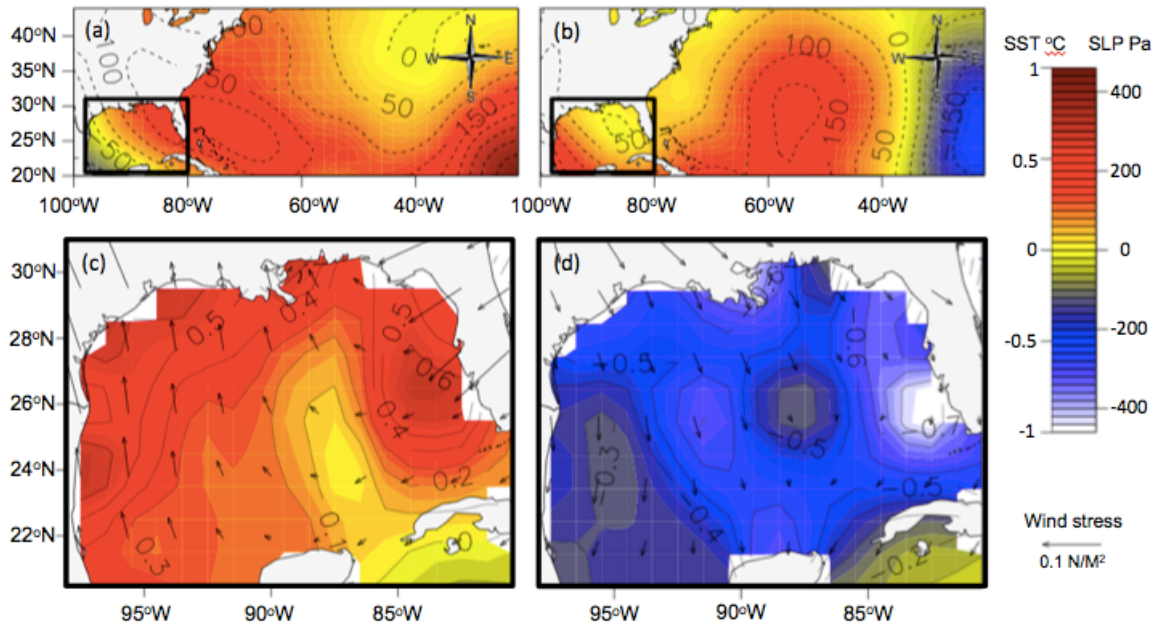


Figure 4. Average March climate conditions expressed as (a, b) SLP anomalies and (c, d) SST and wind stress. The four highest years are shown in (a) and (c). The four lowest years are shown in (b) and (d).

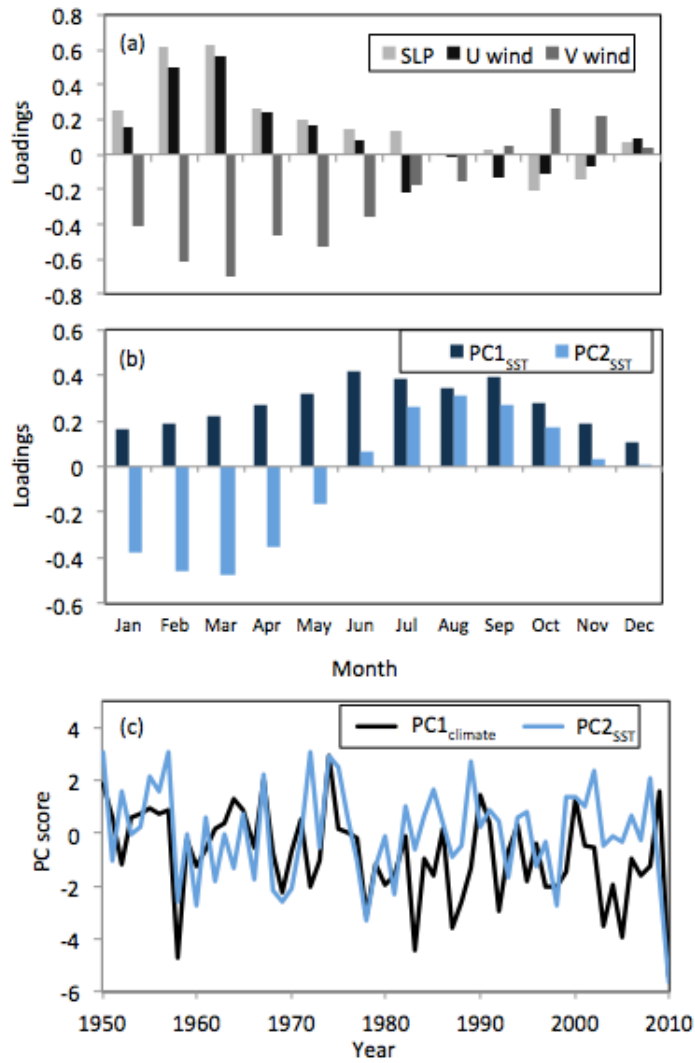


Figure 5. Principal component loadings between (a) $PC1_{climate}$ and monthly SLP, U wind stress, and V wind stress data used to generate the principal component and (b) $PC1_{SST}$ and $PC2_{SST}$ and the monthly SST data used to generate the principal component. (c) Scores on $PC1_{climate}$ and $PC2_{SST}$. $PC2_{SST}$ is inverted to show synchrony.

Table 3. Pearson correlation coefficients between $PC1_{Climate}$ and all chronologies developed for the Gulf of Mexico. Significant correlations are bold.

Species	Correlation
GS	0.61
RS	0.50
LABD	0.50
TXRS	0.58
KMK	-0.097
$PC1_{fish}$	0.60

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Vita

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