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Changing climate associated with the range-wide decline of an estuarine finfish

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Abstract

Southern flounder (*Paralichthys lethostigma*) are a coastal flatfish species that supports recreational and commercial fisheries but are currently experiencing range-wide declines. To quantify the range-wide declines and investigate the role of climate in these declines, fishery-independent sampling data of age-0 flounder were obtained from 34 estuaries representing four states in the Gulf of Mexico (TX, LA, AL, FL) and three states in the Southeastern United States Atlantic Ocean (FL, SC, NC) spanning from 1976 to 2019. Generalized additive models (GAM) were used to estimate age-0 recruitment trends. Spatial and temporal synchrony analyses were then conducted using annual GAM-predicted values to determine if variances in trends were similar between estuaries in close proximity, and if declines occurred at the same time. Because the species is dependent on physical transport (i.e., winds and tides) for recruitment, hourly wind speed, wind direction, water temperature, and air temperature were obtained for estuaries with non-zero sampling totals and long-term data sets. Only six estuaries showed significant relationships between age-0 flounder indices and growing degree days. However, all estuaries with wind data showed significant relationships between age-0 flounder indices and hourly summed wind speed. Southern flounder also have environmental sex-determination, meaning warming estuaries could also account for population changes and declines. We document that water temperatures in the same space and time where southern flounder sexually-determine are warmer now than even a decade ago, which could masculinize populations and substantially change population demographics. These results illustrate the vulnerability of estuarine finfish populations to climate change and increased climate variability. Understanding how climate acts on southern flounder biology may help managers respond to and prevent fishery collapses.

Introduction

Climate change and increasing climatic variability pose threats to natural systems and their inhabitants through numerous expected impacts, including increased land and ocean surface temperatures, greater variability in rainfall patterns, and the potential for stronger extreme weather events (IPCC, 2014). Aquatic ecosystems are specifically vulnerable to climate change as rising temperatures can lead to changes in wind patterns (Barth *et al*., 2007), acidification (Doney *et al*., 2009; Raven *et al*., 2005), and reduced oxygen concentrations (Bopp *et al*., 2002; Matear *et al*., 2000), among other effects that may impact aquatic species' abundance and distribution (Bijma *et al*., 2013; IPCC, 2019). In freshwater environments, climate change has been linked to growth rate variability in Walleye (*Stizostedion vitreum*) and Smallmouth Bass (*Micropterus dolomieu*) recruitment (Shuter *et al*., 2002), altered timing of reproductive investment and migration in Arctic Whitefishes (*Coregonus* spp.; Reist *et al*., 2006), and species-specific range shifts, contractions, and expansions (Comte & Grenouillet, 2015). In marine fish populations, long-term monitoring has established strong relationships between temperature changes and habitat range shifts (both latitude and depth; Pinsky *et al*., 2013; Fredston-Hermann *et al*., 2020). Additionally, water temperature has been confirmed as a significant predictor of species occurrence, which is concerning as warming temperatures are expected to decrease habitat suitability for most fish species (Rogers *et al*., 2019). Climate change can also affect marine fisheries production, resulting in reduced recruitment success (Munday *et al*., 2010) and maximum sustainable yield (MSY; Free *et al*., 2019). Understanding the impact of climate change on marine fisheries is important, not only for conservation, but also to protect economies that rely on commercially and recreationally exploited species (Allison *et al*., 2009; Lam *et al*., 2012).

Climate-driven changes in water temperature also affect the individual biology of several vertebrate taxa, including fish. Temperature-dependent sex determination (TSD) is a type of environmental sex-determination (ESD; Charnov & Bull, 1977) where the ambient temperature influences an organism's sex. TSD in fishes was initially reported in Atlantic Silversides (*Menidia,menidia*) from both laboratory and wild stocks (Conover & Kynard, 1981). Researchers established that while TSD is present in some species, a majority of fish species exhibit ESD as genetic sex determination with temperature effects (GSD + TE; Ospina-Álvarez & Piferrer, 2008). GSD + TE occurs when one genotype, often the genotypic female (XX), is unstable and differentiates phenotypically into the opposite sex under thermal stress, commonly leading to population masculinization (Ospina-Álvarez & Piferrer, 2008). This is relevant to current climate change patterns as an increase of only 2°C during the critical window for development in Atlantic Silversides resulted in a 50% male population at 15°C shifting to 69% males at 17°C (Conover & Heins, 1987). A lower proportion of females could negatively impact measures of recruitment such as spawning stock demographics (Secor, 2000) and egg production (Cubillos *et al*., 2007; Lasker, 1985), which could lead to lower quality and quantities of recruits produced. Ultimately, for species with TSD and GSD + TE, climate change holds the potential to induce skewed sex ratios and a host of other substantial population changes.

Southern flounder (*Paralichthys lethostigma*), a recreationally and commercially exploited estuarine flatfish found in both the US Southeastern Atlantic and Gulf of Mexico (Gilbert, 1986; Ginsburg, 1952), exhibit ESD. Southern flounder experience ESD via GSD + TE (Ospina-Álvarez & Piferrer, 2008) and sexually determine during a narrow development window, 35–65 millimeters total length (TL), a size that is typically reached in the spring after spawning (Montalvo *et al*., 2012). In southern flounder, XY males will always develop as male. However, XX females can develop as phenotypic males when exposed to suboptimal water temperatures for growth during the developmental window (Honeycutt *et al*., 2019; Luckenbach *et al*., 2009). In laboratory studies, increased proportions of juvenile southern flounder were phenotypic males following exposure to elevated temperatures during the development window (as well as lower temperatures; Luckenbach *et al*., 2003). Similar findings of juvenile southern flounder masculinizing at warmer temperatures were reported in natural settings in North

Carolina estuaries (Honeycutt *et al*., 2019). Because female southern flounder attain larger sizes than males, climate-driven changes in sex ratios would also change the size structure and biomass of the population (Fischer & Thompson, 2004; Wenner *et al*., 1990). These changes to the population size structure would negatively affect the fishery as southern flounder harvest is dominated by larger females. Combined, these studies highlight the species' susceptibility for warming environments to masculinize individuals and possibly change the sex ratios of year classes (Montalvo *et al*., 2012).

Other aspects of southern flounder's life history further highlight the susceptibility of the species to climate change. In the fall, southern flounder migrate offshore to spawn (Craig *et al*., 2015; Ginsburg, 1952), typically preceded by a cold front (Gilbert, 1986; Stokes, 1977), which is characterized by the passing of a low pressure system followed by sudden shift in air and water temperatures. In laboratory studies at the northern edge of the species range, spawning, hatching success, and larval growth were all optimal during winter water temperatures and photoperiods, with reduced spawning as conditions were artificially adjusted (Smith *et al*., 1999; van Maaren & Daniels, 2001; Watanabe *et al*., 2006). Recruits and most spawners then return to coastal estuaries in the following months to grow and mature. Similar to many marine fish larvae, flounder recruits rely on physical transport mechanisms to reach estuaries and thus are impacted by changes in late winter and early spring tidal patterns (Burke *et al*., 1998; Enge & Mulholland, 1985), river discharge, and wind speed and wind direction (Taylor *et al*., 2010). These environmental factors are in addition to fishing pressure that depresses populations in areas such as North Carolina (Flowers *et al*., 2019). Although southern flounder are exploited throughout their range, fishing pressure is relatively low in other places, such as Louisiana (West *et al*., 2020). The need to better understand drivers of southern flounder abundance has been highlighted by the reports of recent declines in their recruitment (Froeschke *et al*., 2011) and stock status (Davis *et al*., 2015; Flowers *et al*., 2019; Herdter-Smith & Addis, 2019; Lee *et al*., 2018; West *et al*., 2020) throughout their range.

The objective of this study was to characterize the recruitment trends in southern flounder across the species' range in the US Southeastern Atlantic and US Gulf of Mexico, and specifically document any declines in recruitment that have been anecdotally reported by numerous monitoring agencies. After quantifying any recent changes in estuarine recruitment trends, we chose three analyses through which to investigate the identified trends:

1) spatial synchrony to understand if the dynamics of trends are conserved across space,
2) environmental correlates such as wind and air temperature to measure the possible effect of the local environment on recruitment, and
3) winter duration as a proxy to the temperatures juvenile southern flounder are exposed to during the sizes when they sexually differentiate.

Materials and Methods

Data Sources

We used data from US state agencies' fishery-independent sampling programs in both the Gulf of Mexico and US Southeastern Atlantic to evaluate range-wide, long-term trends in age-0 southern flounder abundance. Data in the Gulf of Mexico were received from Texas, Louisiana, Alabama, and Florida, while data for the US Southeastern Atlantic were provided by Florida (same agency for both coasts), South Carolina, and North Carolina. All six states conduct ongoing fishery-independent sampling programs encountering southern flounder. While three states use a stratified-random design (TX, FL, SC), with major bays or estuaries as the strata, Louisiana, Alabama, and North Carolina had fixed station designs (**Supplemental Table S.1**). Due to the unique and specific designs of individual state sampling programs, a variety of sampling gears are employed to collect southern flounder age-0 relative abundance data. We selected data from inshore otter trawls unless state agency expertise recommended a different sampling gear that was more effective and trusted to sample southern flounder in their waters (**Table 1**). Ideally, the same gear would be used by all sampling programs; however, this is rarely the case across multiple agencies, often due to the fact an effective gear in one state may not be effective in another state (due to habitat, sampling logistics, or other reasons). North Carolina is the only state not to sample year-round, conducting sampling only during May and June of each year.

For every sampling event, all southern flounder were enumerated. However, beyond counts, processing protocols varied. To study the effects of a changing environment on southern flounder, we only included age-0 fish in our analysis to avoid demographic variability that could mask year-class strength. We established state-specific total length (mm) and time period cutoffs to subsample states' total southern flounder catches for only age-0 fish because not all states aged their samples. Age-0 cutoff criteria were adopted directly from the sampling agencies due to variability in southern flounder spawning timing and estuarine conditions that influence growth **(Table S.2)**. Cutoffs allowed us to use the year-round data provided by state agencies, while preventing the mixing of age-1 or older fish in the sample. All southern flounder captured using bag seines in Texas were considered to be age-0 based on previous similar usage of bag seines in Texas (Froeschke *et al*., 2011) and the lack of a cutoff provided by the Texas Parks and Wildlife Department (TPWD). Any sampling event missing data was removed and excluded from future analyses. Finally, we attributed all samples to the estuary in which they were captured (**Figure 1**). This spatial attribution was adopted because southern flounder show high site fidelity to specific estuaries up to the age of maturity (Craig *et al*., 2015; Furey *et al*., 2013) and our analysis relied on modeling the dynamics within individual estuaries. Attribution utilized major bay or zone designations as assigned by agencies, which generally matched up with geographic breaks for estuarine systems. The data we used initially represented 23 estuaries in the Gulf of Mexico and 11 in the Atlantic. We removed one area that was poorly defined (referred to as Gulf of Mexico, AL) and two estuaries where no flounder were caught (Tampa Bay, FL and Charlotte Harbor, FL). All further analyses were applied to the remaining 31 estuaries, 20 of which were along the Gulf of Mexico.

Quantify Age-0 Relative Abundance Trends

To quantify trends in southern flounder age-0 relative abundance, we evaluated several time-series models using both explicit (AIC, residual plots, convergence) and implicit (model form, data requirements) model selection. Relative abundance was measured in catch per unit effort (CPUE), which we defined as the number of southern flounder enumerated per sampling event (e.g., tow, set, haul, etc.). GAMs were identified as the best statistical tool to model age-0 southern flounder abundance for four primary reasons: 1) The smoothing function of GAMs allowed us to input multiple points at the same time step without aggregation; 2) As semi-parametric models, GAMs possess a large amount of flexibility to fit different trends as the data determines the shape of the model. This flexibility serves in contrast to parametric models where the shape of trends is constrained by the model (Yee & Mitchell, 1991); 3) GAMs can be applied to data with a variety of statistical distributions (Guisan *et al*., 2002), which is an appealing characteristic given the large number ($N = 31$) of variable data sets used; and 4) The smoothing function of GAMs better captured the general, long-term trend the study was interested in examining, as opposed to other time series models where year-to-year variability can be overwhelming.

For each of the 31 estuaries, a GAM was fit with the general formula:

$$\textbf{Eq. 1}\ Y_{ij} = \alpha_j + S(x_j) + \varepsilon_j,$$

where Y_{ij} are the observations, i, of age-0 flounder CPUE in each estuary, j, α_j is the group intercept, $S()$ is the smoothing function, x_j is the year in each estuary, and ε_j is the estuary specific error.

As the GAM smoothed the multiple observations, the model structure that emerged was:

$$\textbf{Eq. 2}\ g(E(Y_j)) = \alpha_{0_j} + \sum_{j=1}^{j} f_j(x_j),$$

where $E(Y_j)$ is the expected value of age-0 southern flounder CPUE, with a negative binomial distribution and a canonical log-link function $g()$, α_{0_j} is the intercept for each group (estuary), j, and f_j is the smooth function of the covariate (year), x_j, for each estuary. GAMs were fit with a negative binomial distribution to account for the frequent occurrence of zero-samples in the data. Models were also fit with a thin plate spline smoothing function (Wood, 2003). Thin plate splines were selected for their advantages as the most general and widely applicable spline (Pedersen *et al.*, 2019). Thin plate splines provided an appropriate option to maintain statistical integrity and avoided conflicts with knot placement while investigating non-seasonal, unknown trends. Knots were selected through an automated procedure using restricted maximum likelihood (REML) during model fitting. REML was selected over other fitting criteria for its greater penalization of overfitting and reduced smoothing variability (Wood, 2011). Additionally, we used diagnostic tools to check residuals, percent deviance, and compare the maximum degrees of freedom (k') to the effective degrees of freedom (edf). These diagnostics provided another check for overfitting and prevented underfitting by determining if the k' was optimal. Ultimately, all models were fit using the default k', k' = 9, as a compromise to provide sufficient model space, but also limit overfitting. The exception was Port Royal Sound, SC (k' = 8) due to its shorter duration. All models were fit in R (R Core Team, 2020) using the *mgcv* package (Wood, 2011).

After fitting the models, each was visually inspected to determine the direction of the trend. Statistically, trends were evaluated using the additive effects of the model, where a positive effect indicated a positive trend and a negative effect indicated a negative trend. Further, model fit was determined through the traditional means of percent deviance and statistical significance ($\alpha = 0.05$). Residual plots were examined for a normal distribution and consistency of variance over time. Finally, as a simple comparison of change in the time series, we used the coefficients from our GAMs to predict fitted annual values (means) and standard errors of age-0 southern flounder CPUE for each estuary. GAM-predicted annual CPUE values were used to calculate relative percent differences in the equation:

$$\textbf{Eq. 3} \left(\frac{CPUE_F - CPUE_I}{CPUE_I}\right) * 100$$

where $CPUE_F$ is the final fitted GAM value for the time-series and $CPUE_I$ is the initial value. Relative percent difference was a useful metric to measure change since sampling methods varied from state to state and raw CPUE values were not directly comparable.

Spatial Synchrony

We measured synchrony to understand the relationships between our fitted GAM values over spatial scales. In order to analyze pairwise synchrony across estuaries, we first needed to subset each estuary pair such that only the years in common were included. One additional estuary (Port Royal Sound, SC) was removed due to limited sampling (9 years). In total, 435 unique pairwise synchrony analyses were conducted based on pairings of 30 estuaries. Pearson's product-moment correlation coefficient was used as a metric of synchrony and a mean value was calculated for each estuary pair (Gouhier & Guichard, 2014). The use of Pearson's correlation coefficient for synchrony has been applied in similar studies examining spatial patterns of synchrony for juvenile abundance indices in fisheries (e.g., Bacheler *et al*., 2008). We did not calculate significance of the correlations because of the added statistical machinery required, opting to instead establish the strength and direction of correlations with an understanding that shorter time-series can inflate correlation strength.

To determine if estuaries in close proximity were more synchronous than estuaries farthest apart, correlations from within both the Gulf of Mexico and Atlantic were split. *t*-tests were performed between neighboring estuaries (the two closest estuaries in the respective basin) and distant estuaries (the two furthest in the respective basin) to test for local patterns in synchrony. Significant differences were defined by a test statistic that yielded a p-value < 0.05. No multiple comparison adjustments were conducted on the *t*-tests because each test was conducted on a unique set of correlation values. Additionally, to investigate if the level of synchrony was increasing in recent years—hypothesized by widespread reports of declining southern flounder populations (Flowers *et al*., 2019; West *et al*., 2020)—we repeated all synchrony procedures limiting the data to the most recent five years.

Environmental Correlates

Data Collection

All environmental data was obtained from the National Oceanic and Atmospheric Administration's National Data Buoy Center (NDBC)[1]. While many of the sampling programs collected environmental variables, monitoring programs only took measurements, of different variables by state, at the date and time of sampling. Our analyses required continuous, hourly and year-round measurements from monitoring programs, like the NDBC. Specific buoys selected were those in an estuary (or immediate vicinity) that contained the longest, consecutive data set. Fields of interest were date, time, wind direction (degrees), wind speed (m/s), atmospheric temperature (°C), and water temperature (°C). Due to data transmission issues, extreme weather events, and maintenance, there existed a significant amount of missing data. In cases where less than three consecutive days were missing, blanks were filled in with the value from the succeeding entry (day). In cases where more than three consecutive days of data were missing, we excluded that month from future analyses. We only conducted analyses on estuaries with at least seven years of data from the NDBC for the variable(s) of interest to ensure enough data points for interpretation.

Growing Degree Days

We used growing degree days (GDD) to examine the relationship between air temperature and southern flounder age-0 abundance. Although real-time water temperature would be most appropriate for this relationship, its availability was scarce over a large geographic range. Air temperature, however, was more widely available and strongly correlated with water temperature, making it a useful proxy (Caissie *et al*., 2001; Stefan & Preud'homme, 1993). GDD is an index of the metabolically relevant thermal energy a fish, or in this case a population of fish, would experience over a given time period (Chezik *et al*., 2014a). Thermal energy can affect organismal development (Trudgill *et al*., 2005), including fish growth (Neuheimer & Taggart, 2007) and maturity (Venturelli *et al*., 2010). We calculated the GDD for an individual day (°C-days) as:

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[1] All data from the National Data Buoy Center can be accessed at the following URL: https://www.ndbc.noaa.gov/.

$$\textbf{Eq. 4}\ GDD = \left(\frac{T_{max} + T_{min}}{2}\right) - T_0,$$

where $T_{\max}$ and $T_{\min}$ are the maximum and minimum daily temperatures respectively, and T_0 is the temperature threshold at which thermal energy affects biological functions and processes. The form of GDD used in our analyses is cumulative GDD, where non-negative GDD values are summed over the period of interest. We tested all relationships using standard T_0 values of 10°C, 15°C, and 20°C as recommended by Chezik *et al.* (2014a). Testing relationships against different T_0 values is important given the wide spatial coverage of the data because thresholds can vary with location and using an incorrect threshold can artificially generate or suppress an effect (Chezik *et al.*, 2014b). In addition, there is not much existing guidance on varying T_0 for broadly distributed species and since southern flounder lack an established T_0 reference, it was most appropriate to test at all levels mentioned above. The best T_0 value was the highest threshold at which GDDs could be calculated in all months.

The periods of interest for this study were winter and early spring months, which contain the time period during which environmental correlates are thought to have the greatest impact on recently spawned and developing juvenile southern flounder. However, recruitment timing is highly variable, even in the same location (Flounder Technical Task Force, 2015), providing no pre-determined time frame to examine at each location. As a solution, we conducted multiple comparisons for periods of an individual month and two consecutive months for the preceding December through April. Linear models with the notation:

$$\textbf{Eq. 5}\ Y_i = \alpha_A + x_1\beta_1 + \varepsilon_i,$$

where Y_i is the annual GAM predicted value of CPUE from **Eq.2**, α_A is the intercept, x_1 is the value of cumulative GDD, β_1 is the slope, or effect of GDD on the annual CPUE value, and ε_i is error, were fit for each estuary, in each set of time periods, to evaluate any effect of GDD on southern flounder age-0 relative abundance. Models with a significant effect of GDD ($p < 0.05$) were identified as estuaries where temperature may affect age-0 southern flounder abundance.

Wind Direction and Speed

The wind speed data were represented by summed hourly, directional wind speeds for the same periods of time discussed in the GDD methodology. We separated wind direction into eight directions by 45° increments (NNE, NEE, ESE, SES, SSW, SWW, WNW, and NWN). Linear models with the notation:

$$\textbf{Eq. 6}\ Y_i = \alpha_{Bj} + x_{2j}\beta_{2j} + \varepsilon_{ij},$$

where Y_i is the annual GAM predicted value of CPUE from **Eq.2**, α_{Bj} is the intercept, x_{2j} is the value of summed, directional wind speed, β_{2j} is the slope, or effect of wind on the annual CPUE value, and ε_{ij} is error, were fit for each estuary, in each set of time periods, to elucidate the effect of wind speed and direction on southern flounder age-0 recruitment. Models and thus parameters were estimated separately, using corresponding unique x_{2j} values, for each of the eight wind directions, j. Models with a significant effect of wind ($p < 0.05$) were identified as estuaries where wind speed and direction may have an effect on age-0 southern flounder abundance in that estuary.

Closing Window for Development

Although we did not have observed sex ratios in our data, we wanted to develop an analysis to evaluate the possible relationship between water temperatures at the time of sex determination and age-0 relative abundance later in the year. We limited this analysis to water temperature measurements (as opposed to air temperatures) because water temperatures related to shifting sex ratios have been published and therefore can be directly referenced (Honeycutt *et al*., 2019; Luckenbach *et al*., 2003; Montalvo *et al*., 2012). Furthermore, we recognize that southern flounder samples later in the year are of unknown sex ratios; however, it has been well established that catches are increasingly female as fish get older and that as early as age-0 males may occur in habitats different from where females occur (T.F. Farmer, unpublished data; Reagan and Wingo, 1985; Stokes, 1977) and experience different size-dependent mortality (S.R. Midway, unpublished data). Given our requirement of available, high quality and long-term water temperature data, we had to limit our analysis to 12 (6 in both the Gulf of Mexico and Atlantic basins) of the original 31 estuaries. Our criteria for data was at least 10 years in duration and years missing consecutive months of data were excluded. Long-term water temperature data was downloaded from the NDBC by selecting buoys in an estuary (or immediate vicinity) containing the longest consecutive data set. After finding an insufficient number of estuaries with appropriate data from NDBC, we supplemented our sample with data from the National Estuarine Research Reserve System (NERRS) and the United States Geological Survey (USGS) using the National Water Information System **(Table S.3)**. Water temperature was aggregated to calculate the average temperature (°C) for each day.

Consecutive years of water temperature data were paired so that the fall (August–December) of the preceding year were matched with the spring and summer of the following year (January–July). First, we identified cold fronts, although we acknowledge that the resulting temperature change can vary depending on latitude and severity of the frontal system. Cold front occurrence was set as the instantaneous difference in temperature over 48 hours. We were most interested in fronts that would signal flounder egression and thus we chose location-specific reductions in temperature that did not occur frequently (more than once a week), but also occurred more than once per fall. This was tested by initially counting the occurrence of 4°C differences. If any year had less than two occurrences, we tested 3.75°C and if all had more than two, we tested 4.25°C. This continued in a similar stepwise fashion until a cold front criterion was selected that occurred multiple times in each year. From this set of identified cold fronts, the second cold front occurrence was used to mark the start of development, under the assumption that not all spawning flounder will leave at the first cold front, but mature individuals will likely have migrated by the last cold front. We defined the end the development period by identifying dates when water temperatures surpassed warming thresholds (15°C, 18°C, 20°C, 23°C, 25°C, and 28°C) for ten consecutive days. These thresholds were selected because 15°C, 20°C, and 25°C are reasonable water temperatures in the sampling locations, while 18°C, 23°C, and 28°C were used in Luckenbach *et al*. (2003). While the cold front occurrence criteria were unique to each estuary, all five warming thresholds were tested at each location. We utilized different criteria because climate varies over our study area (from south Texas to northern North Carolina) and similar temperature profiles and biological responses are not expected in each estuary. The number of days between the second cold front and warming is referred to as the *development window*, or the period when young of year southern flounder would be vulnerable to temperatures during ESD (Honeycutt *et al*., 2019; Montalvo *et al*., 2012). To determine if the development window changed over time a linear model was fit:

Eq. 7 $Y_i = \alpha_C + x_3\beta_3 + \varepsilon_i$,

where Y_i is the length of the development window, α_C is the intercept, x_3 is the year, β_3 is the slope, or measure of development window change with time, and ε_i is error. Models with a significant negative slope ($p < 0.05$) were identified as estuaries where the development window length could change sex ratios.

Results

Quantify Trends

Of the 31 estuarine-specific GAMs ran to model annual age-0 southern flounder relative abundance, *year* was a significant smoothing factor for 23 models, indicating significant changes in southern flounder abundance over time **(Table 2).** Temporal trends explained between 1.75% (Cape Romain, SC) and 33.9% (Cedar Key, FL) of the deviance in southern flounder abundance **(Table S.4)**. In 20 of the 23 significant GAMs (87%), the relative percent difference was negative, suggesting a long-term decline. Upper Laguna Madre, TX and Sabine Lake, TX were the only estuaries where CPUE of age-0 Southern flounder was greater at the end of the time-series compared to the initial year. Declines were present in both the Gulf of Mexico (**Figure 2**) and US Southeastern Atlantic (**Figure 3**). In the last five years when declines have been reported, Upper Laguna Madre, TX (36.9%) and Charleston, SC (25.8%) are the only estuaries to see a relative increase in southern flounder. The other 21 estuaries are experiencing continued declines over the last five years (**Table 2**). Recent declines in southern flounder recruitment were evident as negative relative percent differences and are also visible in the downward trends in the red-shaded areas of Figures 2 and 3.

Spatial Synchrony

We calculated 435 unique correlations to estimate spatial synchrony between 30 estuaries. Based on these correlations, 305 were positive (70%) and 130 were negative (30%) with an absolute mean correlation of $r = 0.47$ **(Figure 4; upper triangle)**. Based on *t*-tests, there was no evidence for regional synchrony in the correlations, suggesting that proximity between estuaries was not driving the widespread correlations we measured. When we compared neighboring estuaries and distant estuaries, only 2 out of 30 (7%) had a significant difference. Matagorda Bay, TX and Pontchartrain Basin, LA were more synchronous with their neighboring estuaries than distant estuaries and none were more synchronous with distant estuaries. When the last five years of data were examined, 352 correlations were positive (81%) and 83 were negative (19%) with a mean absolute correlation of 0.9, almost double the long-term correlation coefficient (**Figure 4;**

lower triangle). Negative correlations indicated when declines were occurring elsewhere, those locations were moving in a positive direction. The remainder of estuaries were involved in strong positive declines, where downward trends mirrored each other across basins. When neighboring and distant estuaries were compared for the previous five years, none showed significantly stronger correlation with neighboring estuaries, indicating the lack of any regional synchrony in the macroscale pattern.

Environmental Correlates

Growing Degree Days

Out of the 31 estuaries investigated, 17 were analyzed based on available air temperature data for at least seven years. These estuaries included five in Texas, three in Louisiana, one in Alabama, four in Florida, one in South Carolina, and three in North Carolina **(Supplemental Figures 1-4)**. Of those 17, only six showed a significant effect of GDD on age-0 southern flounder abundance. Two estuaries had a positive effect, which took place in early winter months, with January GDD being significant in Corpus Christi, TX, and December GDD being significant in Barataria Bay, LA. Four estuaries, Aransas Bay, TX, Galveston Bay, TX, Mobile Bay, AL, and Pamlico Sound, NC had a negative effect of GDD, where higher temperatures estimated lower age-0 abundance. Significant negative relationships were most common in later months after February and into March and April. Four of the significant relationships were compared to $T_0 = 20$°C, except for Mobile Bay and Pamlico Sound where $T_0 = 15$°C due to the lack of warmer temperatures in some months.

Wind Speed and Direction

Twenty-one of the 31 estuaries had available wind direction and speed data for at least seven years and were included in our analysis. These included eight estuaries in Texas, four in Louisiana, one in Alabama, four in Florida, one in South Carolina, and three in North Carolina **(Supplemental Figures 2–4).** All had at least one significant relationship with wind, with 15 showing significant relationships with multiple directions and six unidirectional relationships. Thirteen showed both positive and negative relationships, either with different wind directions, or the same wind direction at different times of year. Each of the eight direction vectors were significant for at least one estuary. The number of wind directions significant for a given estuary ranged between one and six. The exact timing and directions of significance varied greatly among estuaries.

Closing Window for Development

We acquired long-term water temperature data sets for 12 estuaries. Seven of the 12 estuaries were found to have a significant negative effect of time; in other words, the duration of cold temperatures during spawning was significantly decreasing in at least seven estuaries we studied (**Figure 5**). There was no significant change in the development window for Sabine Lake, LA, Barataria Bay, LA, ACE Basin or Winyah Bay, SC, and Jacksonville, FL. In Aransas Bay, TX, the development window has declined by an average of 58 days between 1991 and 2017, which was the temporal extent of available environmental data. Vermilion Bay, LA had a development window reduced by an average of 30 days from 1998 to 2020. The development window in Pontchartrain Basin, LA has closed by an estimated 50 days between 1996 and 2020. In Apalachicola, FL, the resulting development window declined by an average of 48 days during the extent of available data between 1996 and 2018. In Charleston, SC, the development window has closed by 53 days between 1998 and 2020. For Cape Fear, NC there was a significant negative relationship resulting in the development window closing by 68 days between 1998 and 2019. Finally, the development window in Pamlico Sound, NC has closed by an average of 67 days between 2006 and 2018 (**Table 3)**.

Discussion

Relative Abundance Trends

Southern flounder age-0 relative abundance is declining range-wide in most estuarine systems in both the US Southeastern Atlantic Ocean and Gulf of Mexico. While stock assessments and abundance estimates are often conducted and reported locally, incorporating range-wide data provides macroscale knowledge of southern flounder. In using the relative abundance estimates from state agencies, we not only ensure our data was collected using scientifically sound methods, but we also use the same data that informs stock assessments and fishery management decisions (Conn, 2011). While all data collection and fishery monitoring are important, our study presents the unique opportunity to examine multiple data sets of over 30 years. Not only are long-term studies rare in ecology, but long-term monitoring is essential to informed fishery management and provides the opportunity to accurately and historically compare stocks (Makinster *et al.*, 2010). We used age-0 relative abundance as a proxy for southern flounder annual recruitment because most of the variability in recruitment is determined at the egg and larval stages (van der Veer, 1986; van der Veer *et al.*, 2000). By the time age-0 fish are vulnerable to the gear, they are settled into estuarine nurseries and likely large enough to index year class strength prior to the adult stage. Abundance of the age-0 year class serves as a crucial index of the smaller fish that survived the most vulnerable stage of recruitment and will be needed to replace spawning adults (Ricker, 1975; van der Veer *et al*., 2000). Use of recruitment indices is common in stock assessments and management decisions and the presence of a recruitment decline indicates the need for remedial action (Sammons & Bettoli, 1998).

We believe this study is important because it was initiated at the same time news media and state management agencies reported problems in the fishery (Davis *et al*., 2015; Lee *et al*., 2018). Often, fish stock collapses are not identified until after recruitment and spawning stock biomass (SSB) bottom out and drastic management measures, such as moratoriums have been enacted. In these cases, studies often focus on a retrospective analysis of the causes (Myers *et al*., 1997) or the recovery of a declined stock (Fernandes & Cook, 2013; Hutchings, 2000). Our opportunity was to study a potential fishery decline as it was happening and deliver results relevant to fishery managers. These results are reported at a time when many states are considering or implementing new regulations on southern flounder (Murphey, 2020a; Murphey, 2020b; Texas Parks and Wildlife Commission, 2020) and will inform future management decisions, and potentially with evident range-wide declines, encourage collaboration and data-sharing between agencies.

While fishery collapses are often associated with high fishing pressure (Fernandes & Cook, 2013; Myers *et al*., 1997; Vasilakopoulos *et al*., 2014), it rarely fully explains the trend and there are often a number of interactive components affecting fish populations. These include species' life histories and trophic levels (Pinsky *et al*., 2011), genetics, habitat alteration (Hutchings, 2000), and environmental changes (Payne *et al*., 2009). Also, fishery monitoring programs like fixed station surveys can add bias due to habitat change (Lee and Rock, 2018); however, we detected southern flounder declines in both fixed station and stratified random survey designs, suggesting sampling station inclusion was not a factor. In a species such as southern flounder, we acknowledge fishing pressure is high in some areas and certainly has a role to play in reducing biomass in state waters in the Atlantic (Flowers *et al*., 2019). However, it is known that fishing pressure does not account for declines everywhere (West *et al*., 2020), likely meaning other factors are at play.

Even in cases of high fishing mortality, flatfishes exhibit high steepness values, where steepness is a parameter representing the slope at the start of the stock-recruit curve (Myers *et al*., 1999). The steepness of the stock-recruit slope is used to measure the degree of density-dependent compensation in the population. High steepness values have been estimated for similar species, such as summer flounder (*Paralichthys dentatus*), where recruitment was determined to be mostly independent of spawning stock biomass (Maunder, 2012). Specific to southern flounder, Midway *et al*., (2018) determined that in order to maintain population levels seen in North Carolina under high levels of fishing pressure, southern flounder not only were exhibiting a high degree of compensatory recruitment, but there also was likely a cryptic population offshore contributing to reproduction. The assumed high degree of density-dependent compensation makes southern flounder more resilient to overfishing (Davis *et al*., 2015). Finally, fishing pressure is not applied synchronously throughout the range of southern flounder. If fishing pressure were the driving force behind these declines, we would expect negative trends in areas of high fishing pressure, but areas of lower fishing pressure remain relatively stable. Instead, we see synchronous declines, especially over the most recent 5-year period, in areas with and without (over)fishing.

Spatial Synchrony

Spatial synchrony quantifies the concurrent changes in abundance of geographically distinct populations (Liebhold *et al*., 2004). By adding a synchrony component to our study, we were able to answer the question of whether temporal trends in southern flounder recruitment were spatially correlated with other estuaries and, if so, to what extent. First, we established that 70% of correlations were positive, indicating age-0 flounder recruitment has generally been synchronously declining in the long-term across their range, as evident by only two estuaries showing an increase in flounder recruitment over time. Out of 30 *t*-tests using pairwise specific values, only Matagorda Bay, TX and Pontchartrain, LA showed greater synchrony with their neighboring estuaries than more distant estuaries. This indicates distance is not strongly correlated with age-0 relative abundance correlations for southern flounder. This contrasts with the synchrony of another estuarine fish with a similar range as southern flounder, red drum (*Sciaenops occelatus*), where populations were synchronous at intrastate levels, but not across broader distances (Arnott *et al*., 2010; Bacheler *et al*., 2008).

Secondly, when we evaluated only the last five years of available data (understanding that reduced time-series result in inflated correlations, but wanting to make a broader point without additional statistical analyses), we see 81% positive correlations, indicating more estuaries are exhibiting declines at the same time. Mean correlation coefficients from the 5-year analysis are almost double the mean long-term value ($r = 0.47$ vs $r = 0.9$), meaning declines have become more strongly correlated in recent years. For the recent time-series, the lack of correlation with neighboring estuaries and curious occurrence of correlation with furthest distance estuaries again indicates the lack of a regional pattern to this synchrony. The absence of a relationship with neighboring estuaries could be explained by the life history of southern flounder, a relatively short-lived fish that matures by age-1 or age-2 (Corey, 2016; Midway & Scharf, 2012), as faster life history species (early reproduction, shorter generation time, short longevity) exhibit less spatial synchrony than slower life history species (Marquez *et al*., 2019). The lack of local scale spatial synchrony, combined with the evidence for a range-wide decline is concerning as increased synchrony among interacting spatial populations can reduce the resilience of declining stocks (Koenig & Liebhold, 2016). Two potential primary drivers of the range-wide synchrony seen here are dispersal among populations and shifts in environmental variables that influence population dynamics (Liebhold *et al*., 2004). Although not much is known about southern flounder's offshore spawning locations and dispersal, the range gap around southern Florida (Gilbert, 1986; Ginsburg, 1952) and genetic differences between basins (Anderson & Karel, 2012; Anderson *et al.*, 2012) would indicate widespread dispersal is not responsible for the synchrony in range-wide declines. This leads us to consider a changing climate as the most likely explanation for widespread declines. While additional tests would be required to use synchrony as an explanation for the decline, this analysis does provide further evidences of a decline occurring.

Changing Climate Effects

Southern flounder spawn and recruit in winter months, which maximizes their chance for survival by taking advantage of cooler water temperatures associated with favorable oceanic currents (Miller *et al*., 1984). However, we found GDD plays a localized role in explaining the age-0 relative abundance trends. Five of the six GDD relationships and both winter severity relationships were in the Gulf of Mexico, which suggests temperature is a more important factor for survival in southern areas with higher extreme temperatures. Wind was significant in all 21 of the estuaries, with both positive and negative effects on age-0 relative abundance in 13. This aligns with physical factors southern require for transport from offshore waters into estuaries (Burke *et al*., 1998; Enge & Mulholland, 1985; Taylor *et al*., 2010). The significant wind directions were highly variable by location, which is likely a function of the entrance to each estuary facing in a unique direction and having openings at different orientations. Winds with a positive affect would likely be pushing flounder into and toward the estuaries where they settle, while negative affecting winds would keep flounder from settling in estuaries. Ultimately, range-wide and synchronous southern flounder declines are not well attributed to local environmental variables, both of which are heterogenous and local-scale.

In addition to the effects of wind and temperature on survival and recruitment, we also wanted to address the hypothesis that declines in relative abundance could be driven by changing sex ratios associated with warm waters masculinizing the population. Masculinization is relevant to declines in abundance and fishery catches because southern flounder exhibit sexually dimorphic growth (Fischer & Thompson, 2004; Wenner *et al*., 1990). Males are smaller than females and thus less susceptible to both fishery and sampling gears. Males may also spend more time in offshore habitats (T.M. Farmer, unpublished data; S.R. Midway, unpublished data; Reagan & Wingo, 1985; Stokes, 1977). As a result, masculinized populations may be more cryptic to fishery-independent and fishery-dependent surveys, resulting in lower indices of relative abundance. Our hypothesis was informed by previous work that clearly established balanced sex ratios at intermediate temperatures (23°C) and masculinization at 5°C cooler or warmer temperatures (Luckenbach *et al*., 2003). The confirmation of GSD + TE occurrence in natural populations furthered the interest in ESD as an explanatory factor for trends in southern flounder relative abundance (Honeycutt *et al*., 2019). In addition, recent studies have gained a better understanding of the GSD + TE mechanism southern flounder exhibit (Luckenbach *et al*., 2009; Ospina-Álvarez & Piferrer, 2008). Similar findings of GSD + TE in a related species, the Japanese flounder (*Paralichthys olivaceus*), added further evidence to a potential masculinization event and contributed knowledge that the masculinization may be associated with elevated cortisol levels in XX genotype, phenotypic males under high temperatures (Yamaguchi *et al.*, 2010).

One key limitation of our analysis was the lack of sex ratio data. Most of the states' fishery-independent sampling programs simply enumerated fish for the surveys we received, as their primary objectives are to monitor population dynamics. Without sex ratio data, we could not conduct similar analyses directly comparing sex ratios and water temperature in estuaries throughout the range. In this absence, we sought to identify a simpler analysis that could serve to contribute to future work with sex ratio data and focus on the locations where ESD would most explain southern flounder population variation. In Atlantic Silversides, it was a critical period during juvenile development where the environment controlled sex determination (Conover & Kynard, 1981). In southern flounder, this critical period has been identified as 35–65mm TL (Montalvo *et al.*, 2012), a length southern flounder are likely to reach in the spring after being spawned in the winter. We examined the closing window of development to determine if juvenile southern flounder had a longer or shorter window (by number of days) to develop at the mid-range temperatures responsible for even sex ratios.

We defined this window of development as the time-period between the cold fronts that are often associated with fall spawning egress (Stokes, 1977) and the time in the spring when long periods of warm temperatures re-establish. If southern flounder have a shorter period between spawning and warming, then we hypothesized juvenile exposure to warm, masculinizing temperatures during spring would be lengthened, increasing the chances of a male-skewed sex ratio. A long-term review of water temperature data was previously used to show that grayling (*Thymallus thymallus*) had experienced a 20% increase in the proportion of males between 1993 and 2011, which was best explained by the water temperatures experienced during this species' juvenile window of development (Wedekind *et al.*, 2013). While it would perhaps be stronger to use consistent criteria, individual estuaries themselves are unique systems and when examined range-wide, climates vary amongst states and latitudes. To quantify the window of development for each estuary, the use of a flexible criteria was necessitated as the temperatures found in one estuary, may not be achieved at another (ex: Pamlico Sound, NC vs Lower Laguna Madre, TX). We did however consistently use the second cold front in the fall as the proxy for spawning egress start. The second occurrence was used because the first front may occur early in the year and not all spawning flounder are expected to leave in response to the first front. However, we anticipate by later cold fronts in December, most flounder that are going to spawn will have already departed the estuaries for offshore sites. The use of the second cold front was designed to create a developmental window that closely tracked the actual timing of offshore spawning activity. The warming thresholds were designed to represent a variety of temperatures associated with GDD and ESD studies. Each value was tested as warming patterns and sustained spring temperatures vary by location and thus different values were significant to flounder development.

Ultimately, we show the window of development is closing in a majority of estuaries with long-term water temperature data. This means flounder are being exposed to shorter periods of cool temperatures, giving them less time to develop in equal sex ratios between 35–65mm TL. Most of the windows have closed dramatically, by greater than 30 days over the time-series, including a 67-day reduction in the window in only 12 years for Pamlico Sound, NC. Concerns for southern flounder masculinization will only continue to grow with climate change, as warmer temperatures are a threat to natural populations if the skewed sex ratios reduce female reproductive capacity (Geffroy & Wedekind, 2020). These examples of closing development windows further expand the possibility that southern flounder masculinization is occurring range-wide and could be leading to both declining populations and an increase in cryptic individuals. We acknowledge this analysis cannot confirm sex ratios are changing in these locations without the proper data, but we do think it argues for the necessity to include sex ratio changes in the discussion of southern flounder stocks. We hope future studies will be able to gather sex ratio data in these locations, as well as conduct their own closing window analyses when consistent, long-term data are available, to further investigate this hypothesis.

Conclusion and Summary

We provide evidence that southern flounder are declining in both the long- and short-term throughout their range. Our study examined a diversity of factors that could be contributing to range-wide declines in southern flounder. Many of the investigated variables (i.e., GDD and closing development window) were not universally important and instead significant at the individual estuary level. Wind was the only environmental variable to be significant in every estuary tested, supporting the importance of physical transport on age-0 southern flounder relative abundance. Including the asynchronous application and effect of fishing mortality, we did not identify any clear and leading cause of the southern flounder collapse. However, as with many fishery collapses, it is likely that a multitude of factors, including fishing mortality, temperature, wind, seasonality, and biological development, are acting in concert to increase stress on southern flounder and contribute to negative trends in their populations. Future studies should seek to conduct localized evaluations of fishing pressure, environmental correlates, and sex ratio changes to contribute better data and analysis to our knowledge and management of southern flounder stocks. These studies are needed to evaluate and monitor the role climate change and variability are having on estuarine finfish. Finally, macroscale studies would be useful in other fisheries of concern by fostering greater intra-agency collaboration and understanding the full picture of a species' dynamics. By taking a macroscale view and applying consistent methodologies to local estuarine systems, fishery managers can more sustainably manage the southern flounder fishery and incorporate climate variability into management plans.

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Tables

Table 1. Programmatic details for state fishery monitoring surveys sampling young-of-year southern flounder in six states that provided data to the study. Note that the program timeframes in the table reflect the months in which samples used in this study were collected and not the entire timeframe of the overall program.

States	Estuaries	Years	Gear Type	Timeframe	Sampling Sites
Texas[1]	9	1976–2017	Bag Seine	Year-Round	20/month[b]
Louisiana[2]	5	1980–2017	4.88m Otter Trawl	April–September	Basin-specific
Alabama[3]	4	1981–2017	4.88m Otter Trawl	May–June	24 routine sites
Florida[4]	5	1996–2017	6.1m Otter Trawl[a]	Year-Round	Basin-specific
South Carolina[5]	5	1991–2018	Trammel Net	Year-Round	Basin-specific
North Carolina[6]	3	1978–2017	3.2m Otter Trawl	May–June	104 routine sites

a. In the South Indian River, no flounder were caught in the 6.1m trawl over a short period of available sampling, so data comes from a 183m haul seine.
b. Only 10 samples per month are taken in East Matagorda Bay, TX.
1. (Martinez-Andrade *et al.*, 2005)
2. (Louisiana Department of Wildlife and Fisheries, 2017)
3. (Alabama Marine Resources Division, 2013)
4. (Allen, 2019)

5. (Arnott, 2014)
6. (Lee, 2018)

Table 2. Outputs from the 31 estuary-specific generalized additive models of age-0 southern flounder catch per unit effort over time. These outputs examine the significance or non-significance of *year* ($\alpha < 0.05$), as well as the changes over the entire length of the time series. Bold text indicates a significant effect of *year* on southern flounder CPUE, and non-bolded font indicates an insignificant effect. The 5-Year Reference starts in 2013 with a Last Sampling Year in 2017, unless noted by *, in which case those headings are 2014 and 2018 respectively. Negative Relative % Difference indicates a decline, while a positive value indicates an increase in CPUE.

Estuary	Sampling Start Estimate	5-Year Reference Estimate	Last Sampling Estimate	Relative % Difference (All Data)	Relative % Difference (5 yrs)
Lower Laguna Madre, TX	1976: 0.360	0.045	0.044	**-87.8**	**-2.2**
Upper Laguna Madre, TX	1976: 0.057	0.046	0.063	**10.5**	**37.0**
Corpus Christi, TX	1976: 0.041	0.047	0.043	**4.9**	**-8.5**
Aransas Bay, TX	1976: 0.317	0.051	0.041	**-87.1**	**-19.6**
San Antonio Bay, TX	1976: 0.066	0.062	0.055	**-16. 7**	**-11.3**
Matagorda Bay, TX	1976: 0.103	0.051	0.031	**-69.9**	**-39.2**
East Matagorda Bay, TX	1983: 0.129	0.048	0.020	**-84.5**	**-58.3**
Galveston Bay, TX	1976: 0.123	0.151	0.077	**-37.4**	**-49.0**
Sabine Lake, TX	1976: 0	0.205	0.061	**NA**	**-70.2**
CSA7/Calcasieu Lake, LA	1980: 0.248	0.156	0.069	**-72.2**	**-55.8**
CSA6/Vermilion Bay, LA	1982: 0.999	0.124	0.023	**-97.7**	**-81.7**
CSA5/Terrebonne Bay, LA	1980: 0.207	0.248	0.011	**-94.7**	**-95.6**
CSA3/Barataria Bay, LA	1980: 0.019	0.028	0.029	52.6	3.6
CSA1/Pontchartrain, LA	1980: 0.269	0.094	0.012	**-95.5**	**-87.2**
Mississippi Sound, AL	1981: 0.044	0.002	0.001	-97.7	-50.0
Mobile Bay, AL	1981: 0.586	0.036	0.019	**-96.8**	**-47.2**
Little Lagoon, AL	1992: 0.082	0.086	0.084	2.4	-2.3
Perdido Wolf System, AL	1981: 0.004	0.106	0.079	1875.0	-25.5
Apalachicola, FL	1998: 0.032	0.073	0.022	**-31.3**	**-69.9**
Cedar Key, FL	1996: 0.006	0.002	0	**-100.0**	**-100.0**
Southern Indian River, FL	1998: 0.074	0.001	0	**-100.0**	**-100.0**
Northern Indian River, FL	1996: 0.003	0.001	0	-100.0	-100.0
Jacksonville, FL	2001: 0.103	0.112	0.028	**-72.8**	**-75.0**

Port Royal Sound, SC	2010: 0.064	*0.086	*0.088	37.5	2.3
ACE Basin, SC	1994: 0.428	*0.194	*0.105	**-75.5**	**-45.9**
Charleston Harbor, SC	1991: 0.492	*0.120	*0.151	**-69.3**	**25.8**
Cape Romain, SC	1994: 0.102	*0.051	*0.040	**-60.8**	**-21.6**
Winyah Bay, SC	2003: 0.214	*0.230	*0.175	-18.2	-23.9
Cape Fear, NC	1978: 1.90	0.406	0.240	**-87.4**	**-40.9**
Pamlico, NC	1978: 1.530	2.763	1.075	**-29.7**	**-61.1**
Albemarle, NC	1981: 1.156	0.686	0.515	-55.4	-24.9

Table 3. Combinations of cold fronts and progressive warm water thresholds evaluated for the developing window. The cold front is defined by a temperature drop of that magnitude and we used the date of the second fall cold front, which was tested against the progressive warming thresholds that needed to persist for 10 days. Blank "Cold Front" cells with a dash (–) indicate no cold front was significant. Green cells indicate a significant reduction in the development window over years in each data set and red indicates the absence of a significant relationship.

Estuary	Cold Front	15°C	18°C	20°C	23°C	25°C	28°C
Pamlico Sound, NC	4°C	🟥	🟩	🟩	🟩	🟩	🟥
Cape Fear, NC	3.25°C	🟥	🟥	🟥	🟥	🟩	🟥
Winyah Bay, SC	—	🟥	🟥	🟥	🟥	🟥	🟥
Charleston, SC	1.25°C	🟩	🟥	🟩	🟩	🟩	🟩
ACE Basin, SC	—	🟥	🟥	🟥	🟥	🟥	🟥
Jacksonville, FL	—	🟥	🟥	🟥	🟥	🟥	🟥
Apalachicola, FL	4°C	🟥	🟥	🟩	🟥	🟥	🟥
Pontchartrain Basin, LA	2.5°C	🟥	🟩	🟩	🟩	🟩	🟥

Barataria Bay, LA	—	🟥	🟥	🟥	🟥	🟥	🟥
Vermilion Bay, LA	3.5°C	🟥	🟥	🟩	🟥	🟥	🟥
Calcasieu Lake, LA	—	🟥	🟥	🟥	🟥	🟥	🟥
Aransas, TX	2°C	🟥	🟩	🟩	🟩	🟩	🟩

Figure Captions

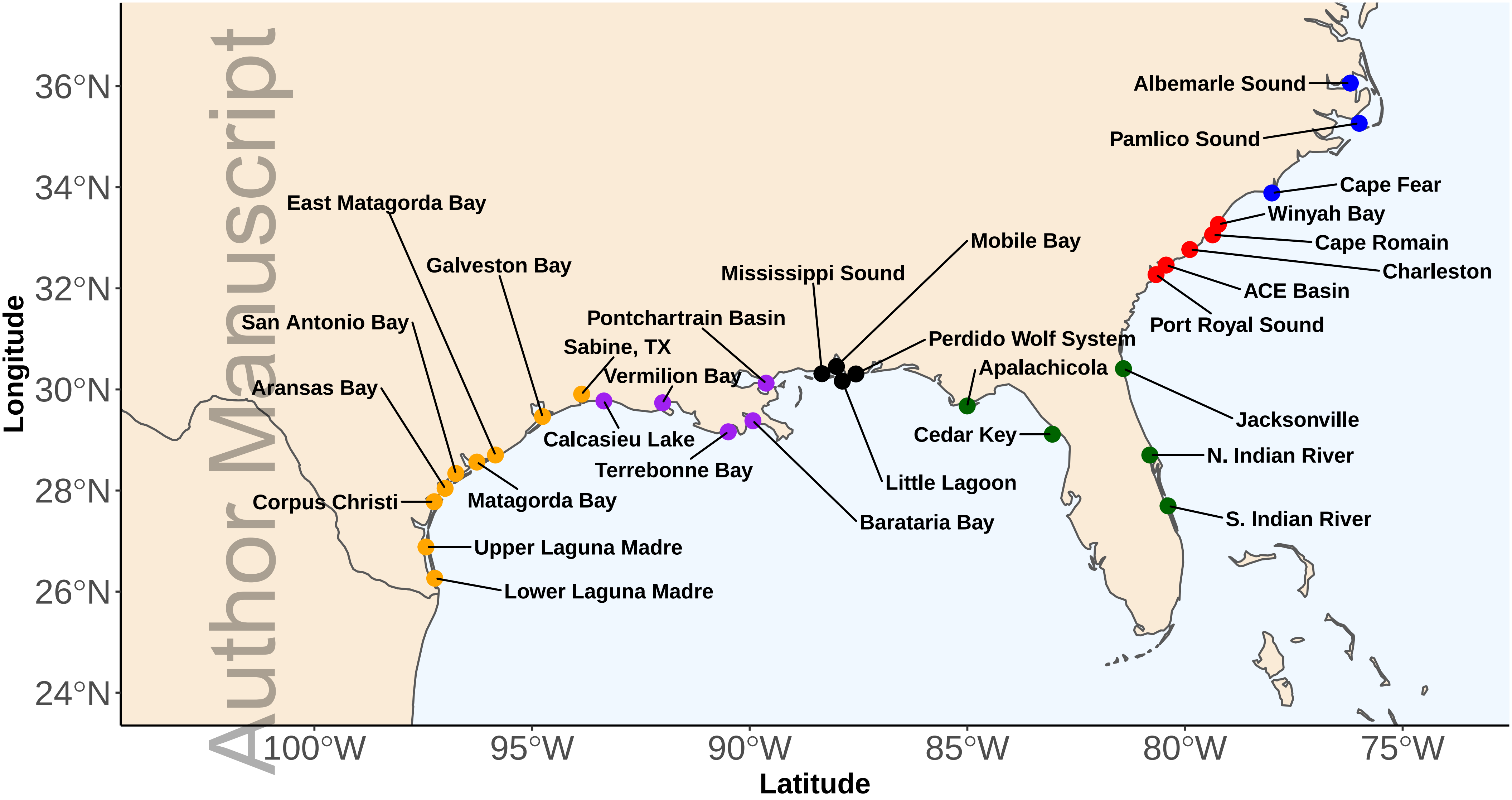
Figure 1. Map of estuaries in the Gulf of Mexico and US Southeastern Atlantic with age-0 southern flounder data used in this study. There are *N* = 31 total estuaries, *n* = 11 in the Atlantic and *n* = 20 in the Gulf of Mexico. Dots are colored according to their respective states, placed on the estuaries, and labeled by the connecting lines. Please note that the dot sizes are uniform and not related to the size of the estuary.

Figure 2. Generalized Additive Models (GAMs) of fishery-independent, age-0 southern flounder CPUE for 20 estuaries in the Gulf of Mexico (TX–Orange, LA–Purple, AL–Black, and FL–Green). All models were fit using a negative binomial distribution and restricted maximum likelihood to select the number of knots. Red shading highlights the last five years of data.

Figure 3. Generalized Additive Models (GAM) of fishery-independent age-0 CPUE of southern flounder for 11 estuaries in the US Southeastern Atlantic (FL–Green, SC–Red, NC–Blue). All models were fit using a negative binomial distribution and restricted maximum likelihood to select the number of knots. Red shading highlights the last five years of data. Note that Figure 2 uses standardized axes, whereas both the years of sampling and CPUE were much more variable in the Atlantic estuaries, necessitating estuary-specific axes.

Figure 4. Correlation plot showing the Pearson product-moment correlation between annual predicted values of southern flounder CPUE for pairs of estuaries. The upper triangle is the correlations over the entire range of data and the lower triangle is the correlations from the last five years. Larger, darker circles indicate stronger correlations and smaller, lighter circles indicate weaker correlations. Blue circles are positive correlations, while red circles are negative correlations. Empty boxes are correlations close to zero and the diagonal has also been left blank to better define the difference between halves. States start with Lower Laguna Madre, TX as TX1 and move eastward, then north on the Atlantic Coast to Albemarle Sound, NC as NC3 (the sequence of estuary codes follows the sequence of estuary labels in Figure 1).

Figure 5. Linear models of development window length over time for seven estuaries with significant negative relationships. Each colored line represents the model's best fit and the corresponding shaded area is the 95% confidence interval (note that colors match states in Figure 1). Each pink strata in the background represents 30 days (i.e., one month), and are included to aid in interpretation such that the best fit line passing through one pink strata estimates a development window that has been shortened by one month.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Pamlico Sound
Cape Fear
Winyah Bay
Cape Romain
Charleston
ACE Basin
Port Royal Sound
Mobile Bay
Mississippi Sound
Perdido Wolf System
Apalachicola
Jacksonville
Cedar Key
N. Indian River
S. Indian River
Little Lagoon
Barataria Bay
Pontchartrain Basin
Vermilion Bay
Sabine, TX
Calcasieu Lake
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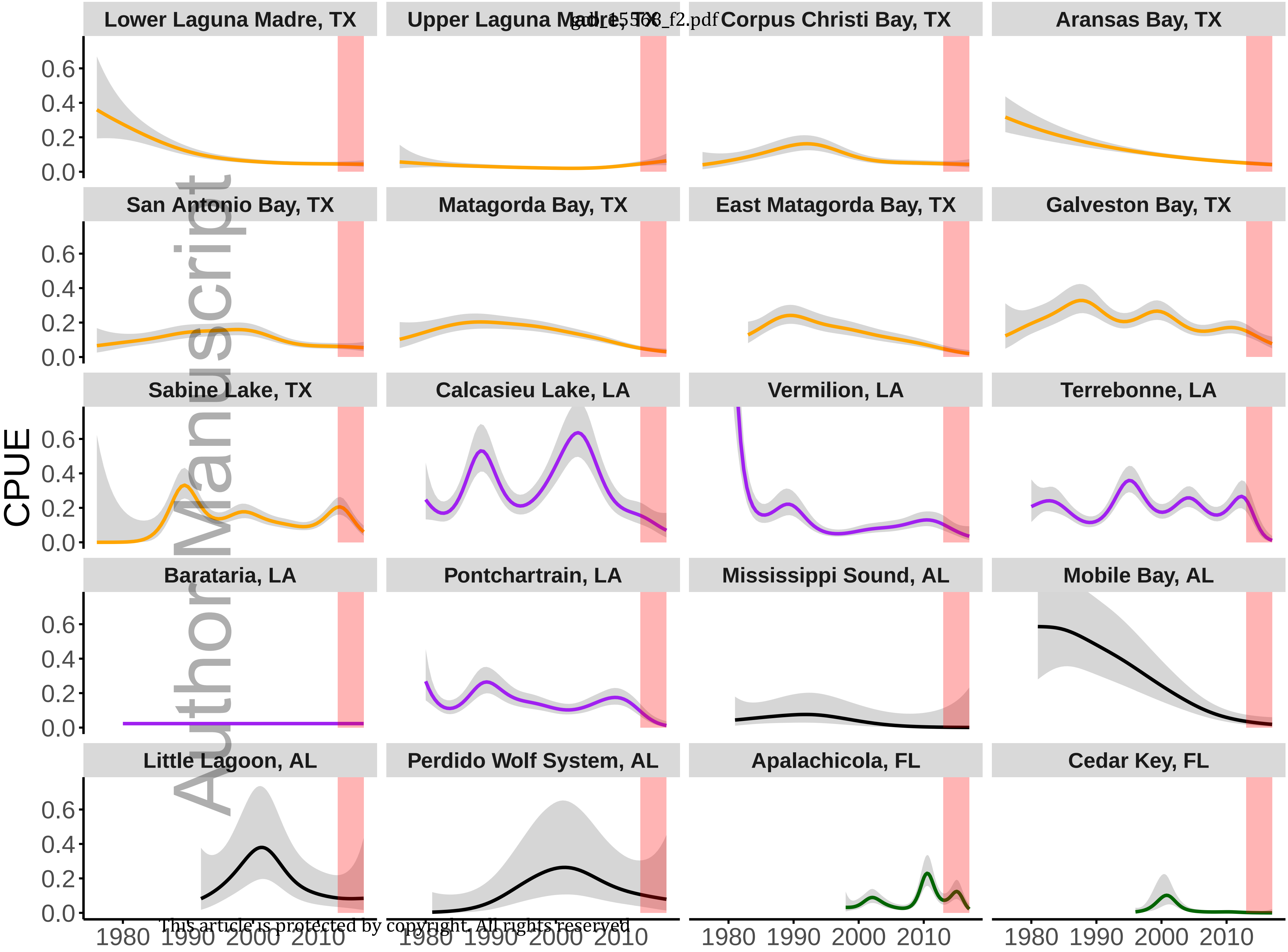
San Antonio Bay
Aransas Bay
Corpus Christi
Matagorda Bay
Upper Laguna Madre
Lower Laguna Madre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Matagorda Bay, TX
East Matagorda Bay, TX
Galveston Bay, TX
Sabine Lake, TX
Calcasieu Lake, LA
Vermilion, LA
Terrebonne, LA
Barataria, LA
Pontchartrain, LA
Mississippi Sound, AL
Mobile Bay, AL
Little Lagoon, AL
Perdido Wolf System, AL
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Cedar Key, FL
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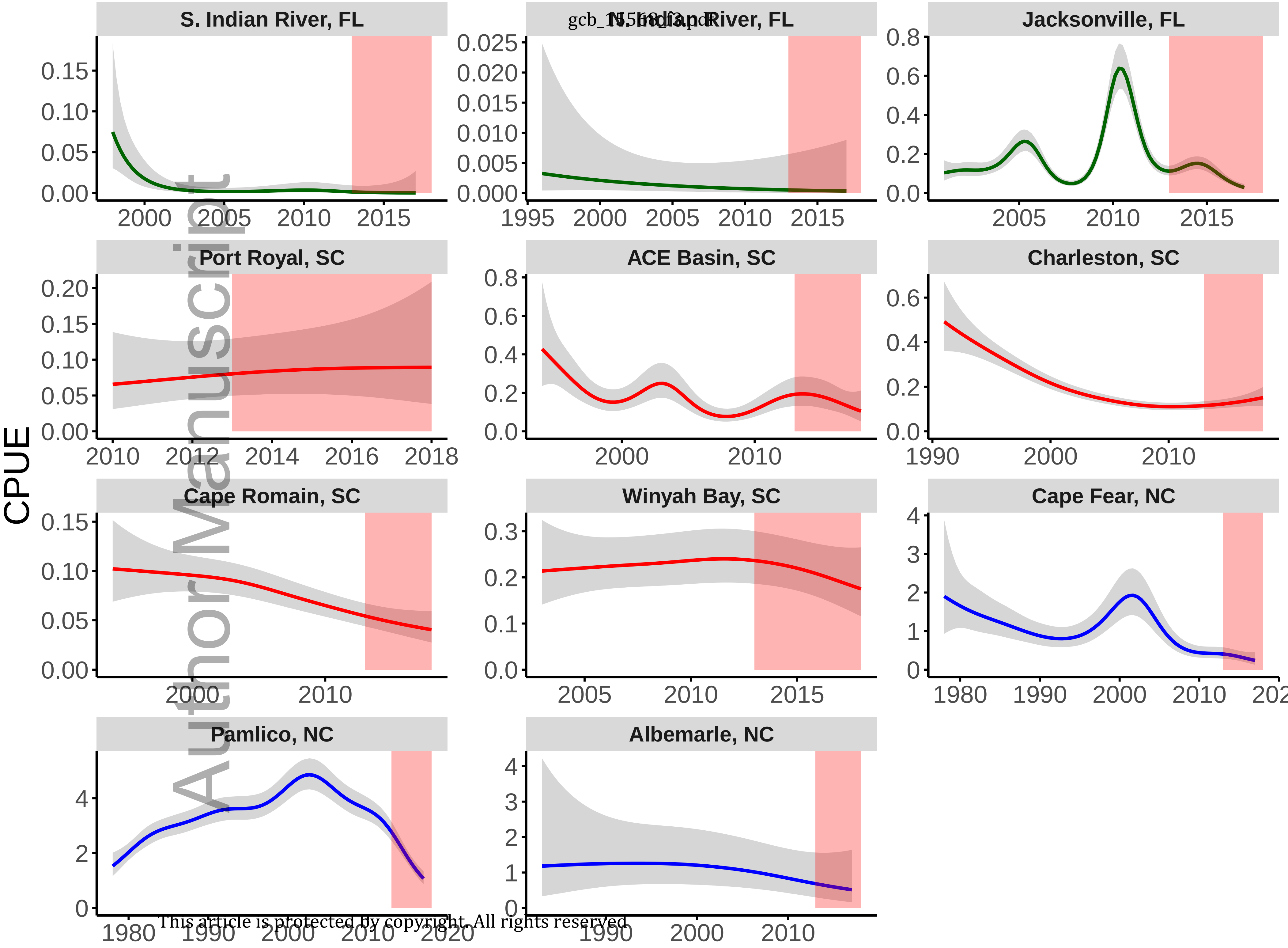
CPUE
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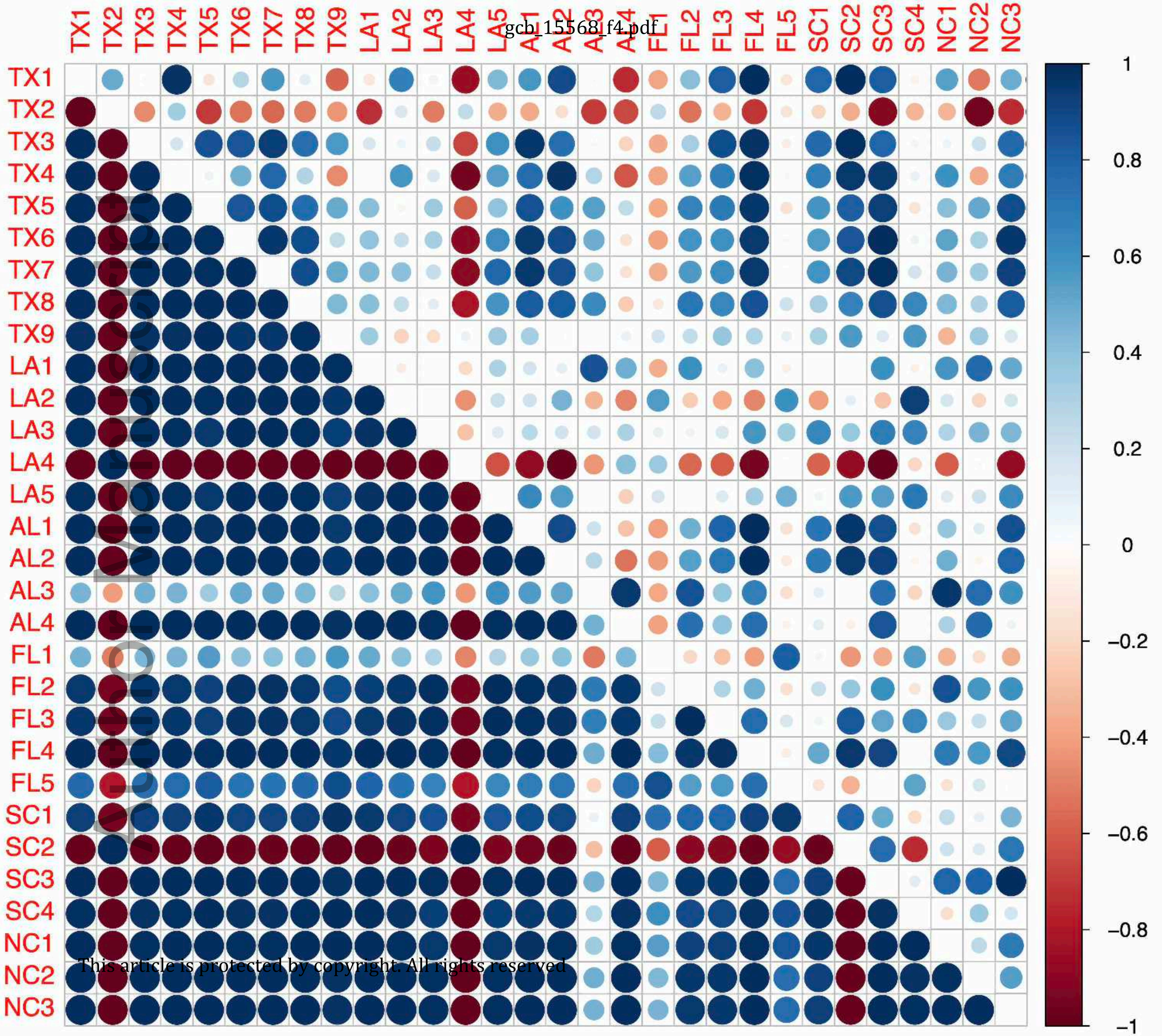
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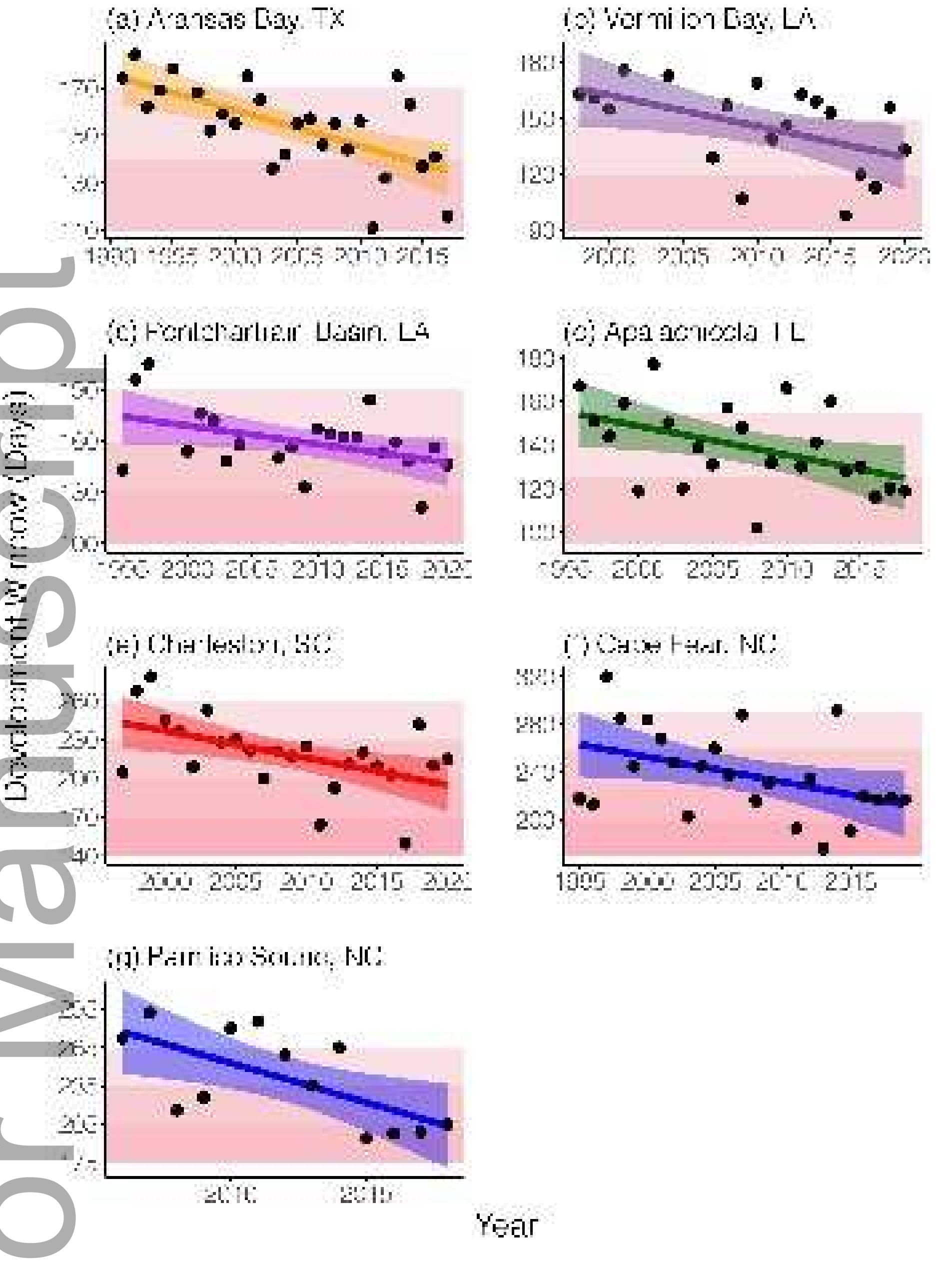

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