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Environmental Drivers of Southern Flounder (Paralichthys lethostigma) Growth, Condition, and Juvenile Recruitment Along the Northern Gulf of Mexico

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ENVIRONMENTAL DRIVERS OF SOUTHERN FLOUNDER (*PARALICHTHYS LETHOSTIGMA*) GROWTH, CONDITION, AND JUVENILE RECRUITMENT ALONG THE NORTHERN GULF OF MEXICO

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by
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Accepted by:
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ABSTRACT

Southern Flounder (*Paralichthys lethostigma*) is an economically important species that uses habitats across salinity gradients along the Atlantic Ocean and Gulf of Mexico. During winter, adults spawn offshore, and larvae migrate to estuaries. During spring, larvae settle, grow, and metamorphose into juveniles. Juveniles and adults continue to use estuaries until adults mature and migrate offshore to spawn. This presumed, migratory life history indicates that Southern Flounder is an estuarine-dependent species. As with many estuarine-dependent species, growth, condition, and juvenile recruitment are highly variable across time and space. In response to declines across the species range, state managers have imposed a series of increasingly stringent regulations on Southern Flounder fisheries. However, recent stock assessments show no signs of recovery thus far, suggesting that factors other than fishing mortlity, such as environmental conditions and habitat-use patterns, may be contributing to the decline. My objectives were to 1) develop an index of juvenile Southern Flounder abundance to investigate relationships with environmental factors, and 2) use back-calculation and condition indices to investigate how observed patterns in growth and condition relate to habitat-use patterns.

We developed an index of juvenile Southern Flounder abundance in Mobile Bay (1981 – 2018) and Perdido Bay (1988 – 2018) using historical Alabama survey data. Generalized additive models tested mechanistic hypotheses by relating environmental variables to juvenile abundance for short- and long-term analyses in Mobile and Perdido Bays. Models that included winter covariates were selected as best for all three analyses, suggesting that environmental conditions during spawning and larval stages explain the most variation in year-class strength. Specifically, westerly winds, river discharge, and intermediate winter durations were positively correlated with juvenile abundance, and recent suboptimal conditions helped to explain dramatic declines in juvenile recruitment.

We used 313 otoliths from Southern Flounder collected in Alabama’s coastal waters in 2004 – 2007 and 2018 – 2019 to investigate how age-specific contingent types impacted age-specific back-calculated growth rates and condition. We used linear mixed effects models with various random effect structures to account for age, growth, year, and individual effects. Age-0 and first-year estuarine and transient contingents had higher growth rates than freshwater contingents, but there was no difference in growth among contingents during the second year of life. Age-0 and age-1 estuarine and transient contingents had higher condition than freshwater contingents, but there was no difference in condition for age-2 Southern Flounder.

Over the next century, the Gulf of Mexico is expected to see increased drought conditions, more intense storms, and warmer winter temperatures. This could impact the amount of river discharge that enters the estuary, thus impacting growth rates and overall abundance of young Southern Flounder. Warmer winters could interfere with reproductive success and the number of recruits surviving to the juvenile stage. As recruitment dynamics strongly influence adult abundance, our results should help inform expectations for Alabama’s Southern Flounder fishery in response to changing environmental conditions. Growth and condition are products of good estuarine habitat, and our results could assist in identifying high-quality estuarine habitats that could be used for recently developed stocking programs and continued habitat restoration efforts in Alabama.

DEDICATION

To my parents, Michael and Mary Angelina, for giving me the means to "let my dream lead me on a journey to discover who I'm meant to be." I would not be here without your unending love and support. Thank you for raising me by the sea with a sense of curiosity and adventure, and always encouraging me to leave the world a little better than I found it. I promise to keep "going the distance," and know that no matter what "you'll be here in my heart, always."

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CHAPTER ONE

WINTER CONDITIONS SHAPE SOUTHERN FLOUNDER (*PARALICHTHYS LETHOSTIGMA*) JUVENILE RECRUITMENT ALONG THE NORTHERN GULF OF MEXICO

1. Introduction

Biological recruitment of marine fishes occurs when offspring survive through early life stages, which have high and variable mortality, to a given size or age when mortality declines and stabilizes at a constant rate (Miller et al. 1991, Bradford & Cabana 1997, Van der Veer et al. 2000). At this point during early life, the abundance of a cohort represents the annual level of recruitment to the population, which is also referred to as year-class strength (Bradford & Cabana 1997). It has been well established that annual variations in recruitment will fluctuate by orders of magnitude for most marine fishes (Pope & Macer 1996, Houde 2008, Houde 2009). This extreme annual variability in recruitment results from large numbers of eggs being produced each year by highly fecund females and high mortality during early life due to starvation, predation, or natural causes (Cushing 1975, Rijnsdorp et al. 1995, Van der Veer et al. 2000, Houde 2008). Given the importance of recruitment in forecasting future population sizes, much effort has been devoted to investigating biological and environmental variables affecting recruitment dynamics (Hjort 1914, Houde 2008). However, successfully predicting annual fluctuations in recruitment remains an elusive goal, especially as the climate continues to change (Bakun 1985, Houde 2008, Houde 2009). Nevertheless, continued research that investigates the causes of recruitment variability is needed to inform sound management (Subbey et al. 2014). This requires retrospective analyses of long-term juvenile surveys, which can assist fisheries ecologists and managers in understanding the impacts of physical and biological factors affecting survival during early life stages (Houde 2008).

Flatfish, like many other marine fishes, have the potential for high recruitment variability because of their migratory life history across marine and estuarine ecosystems, where larvae and juveniles encounter a diverse suite of predators, prey, and abiotic factors in many different habitats throughout early life (Miller et al. 1991). Generally, for flatfish, the importance of density-independent and -dependent factors differs with each stage during early life. Density-independent factors, such as wind, salinity, and temperature, can affect recruitment by altering the connectivity between offshore spawning grounds and estuarine nurseries, and are thought to play an important role in determining flatfish survival rates during the pelagic larval stage (Rijnsdorp et al. 1995, Cowen & Sponaugle 2009, Amorim et al. 2016, Coogan et al. 2019). Conversely, survival during the demersal juvenile phase is thought to depend on density-dependent factors, such as competition for optimal habitat and prey resources (Gibson 1994, Rijnsdorp et al. 1995). Density-independent abiotic factors likely generate recruitment variability during the egg and larval stages, while density-dependent biotic factors likely dampen recruitment variability during the juvenile stage (Van der Veer 1986, Miller et al. 1991). Factors that generate variability are known as controlling factors, while those that dampen variability are known as regulating factors (Miller et al. 1991, Van der Veer et al. 1994, 2000, Houde 2008). Year-class strength, therefore, is likely determined before the juvenile stage for flatfish when controlling factors act on eggs and larvae (Van der Veer 1986, Miller et al. 1991, Van der Veer et al. 2000).

Southern Flounder (*Paralichthys lethostigma*) is an economically important species that use a variety of habitats across salinity gradients in and along the Atlantic Ocean and Gulf of Mexico. The species is distributed from North Carolina to Texas, but is absent from waters off the southern tip of Florida (GSMFC 2015). The presumed life history for Southern Flounder includes offshore spawning as adults and migrating to estuarine nurseries as larvae where they will settle, grow, and metamorphose into juveniles before moving offshore as adults and beginning the process again (Burke et al. 1991, Fischer & Thompson 2004). This presumed life history indicates Southern Flounder is a marine estuarine dependent species (Elliott et al. 2007).

Over the past several decades, recreational and commercial fishery landings and the adult abundance of Southern Flounder have declined across the species' range for unknown reasons (Froeschke et al. 2011, Chagaris et al. 2012, GSMFC 2015, Flowers et al. 2019). In response, many state agencies tasked with the management of Southern Flounder have increased the minimum harvestable size, restricted gear types, decreased bag limits, and implemented full or partial season closures. Despite these changes in regulations, angler landings and fishery independent monitoring have shown few signs of recovery and some areas along the Gulf and Atlantic Coasts are seeing further declines (GSMFC 2015, Flowers et al. 2019). This suggests that other factors besides exploitation may be playing a role in determining Southern Flounder year-class strength, and the roles of environmental drivers should be investigated.

Several previous studies have found strong correlations between offshore wind and juvenile flatfish abundance (e.g. Nielsen et al. 1998, Taylor et al. 2010, Wilderbuer et al. 2013), and Werner et al. (1997) attributed it to possibly being the most studied abiotic factor affecting year-class strength of marine fishes. The hypothesized mechanism underlying these relationships is that wind-driven currents and circulation patterns influence the transport and feeding abilities of larval Southern Flounder. Therefore, wind blowing at the right time and direction may act as a controlling factor by positively affecting the number of larvae reaching coastal estuarine nursery habitats and surviving to the juvenile stage.

River discharge could also act as a controlling factor for Southern Flounder in the northern Gulf of Mexico. Freshwater inflow into estuaries can potentially generate recruitment variability in several ways. Specifically, river discharge may advance larval ingress into estuaries by causing the stratification of the water column, which can result in bottom currents flowing upstream (Hare et al. 2005, Schieler et al. 2014). This could promote Southern Flounder larval transport into estuaries via selective tidal stream transport (i.e., using bottom currents and ebb tides), which may be enhanced during periods of high flow (Weinstein 1980, Boehlert & Mundy 1988, Burke et al. 1998, Jager 1999, Taylor et al. 2010). Additionally, river discharge effects on estuarine salinities can impact the development and survival of Southern Flounder larvae and juveniles. While larvae have a zero tolerance of freshwater, juveniles and adults appear to use a variety of habitats across salinity gradients, from tidal freshwater to polyhaline habitats (Smith et al. 1999a, Lowe et al. 2011, Farmer et al. 2013, Nims & Walther 2014). Although they have a wide tolerance, the optimal salinities for juvenile Southern Flounder specific growth rates was found to be between 10 and 30‰ during a controlled laboratory experiment, and growth can subsequently influence the survival of juveniles (e.g., size-dependent predation and greater ability to escape; Howson & Targett 2020). Elevated river discharge during spring could also increase productivity in estuarine nursery habitats through subsidies of terrestrial nutrients (Cloern et al. 2001, Connolly et al. 2009), which could positively affect growth and survival of juveniles.

Environmental temperature may act as a controlling factor on Southern Flounder recruitment by regulating the timing and duration of spawning events, hatching success, and overall growth potential during early life stages. Offshore migrations of reproductively mature Southern Flounder begins in response to a 4 – 5 °C drop in water temperature during the late fall months in the Gulf of Mexico (Reagan & Wingo 1985), and a prolonged period of batch spawning occurs in the Atlantic Ocean and Gulf of Mexico occurs during winter months when the temperature is between 14 and 18 °C (Miller et al. 1991, Smith et al. 1999b, Van Maaren & Daniels 2001, Watanabe et al. 2006). The thermal conditions at which spawning and hatching occur could impact juvenile abundance by influencing the length of the spawning window, hatching success and timing, and ultimately, larval growth rates (GSMFC 2015). In a laboratory experiment, fertilized Southern Flounder eggs, acclimated to temperatures of 13, 17, 21 and 25 °C, had highest hatching success and fastest larval growth at 17 °C (Van Maaren & Daniels 2001). Both hatching success and larval growth rates decreased with increasing temperature (Van Maaren & Daniels 2001), indicating that optimal conditions for hatching and larval growth occurred at temperatures below 18 °C. Thus, a longer period of cold temperatures during winter may lead to a longer window of optimal thermal conditions for spawning and larval growth, increasing the probability of Southern Flounder larvae surviving to the juvenile stage (Cushing 1990, Mertz & Myers 1994).

Environmental temperatures could also impact recruitment during the juvenile stage. After larval Southern Flounder ingress into estuaries and settle to benthic habitats, they will rapidly grow as juveniles during the spring months. There is a positive correlation between water temperature and metabolic processes during the juvenile stage, which increases growth while reducing stage duration (O'Connor et al. 2007, Del Toro-Silva et al. 2008). Howson & Targett (2020) found the highest specific growth rates of juvenile Southern Flounder occurred at 25 – 26 °C, suggesting that warmer temperatures would be optimal for high growth rates, which would contribute to the likelihood of juvenile survival.

The potential roles of wind, river discharge and seasonal temperature patterns as controlling factors in driving interannual variability of juvenile abundance, and possibly, declines in adult Southern Flounder abundance has not yet been investigated in the northeastern Gulf of Mexico. This work aimed to develop a historical index of juvenile abundance (to serve as an index of year-class strength) and investigate relationships between juvenile Southern Flounder abundance and controlling environmental factors. Specifically, we hypothesized that:

H1. Increased southerly winter winds will have a positive effect on juvenile abundance by promoting the transport of eggs and larvae toward estuarine nursery habitats. Conversely, increased northerly winter winds will have a negative effect on juvenile abundance by causing a divergence from estuarine refuges.

H2. Increased easterly and westerly winter winds will have a positive effect on juvenile abundance by promoting along-shore transport and upwelling events.

H3. Elevated river discharge during winter and spring will have a positive impact on juvenile abundance by facilitating selective tidal stream transport into estuaries, creating optimal salinities for growth, and enhancing estuarine productivity.

H4. Longer, colder winters will result in increased juvenile abundance by lengthening the spawning window and duration of optimal thermal conditions for hatching and larval growth.

H5. Warmer spring conditions (indexed as growing degree-days) will lead to increased juvenile abundance due to positive effects on juvenile growth rates.

Our study used catches of juvenile (age-0) flounder during May and June, and quantified biological recruitment (juvenile abundance during the first spring of life) as opposed to fishery recruitment, which refers to individuals surviving to the size at which they are able to be harvested (Van der Veer et al. 2000, Midway & Scharf 2012). The primary objective of this work was to test the above hypotheses using generalized additive models (GAMs) to quantify the strength and direction of relationships between key environmental variables and our index of recruitment within two estuaries along the northeastern Gulf of Mexico. With improved understanding of these relationships, fisheries managers will be able to better anticipate the impact that large-scale environmental drivers can have on Southern Flounder year-class strength and subsequent population dynamics.

2. Methods

2.1 Study area

Mobile Bay and Perdido Bay are neighboring estuaries along the northeastern Gulf of Mexico and have historically supported large harvests of Southern Flounder (GSMFC 2015, Figure 1). Mobile Bay is located in Alabama, and Perdido Bay is located in Alabama and Florida. Due to their shallow depths, Mobile Bay and Perdido Bay, like many coastal estuaries, are highly influenced by wind, freshwater discharge, and ambient air temperature, all of which could influence the quality of Southern Flounder habitats in these systems.

Mobile Bay has the fourth largest river system in the United States, and receives the sixth largest volume of freshwater discharge in North America (mean daily discharge rate: 1850 m^3/s; Morisawa 1968, Park et al. 2007). This large amount of freshwater input promotes a distinct salinity gradient, and influences salinities in the lower estuary during the high discharge period in winter and spring. There is also a distinct temperature gradient during early spring with waters in upper Mobile Bay being cooler than waters in lower Mobile Bay. During the summer and fall when the freshwater input is considerably lower, the Gulf of Mexico has a greater influence on the estuary's thermohaline dynamics and stratification occurs with large vertical and horizontal ranges of salinities and temperatures in Mobile Bay (Coogan et al. 2019). Perdido Bay can be broken into two salinity zones known as upper and lower Perdido Bay. Upper Perdido Bay is influenced by tidal forcing and freshwater inflow from the Perdido and Styx Rivers (mean daily discharge rate: 56 m^3/s, Schropp et al. 1991, Grubbs & Pittman 1997, Xia et al. 2011). Lower Perdido Bay is influenced by tidal forcing, exhibits a vertical salinity gradient, and can have salinities greater than 30 ppt (Xia et al. 2011).

2.2 Index of juvenile abundance

An index of juvenile (age-0) Southern Flounder abundance was developed from a historical survey conducted monthly by the Alabama Department of Conservation and Natural Resources, Marine Resources Division (ADCNR/MRD) from 1981 – 2018, as part of the Fisheries Assessment and Monitoring Program (FAMP). This survey used 4.88 m bottom trawls with 30.48 m of towline (more towline was used if the depth was greater than 9.14 m) to target benthic fishes, including juvenile and adult Southern Flounder, across Alabama coastal and estuarine waters (Figure 1). The trawls were pulled for 10 minutes at 2 – 2.5 knots with 0.36 m head rope. The bottom trawl consisted of a two-seam net with the innermost one having a 4.76 mm mesh. When flounder were caught, they were placed in ziploc bags that were put on ice and later frozen. In the laboratory, Southern Flounder were thawed, measured to the nearest millimeter standard length, and weighed to the nearest gram.

We examined the average monthly catch per unit effort (CPUE) of Southern Flounder across years to determine the most suitable time period to index juvenile Southern Flounder abundance in Mobile Bay (1981 – 2018) and Perdido Bay (1988 – 2018). Average monthly CPUE was consistently highest during May and June, and the index was limited to these months. We believe this May – June time period allows for juvenile recruits (likely spawned in offshore waters form December to February; Glass et al. 2008) to migrate to estuaries where they will settle, metamorphose, and grow in areas sampled by the FAMP program. This time period is likely prior to any movement toward deeper or offshore habitats (not effectively sampled by the FAMP program) later in the growing season (Stokes 1977).

Since Southern Flounder otoliths were not collected and ages were not assigned during the FAMP survey, we used otoliths and associated lengths from Auburn University's and ADCNR/MRD's historical collections from May and June 2004 – 2010 ($N = 132$) to develop a length cutoff for age-0 juvenile Southern Flounder in the FAMP dataset. Two independent readers estimated age by counting the annuli on each otolith. If disagreement occurred, a third reader aged the otolith at question. The total lengths of age-0 Southern Flounder (no annuli present on the otolith) collected in Alabama during May and June ranged from 52 – 224 mm, while total lengths of age-1 Southern Flounder (one annulus present on the otolith) ranged from 157 – 404 mm. We established a length cutoff of 165 mm for age-0 Southern Flounder collected during May and June. Only 2 of the 67 age-0 Southern Flounder had lengths greater than 165 mm, and only 2 of the 65 age-1 Southern Flounder had lengths less than 165 mm. Since the historical collections recoded total length only and the FAMP survey recorded standard length only, we used a total to standard length regression for Southern Flounder developed by Harrington et al. (1979) (TL = 8.959 + 1.175 SL), and found that the maximum standard length of juvenile Southern Flounder was equal to 132.8 millimeters. Annual collections of flounder were summed together for each station. There was typically one 10-minute trawl per month at each station, but in rare cases, this ranged from 0 – 4 10-minute trawls in the entire May – June period at some individual stations (Mobile Bay: 93.3 % of stations in 1981 – 2018 were sampled once per month in May and June; Perdido Bay: 89.9 % of stations in 1988 – 2018 were sampled once per month in May and June).

We only included stations that were sampled consistently across years in each estuary (surveyed in ≥ 90 % of years) in the analyses. To visually inspect trends in our index of juvenile abundance, catch values were averaged across stations within years (Mobile Bay: 1981 – 2018; Perdido Bay 1988 – 2018). In our statistical analysis using generalized additive models (see section 2.4 below), the annual cumulative catch at each station was the response variable, and the number of trawls at each station in each year was used an offset variable to account for variability in sampling Seffort.

2.3 Environmental covariates

We summarized environmental data for wind speed and direction, river discharge, winter duration, and growing degree-days to test specific hypotheses regarding the mechanisms affecting Southern Flounder recruitment. All environmental variables were mean-centered and scaled (by dividing the centered values by their standard deviations) to standardize each environmental variable and assist with model fitting. Prior to model fitting, we checked to ensure multicollinearity was not present among the environmental covariates (according to Spearman's correlation coefficient, *r* < 0.7)

2.3.1 Wind

Wind speed and direction (recorded every ten minutes) were acquired from the National Data Buoy Center (NDBC) from a buoy off the coast of Dauphin Island (DPIA1; Latitude/Longitude: 30.250° N -88.075° W). The average wind speed and direction were determined for each day. Wind direction was classified as northerly (NW-N: 0 – 45°; N-NE: 316 – 359°), easterly (NE-SE: 46 – 135°), southerly (SE-SW: 136 – 225°), and westerly (SW-NW: 226 – 315°) according to prevailing wind direction. Wind speed (m/s) and direction were summarized across all available years (1993, 1998 – 2001, 2003 – 2018) during winter months (December – February) when larval Southern Flounder are likely in their pelagic stage and susceptible to offshore wind-driven currents. The cumulative wind speeds for each prevailing wind direction were used as individual covariates in our models.

2.3.2 River discharge

We quantified river discharge to serve as an index of estuarine salinity conditions during the larval and juvenile phases, and to investigate its effects on counter-gradient transport of Southern Flounder via bottom waters. Monthly average freshwater discharge values were acquired for the Alabama and Tombigbee Rivers from the United States Geological Survey (USGS) at gauges 02428400 (Latitude/Longitude: 31.615°, -87.551°) and 02469761 (Latitude/Longitude: 31.758°, -88.129°), respectively. These values (m^3/s) were summed since the confluence of these two rivers occurs upstream of Mobile Bay.

For Perdido Bay, we acquired monthly average freshwater discharge values for the Perdido (USGS Gauge 02376500; Latitude/Longitude: 30.690°, -87.440°) and Styx (USGS Gauge 02377570; Latitude/Longitude: 30.606°, -87.547°) Rivers, which were summed together to represent the freshwater input in Perdido Bay. Monthly river discharge values for both Mobile Bay (1981 – 2018) and Perdido Bay (1988 – 2018) were summed for each trimonthly period (December – February and March – May) to minimize the number of explanatory variables (Taylor et al. 2010), and provide representative indices of river discharge as a controlling factor during the larval (December – February) and juvenile (March – May) stages.

2.3.3 Winter duration

Winter duration was defined as the number of days each year that had a mean daily offshore surface water temperature of 18 °C or less. Hernandez et al. (2010) defined the winter season in the northern Gulf of Mexico as anything below 18 °C based on historic water temperature data from a single station located 18 km south of Dauphin Island, Alabama. Water temperature data from 2012 – 2016 were acquired from the NDBC's Orange Beach Buoy (42012; Latitude/longitude: 30.064°, -87.551°). We used mean daily air temperature data collected from NOAA's National Centers for Environmental Information (NCEI) Dauphin Island Number 2, (GHCND: USC00012172; Latitude/Longitude: 30.2505°, -88.0775°), AL, US station to predict the winter durations for years that water temperature data were unavailable (1981 – 2011, 2017, 2018). To accomplish this, we developed an index of winter duration (number of days with a mean daily temperature ≤ 18 °C) for both the buoy and land-based station for

2012 – 2016. Given there was a positive, linear relationship between these two indices (*p* = 0.004, $R^2 = 0.95$), we used the land-based winter duration index to predict the buoy winter duration index for all missing years from 1981 – 2018.

2.3.4 Growing degree-days

Growing degree-days, a method to quantify cumulative thermal conditions, were used as a metric of growth potential for juvenile Southern Flounder in Mobile Bay during each spring (March – June). Growing degree-days were calculated as:

$$GDD = \Sigma (T_{avg} - T_0)$$

where T_{avg} is the average daily temperature and T_0 is the temperature threshold at which growth is nonlinear or equal to zero. These non-negative values were then summed for each year. Although it is unknown what temperatures would cause Southern Flounder growth rates to equal zero, Malloy and Targett (1991) found that Summer Flounder growth rates were equal to zero when temperatures were between 2 and 10 °C in a laboratory study. Chezik et al. (2014) recommended standardized T_0 values of 0, 5, 10 and 15 °C for both freshwater and marine fishes. In this study, T_0 was set to 15 °C. We attained mean daily estuarine water temperature data for March – June from stations at Meaher State Park, Alabama (located in northern Mobile Bay) and Dauphin Island, Alabama (located in southern Mobile Bay), and averaged these values together. This data was available from 2003 – 2018 through Alabama's Real-Time Coastal Observing System (ARCOS; mymobilebay.com).

2.4 Statistical analysis

We used GAMs in package mgcv in R to investigate how these environmental covariates impacted our index of juvenile Southern Flounder abundance from 18 stations in Mobile Bay and 5 stations in Perdido Bay. GAMs are a flexible class of models that use smoothing functions to estimate potential nonlinear relationships between continuous covariates and the response variable (Wood 2017, Pedersen et al. 2019). Such flexible models have proven useful in previous investigations of environmental influences on fish recruitment dynamics (Cardinale & Arrhenius 2000, Stoner et al. 2001, Taylor et al. 2010, Maynou et al. 2014). Due to limited time series of certain environmental variables, we conducted both a short-term (16-year) and long-term (38-year) analysis for Mobile Bay and a single long-term (31-year) analysis for Perdido Bay. The long-term analyses lacked environmental data for winter winds and spring estuarine growing degree-days. The short-term analysis for Mobile Bay included ten models. Eight models comprised of only individual covariates for four directional winter wind variables, winter river discharge, spring river discharge, and spring estuarine growing degree-days. We also tested two combined models, a ‘winter model’ and a ‘spring model,’ that included each of the individual covariates listed above for each season. The ‘winter model’ included all environmental factors during winter, while the ‘spring model’ included all environmental factors during spring. The long-term analyses for Mobile Bay and Perdido Bay included four models: three single-covariate models for winter river discharge, spring river discharge, and winter duration, as well as a combined ‘winter model’ that included winter river discharge and winter duration. Each model that was tested represented a clear hypothesis, previously described.

The time-series of juvenile Southern Flounder data from the FAMP survey contained many zero catches, which caused the data to be overdispersed. Therefore, a negative binomial distribution with a log-link function was used to fit all models. We used thin plate regression splines, which assumed the amount of smoothing in all covariates was the same, and choosing the number of knots was unwarranted (Wood 2017, Pedersen et al. 2019). Station was used as a random effect to account for the lack of independence among observations collected at the same station across years, and it was also used as a smoother in this analysis (Pedersen et al. 2019). Since the number of 10-minute trawls varied at each station per year, the log of effort (in minutes) was included as an offset variable. The best model was selected according to the least value of marginal likelihood. This method was preferred over generalized cross validation (GCV) and Akaike's information criterion (AIC) because there is a greater resistance to overfitting, which leads to less smoothing parameter variability (Wood 2011, Pedersen et al. 2019). We examined partial residuals (the sums of smoothed covariate estimates within the best model and the residuals of the complete best model; Wood 2017) to quantify the direction and magnitude of environment-recruitment relationships. To understand how changes in environmental conditions may be affecting temporal trends in recruitment, we summarized temporal changes in these partial residuals.

3. Results

3.1 Index of juvenile abundance

The index of juvenile abundance in Mobile Bay indicated fluctuating abundance and an overall decline in juvenile Southern Flounder abundance from 1981 – 2018, especially in recent years (Figure 2). Juveniles were collected at upstream and downstream stations in May and June over these 38 years in Mobile Bay (Figure 1). Across all years, the coefficient of variance was 164.42 %, and the mean number of flounder per trawl across years was 0.21. The index of juvenile abundance in Perdido Bay showed high interannual variability from 1988 – 2018 with a decline in recent years, but abundance peaked in 2015 (Figure 2). The coefficient of variance was 160.31 % across all years, and the mean number of flounder per trawl across years was 0.12. Most juvenile Southern Flounder were caught from the upper reaches of Perdido Bay in May and June over these 31 years (Figure 1). The mean cumulative flounder catch across stations in Mobile Bay was not strongly correlated with the mean cumulative flounder catch across stations in Perdido Bay during the 31 years of sampling in which both bays were sampled (1988 – 2018; $r = 0.28$).

3.2 Environmental covariates

Time series of environmental covariates were highly variable and no temporal trends in wind, river discharge, winter duration, and estuarine water temperature were detected (all $r < 0.35$, Figure 3). Environmental variables were also not strongly correlated with one another (all $r < 0.57$) in any of the long-term or short-term times-series analyses. The complete set of eight environmental covariates was maintained in the short-term analysis for Mobile Bay, and winter river discharge, spring river discharge, and winter duration were maintained in the long-term analyses for Mobile Bay and Perdido Bay.

3.3 Sixteen-year Mobile Bay analysis

The winter model was selected as the best model to explain Southern Flounder abundance in Mobile Bay from 2003 – 2018, and the deviance explained by this model was 70.2 % (Table 1). Of the six variables included in the winter model, only river discharge (*p* = 0.026) and prevailing westerly winds (*p* < 0.001) were significant predictors of annual recruitment. Winter river discharge had a nonlinear, parabolic relationship with Southern Flounder juvenile abundance, where juvenile abundance was highest in years of intermediate winter river discharge and lower in years of very low or very high winter river discharge (Figure 4). Westerly winds were positively correlated with Southern Flounder juvenile abundance (Figure 4).

The individual models that included growing degree-days or spring river discharge contained significant covariates within each respective model. Growing degree-days had a significant, negative effect on Southern Flounder juvenile abundance, and the deviance explained by this model was 54.8 % (*p* = 0.006; Table 1). The overall effect of spring river discharge on juvenile abundance was variable, and suggested that highest abundances would likely result from low and extremely high rates of river discharge (*p* = 0.003; Table 1). The deviance explained by the spring river discharge model was 66.4 % (Table 1). However, only growing degree-days was significant in the complete spring model that contained both of these spring covariates. Although these spring covariates were significant, the single-covariate models and complete spring model had higher marginal likelihood values and did not explain as much of the variability in juvenile abundance compared to the complete winter model.

3.4 Thirty-eight-year Mobile Bay analysis

The winter model was also selected as the best model for the long-term analysis of juvenile Southern Flounder abundance in Mobile Bay (1981 – 2018), and the deviance explained by this model was 56.8 % (Table 1). Both covariates included in this model, river discharge ($p < 0.001$) and winter duration ($p = 0.023$), were significant (Figure 5). River discharge had a positive effect on Southern Flounder juvenile abundance in Mobile Bay from 1981 – 2018 (Figure 5). Winter duration had a nonlinear, parabolic relationship with Southern Flounder juvenile abundance, where the shortest and longest winters correlated with low juvenile abundance, and intermediate winter durations were correlated with high abundance (Figure 5).

3.5 Thirty-one-year Perdido Bay analysis

The winter model was selected as best for the 31-year analysis of juvenile Southern Flounder abundance in Perdido Bay (1988 – 2018), and the deviance explained by this model was 37.6 % (Table 1). However, the covariates included in this model, river discharge ($p = 0.845$) and winter duration ($p = 0.306$), were not significant predictors of juvenile abundance in Perdido Bay.

4. Discussion

The declining trend we observed in our index of juvenile Southern Flounder abundance, in conjunction with reports of declining recruitment, adult abundance, and stock size along the Gulf and Atlantic coasts (Froeschke et al. 2011, Chagaris et al. 2012, GSMFC 2015, Powers et al. 2018, Flowers et al. 2019) suggest that Southern Flounder populations across the species' range may be declining due to low recruitment, especially in recent years. A recently completed stock assessment of Southern Flounder in Alabama examined residuals from a stock recruitment relationship, and found below-average recruitment since 2011 (Powers et al. 2018), supporting observed trends in our juvenile abundance index. Likewise, a recent stock assessment of Southern Flounder in the South Atlantic (North Carolina to Florida) indicated a long-term trend of declining recruitment from 13 million estimated recruits in 1989 to only 4 million in 2017 (Flowers et al. 2019). In all but two years since 2005, recruitment of Southern Flounder in the South Atlantic has been lower than expected based on a previously developed stock-recruit relationship (Flowers et al. 2019), suggesting suboptimal environmental conditions may be affecting recruitment across the species' range. Considering our findings and those of recent stock assessments, a more comprehensive analysis of Southern Flounder recruitment trends and key environmental conditions across the Atlantic and Gulf coasts seems warranted.

Our results suggest that environmental conditions during the pelagic larval stage can help to explain variation in Southern Flounder year-class strength and can improve predictions of juvenile flatfish recruitment. This is consistent with findings from other studies of flatfish recruitment, which found that environmental conditions during the egg and larval stages act as controlling factors on recruitment dynamics (Van der Veer 1986, Taylor et al. 2010, Wilderbuer et al. 2013, Amorim et al. 2016). Larval fish are most sensitive to the environment since they are less tolerant of extreme physical conditions compared to their larger counterparts (Lasker 1981, Smith et al. 1999a, O'Connor et al. 2007) and are exposed to greater rates of mortality due to starvation and predation (Anderson 1988, Cushing 1990). Therefore, small changes in environmental conditions can have a large impact on juvenile recruitment. The complete winter models were selected as best in all our analyses, despite the number of years or covariates included. Therefore, the controlling factors of offshore winter winds, winter river discharge, and winter duration appear to be key factors generating variability in Southern Flounder recruitment along the Gulf of Mexico. Years with optimal winds, river discharge, and winter duration may enhance spawning conditions, larval transport, and habitat quality during the Southern Flounder egg, larval, and juvenile periods, which would likely produce the strongest year classes in the Gulf of Mexico. Similar mechanisms have been identified as controlling factors for Southern Flounder recruitment in the South Atlantic Ocean (Taylor et al. 2010), but some estuary-specific differences in the controlling factors of recruitment may exist as we found that environmental covariates that performed well for Mobile Bay did not explain much variability in neighboring Perdido Bay.

The process of recruitment is complex and many factors beyond the physical conditions included here likely played contributing roles in the abundance of juvenile Southern Flounder. Larval and juvenile Southern Flounder are vulnerable to many physical conditions and biological processes, and it is this coupling that ultimately determines recruitment success (Houde 2009). In many studies, the incorporation of environmental variables strengthened the predictions of marine fish abundance (Froeschke et al. 2013, Morrongiello et al. 2014, Brosset et al. 2018). Although we only investigated physical mechanisms, we believed that they would directly impact biological processes occurring during early life stages of Southern Flounder (Amorim et al. 2016).

Many other studies have found strong correlations between offshore winds during the spawning window and indices of flatfish recruitment (Nielsen et al. 1998, Van der Veer & Witte 1999, Taylor et al. 2010). Some of the suggested mechanisms underlying these previously documented relationships may be applicable to the northern Gulf of Mexico. In our study, prevailing westerly winds during winter (December – February) were positively correlated with Southern Flounder juvenile abundance within the winter model for the short-term Mobile Bay analysis, expressing support for our hypothesis (*H2*). Results differed from our hypotheses (*H1* and *H2*) since northerly, southerly, and easterly winds were not significant in predicting juvenile abundance in northern Gulf of Mexico estuaries. Southern Flounder produce buoyant, pelagic eggs, and while exact spawning locations in the Gulf of Mexico are unknown (GSMFC 2015), it is thought that spawning occurs over the inner and central continental shelf at depths between 20 – 60 m (Benson 1982). In the Northern Hemisphere, as winds displace surface water, the Coriolis effect causes the subsequent, deeper water layers to move, forming a clockwise spiral (Ekman 1905). The net movement of water occurs 90 degrees to the right of the wind direction with deeper waters moving up to replenish the displaced surface water (Ekman 1905). These upwelling events can impact physical conditions in the estuary as a result of the mixing of deeper, offshore waters with shallow, inshore waters (Coogan et al. 2019), which could promote the transport of larvae into estuarine habitats (Pitts 1999). When winds blow from the west along the Gulf coast, upwelling of deeper waters potentially carrying Southern Flounder larvae north toward estuarine nurseries would occur as surface waters move offshore. In addition to larval transport, upwelling of nutrient-, phytoplankton-, and zooplankton-rich waters may enhance primary and secondary production in coastal and estuarine environments (Dagg 1988), potentially decreasing starvation, and increasing survival of larval and juvenile fishes. Van der Veer & Witte (1999) concluded that wind-driven circulation may be a key determinant in year-class strength of plaice (*Pleuronectes platessa*) where easterly winds in the North Sea likely prompted upwelling near the Dutch coast. Increased offshore westerly winds can also promote the transport of pelagic eggs and larvae along coasts and barrier islands so that they may have a higher chance of encountering the passages to estuaries (Taylor et al. 2010). If major offshore spawning areas for Southern Flounder are located west of Mobile Bay and Perdido Bay, the positive relationship between increased westerly winds and juvenile abundance found in our study would strongly support this mechanism of along-shore transport. While our study cannot conclusively identify the individual or combined wind-induced processes affecting Southern Flounder recruitment, upwelling events and along-shore transport appear to be plausible mechanisms that deserve further investigation.

Like wind, river discharge may also contribute to egg and larval transport through stratification, movement, and exchange of estuarine and offshore waters (Dzwonkowski et al. 2011, 2015, Coogan et al. 2019). Previous studies of flatfish recruitment have found that such estuarine-shelf exchanges driven by river discharge during the spawning seasons likely influenced settlement into estuarine habitats (Taylor et al. 2010, Martinho et al. 2009). In our short-term Mobile Bay analysis, intermediate levels of river discharge resulted in the highest abundance of juvenile Southern Flounder. However, the range of winter river discharge values in the short-term Mobile Bay analysis (2,317 – 12,818 m^3/s) was limited compared to that in the long-term Mobile Bay analysis (2,056 – 15,895 m^3/s), which included an additional 22 years of data with more years of extreme high and low flows. In the long-term analysis, a significant positive relationship emerged, supporting our hypothesis (*H3*) that high freshwater flows during winter are correlated with high abundances of juvenile Southern Flounder in the northern Gulf of Mexico. In addition to a wider range of discharge rates over many years, interacting effects of the covariates included in each analysis could help to explain the differing relationships between winter river discharge and juvenile abundance in the short- and long-term analyses for Mobile Bay (Stige et al. 2013). During high rates of river discharge, high influxes of new ocean water flows into the estuary generating some counter gradient flows (Du et al. 2018). Southern Flounder are known to use selective tidal stream transport where they vertically move to the bottom and use daytime ebb tides to avoid predation and migrate to the upper reaches of the estuary during periods of high winter river discharge in Mobile Bay (Weinstein 1980, Rijnsdorp et al. 1985, Boehlert & Mundy 1988, Burke et al. 1998, Jager 1999, Taylor et al. 2010).

Winter river discharge may also affect Southern Flounder recruitment by altering the salinity of estuarine waters during settlement periods and enhancing primary and secondary production in estuarine and offshore waters (Gibson 1994, Kimmerer 2002). Stickney & White (1974) found that recently metamorphosed Southern Flounder preferred low salinities (5 – 15 ‰). Therefore, high winter river discharge rates over a longer duration could increase the overall area and diversity of estuarine habitats with these preferred, low salinities, which may increase post-metamorphosis survival and biological recruitment.

To our knowledge, our study is one of the first to consider how winter duration might influence juvenile flatfish recruitment in estuaries along the Gulf of Mexico. Winter duration was found to be an important controlling factor and predictor of juvenile Southern Flounder abundance in Mobile Bay based on the long-term Mobile Bay analysis. Based on our findings, extremely long or short winters were followed by lower abundances of juvenile Southern Flounder, while intermediate winter durations appeared to have a positive effect on juvenile abundance. Winters of intermediate lengths may allow for a prolonged spawning period of optimal thermal conditions that increase hatching success of Southern Flounder eggs and increase larval growth rates (Cushing 1990, Mertz & Myers 1994). Curran & Wilber (2019) observed higher abundance of juvenile Southern Flounder in years following colder winters in an estuarine tidal creek in Georgia, suggesting that these increased occurrences of colder winter temperatures may play a positive role in early life survival across estuarine systems. Rijnsdorp et al. (1992) found that strong year classes of sole (*Solea solea*) followed cold winters, and suggested that cold winters may have a positive impact on reproductive success. However, long, cold winters could also directly increase mortality rates of older adults, which could affect recruitment by reducing the spawning stock size (Rjinsdorp et al. 1992).

These results differed from our hypothesis (*H4*) since there may be a limit to the positive effect that prolonged, cold temperatures during winter have on spawning and early survival. For example, the availability of larval prey can be time sensitive and extremely long winters may interfere with plankton blooms, which typically occur as temperatures begin to rise (Cushing 1990). If winters are longer, these blooms may be delayed, potentially leading to larval starvation. Longer spawning windows during long winters could lead to increased cannibalism among juveniles, thus decreasing the overall number of recruits, as observed for Olive flounder (*Paralichthys olivaceus*) who typically have a long spawning season that lasts up to two months (Minami & Tanaka 1992).

While growing degree-days was significant within the single-covariate model and the complete spring model, the relationship between growing-degree days and juvenile abundance was in the opposite direction of our hypothesis (*H5*). Spring growing degree-days had a negative effect on Southern Flounder juvenile abundance in the short-term analysis. This suggests that extremely warm springs may not be optimal for biological processes, such as juvenile growth. The models that included growing degree-days were not selected as best, and controlling factors during the winter explained most variability in abundance.

The results of this study and the projected changes in the severity and frequency of extreme environmental conditions help explain recent trends in recruitment and may help to predict Southern Flounder recruitment patterns in response to the changing environment. The partial residuals for each significant covariate served as an indicator of covariate effects on juvenile abundance. The partial residuals of westerly winds, winter river discharge, and winter duration within the winter models were all low in recent years (2012 – 2018), suggesting these environmental factors may have played a role in driving the low Southern Flounder juvenile abundance observed in Mobile Bay during recent years (Figure 6). Our study suggests that the low number of Southern Flounder recruits resulting from suboptimal environmental conditions helps to explain the documented population declines in the northern Gulf of Mexico in recent years (Froeschke et al. 2011, Chagaris et al. 2012, GSMFC 2015, Powers et al. 2018).

Over the next one hundred years, the Gulf of Mexico region is expected to see increased durations of dry conditions and increased intensity of precipitation events, as well as increased durations of heat waves and decreased cold snaps (Diffenbaugh et al. 2005, Biasutti et al. 2012). Increased periods of dry conditions or intense rainfall could alter the amount of river discharge that enters each estuary, thus altering habitat availability and physical conditions that affect larval settlement in estuaries. If these prolonged dry periods overlap with Southern Flounder spawning and hatching in winter, we may expect negative impacts on recruitment due to low river discharge. It is anticipated that about 90 % of winters at the end of the 21st century will be warmer than previously recorded (Biasutti et al. 2012). Warmer winter temperatures in the Gulf Coast region may negatively affect Southern Flounder reproductive success by shortening the spawning window, reducing hatching success, and decreasing larval growth rates (Van Maaren & Daniels 2001, GSMFC 2015). Because human activity is typically highest within close proximity to the coasts, estuarine environments are strongly influenced by anthropogenic stressors, which could exacerbate these negative effects of climate change. These changing environmental conditions are concerning for estuarine species, especially those that use estuaries for nurseries or experience ontogenetic habitat shifts throughout their lifetimes (Ong et al. 2015). As recruitment dynamics influence future adult abundance, our results should help inform managers' expectations for the Southern Flounder fishery as environmental conditions continue to change. Managers may be able to better anticipate how environmental changes will affect adult abundance while assisting in setting user group expectations for the productivity of Southern Flounder populations along the northern Gulf of Mexico.

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TABLES

Table 1. Marginal likelihood and deviance explained of models that were run in each of the three analyses. P-values are given in parentheses for each model covariate. (WI= winter covariate; SP= spring covariate).

Model	**Covariate(s)**	**Marginal Likelihood (ML)**	**Deviance Explained (%)**
	Mobile Bay – 16-year analysis		
Winter model	WI Northerly winds (p = 0.248) WI Easterly winds (p = 0.479) WI Southerly winds (p = 0.713) WI Westerly winds (p < 0.001) WI River discharge (p = 0.026) WI Winter duration (p = 0.076)	90.658	70.2
Westerly winds only	WI Westerly winds (p < 0.001)	97.325	59.4
Southerly winds only	WI Southerly winds (p = 0.003)	100.41	55.8
Growing degree-days only	SP Growing degree days (p = 0.006)	101.2	54.8
Spring model	SP River discharge (p = 0.985) SP Growing degree days (p = 0.006)	101.2	54.8
Easterly winds only	WI Easterly winds (p = 0.058)	104	55.6
Spring river discharge only	SP River discharge (p = 0.003)	104.2	66.4
Northerly winds only	WI Northerly winds (p = 0.241)	104.9	50
Winter river discharge only	WI River discharge (p = 0.233)	104.92	49.9
Winter duration only	WI Winter duration (p = 0.501)	105.38	49.5
	Mobile Bay – 38-year analysis		
Winter model	WI River discharge (p < 0.001) WI Winter duration (p = 0.023)	300.48	56.8
Winter river discharge only	WI River discharge (p < 0.001)	302.54	53.8
Winter duration only	WI Winter duration (p = 0.073)	308.27	52.4
Spring river discharge only	SP River discharge (p = 0.344)	309.03	50.4
	Perdido Bay – 31-year analysis		
Winter model	WI River discharge (p = 0.845) WI Winter duration (p = 0.306)	75.644	37.6
Winter duration only	WI Winter duration (p = 0.257)	75.664	37.9
Spring river discharge only	SP River discharge (p = 0.464)	75.834	32.6
Winter river discharge only	WI River discharge (p = 0.608)	75.946	32.5

FIGURES

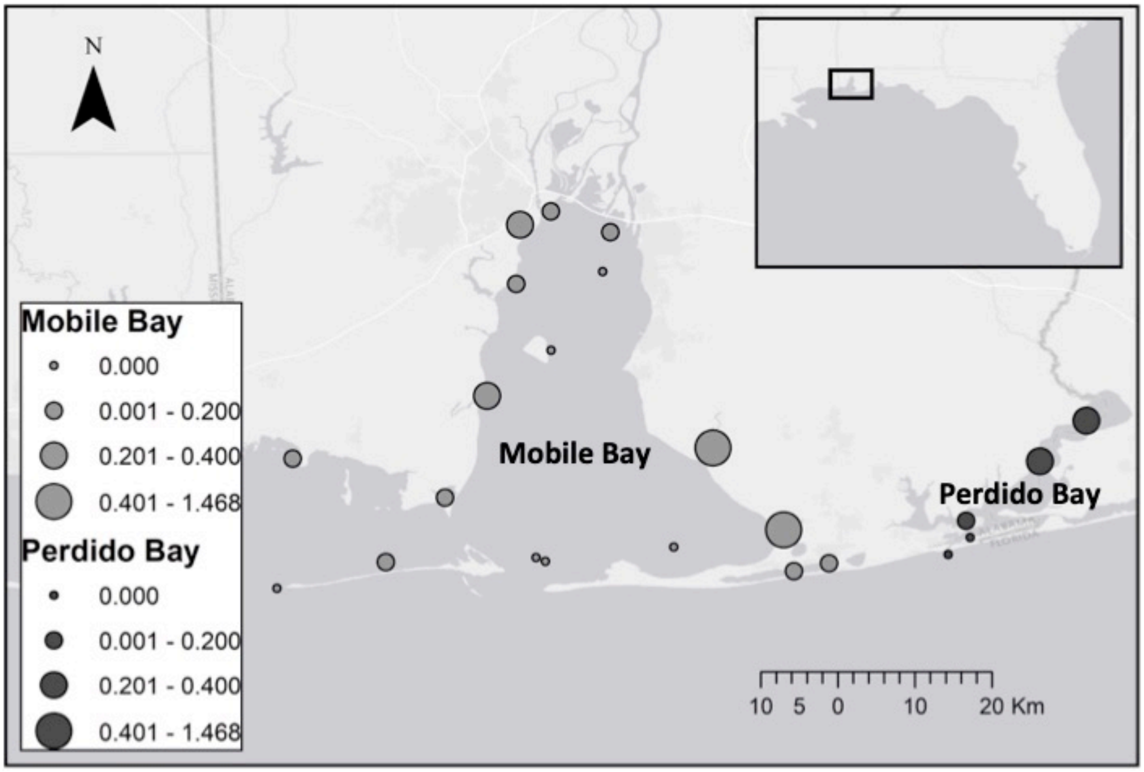

Figure 1. The twenty-three stations surveyed by Alabama Department of Conservation and Natural Resources, Marine Resources Division's (ADCNR/MRD's) Fisheries Assessment and Monitoring Program (FAMP). Eighteen stations were in Mobile Bay (light gray) and five were in Perdido Bay (dark gray). The size of the circle corresponds to the average number of juvenile (age-0) Southern Flounder collected per trawl (1981 – 2018) during May and June.

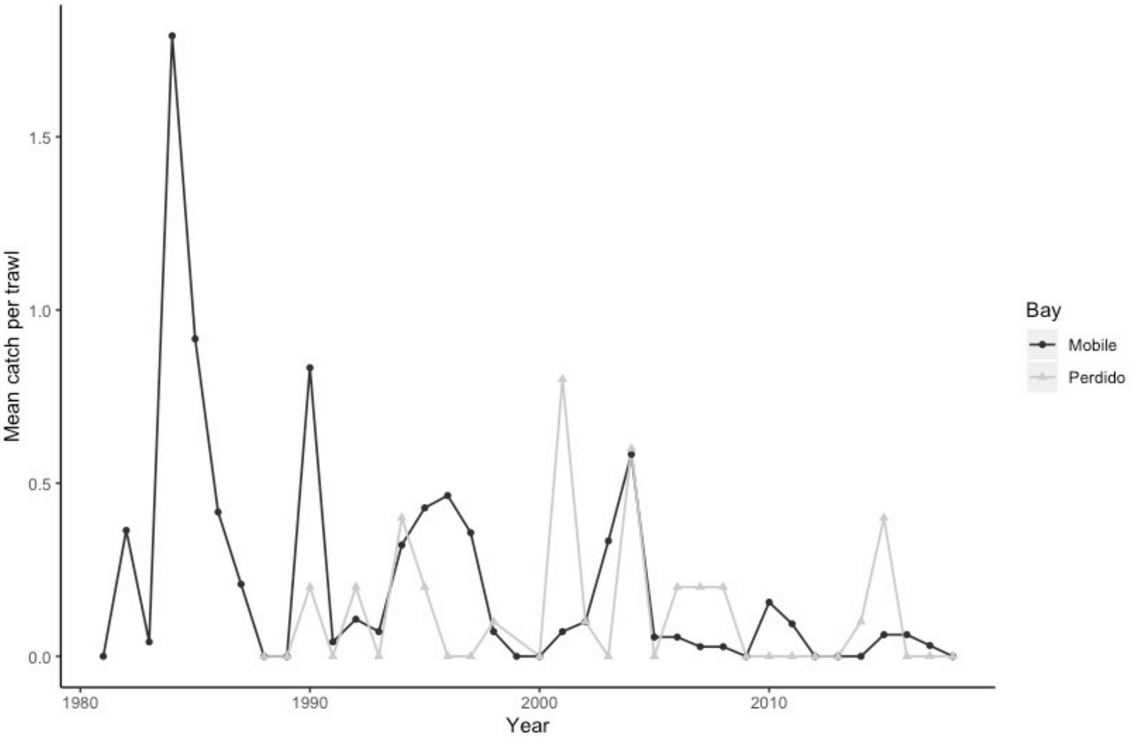

Figure 2. Index of Southern Flounder juvenile (age-0) abundance from Mobile Bay, Alabama (1981 – 2018; black line) and Perdido Bay, Alabama (1988 – 2018; gray line). Juvenile abundance data was collected during bottom trawls conducted by Alabama Department of Conservation and Natural Resources, Marine Resources Division (ADCNR/MRD's) as part of the Fisheries Assessment and Monitoring Program (FAMP). Juvenile abundance is measured as the mean catch of juvenile Southern Flounder per trawl during May – June (1981 – 2018).

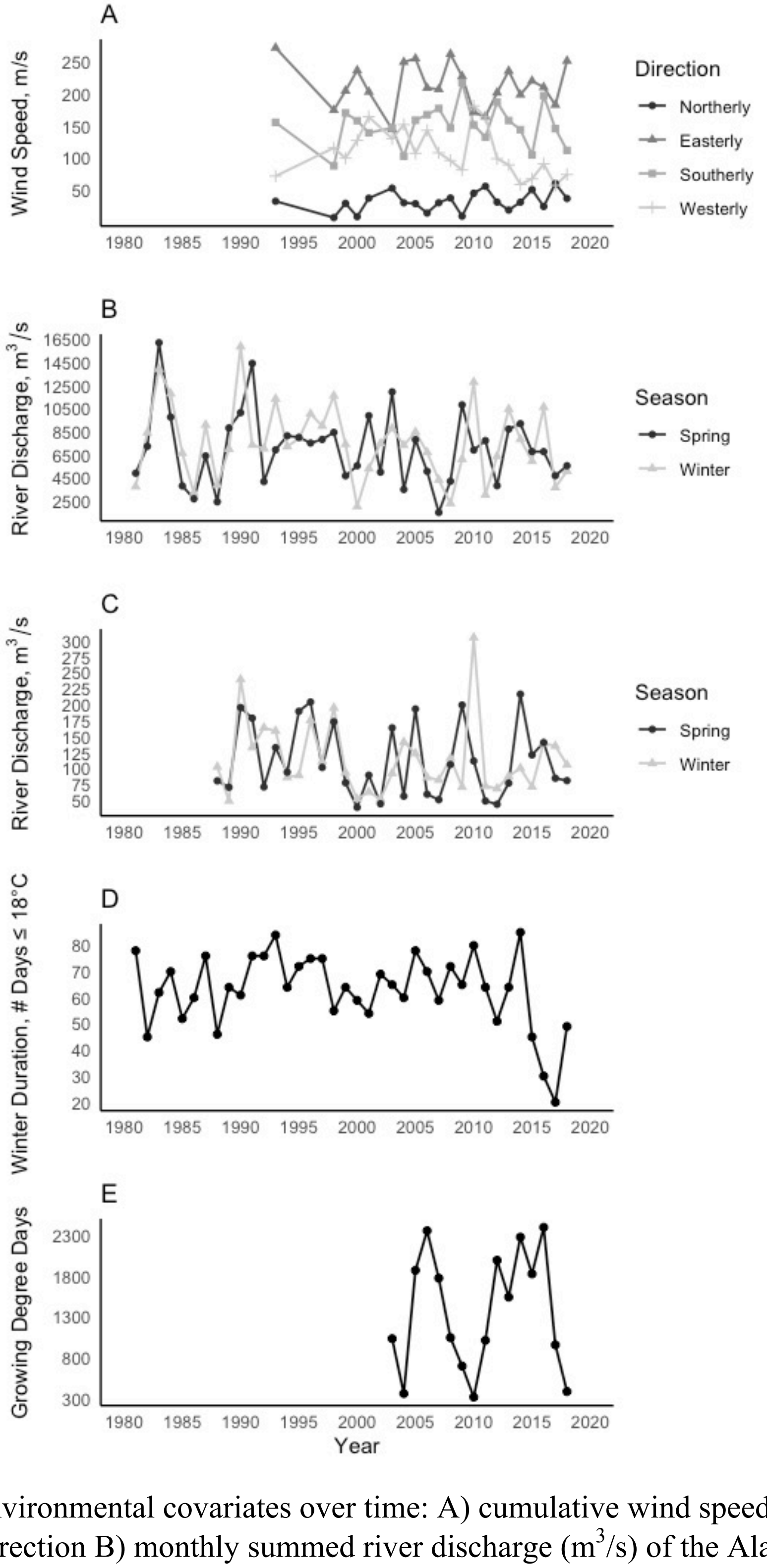

Figure 3. Environmental covariates over time: A) cumulative wind speed (m/s) for each prevailing direction B) monthly summed river discharge (m^3/s) of the Alabama and Tombigbee Rivers during the winter (December – February) and spring (March – May)

C) monthly summed river discharge (m^3/s) of the Perdido and Styx Rivers during the winter (December – February) and spring (March – May) D) winter duration, or the number of days equal to or less than 18 °C E) growing degree days (March – May). Data in plots A, B, C, D, and E were used in the 16-year Mobile Bay analysis. Data in plots B and D were used in the 38-year Mobile Bay analysis. Data in plots C and D were used in the 31-year Perdido Bay analysis.

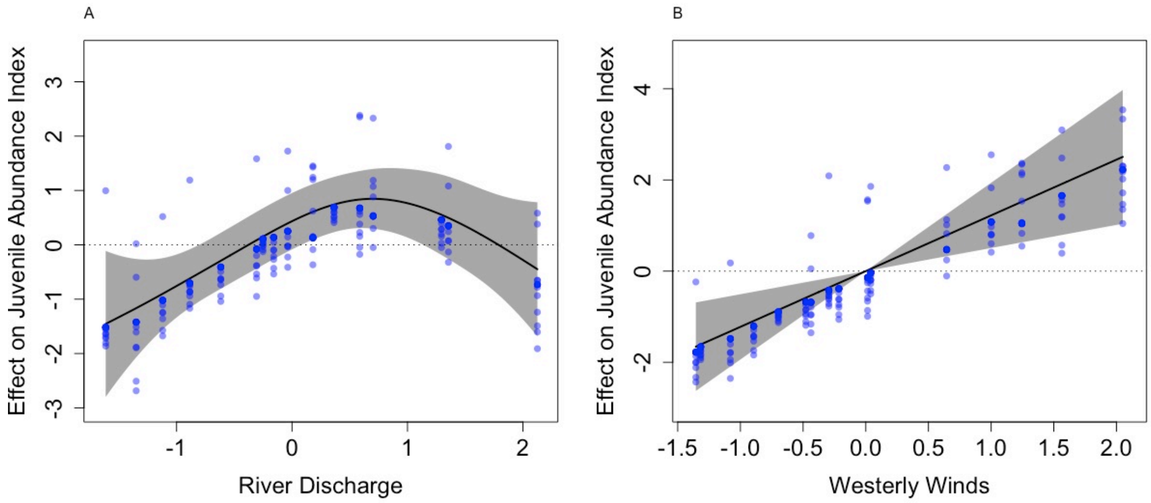

Figure 4. Partial residuals plots from a mixed-effects generalized additive models (GAM) for centered and scaled environmental predictor variables including A) river discharge and B) westerly winds, which both had significant effects on juvenile (age-0) Southern Flounder abundance in Mobile Bay, Alabama for the 16-year analysis (2003-2018). Dots represent partial residuals, or the relationship between the covariate and the model residuals.

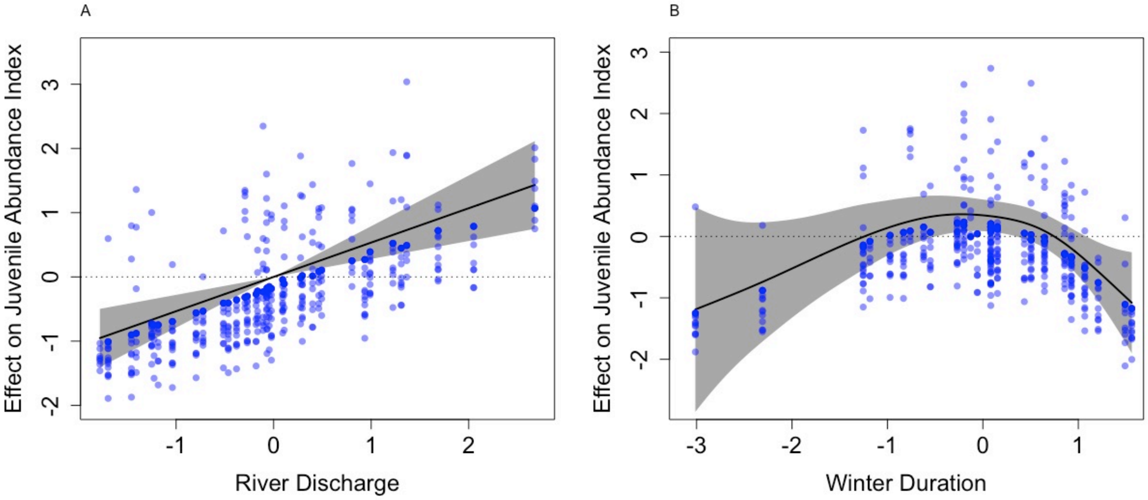

Figure 5. Partial residuals plots from a mixed-effects generalized additive model (GAM) for centered and scaled environmental predictor variables including A) river discharge and B) winter duration, which both had significant effects on juvenile (age-0) Southern Flounder abundance in Mobile Bay, Alabama for the 38-year analysis (1981- 2018). Dots represent partial residuals, or the relationship between the covariate and the model residuals.

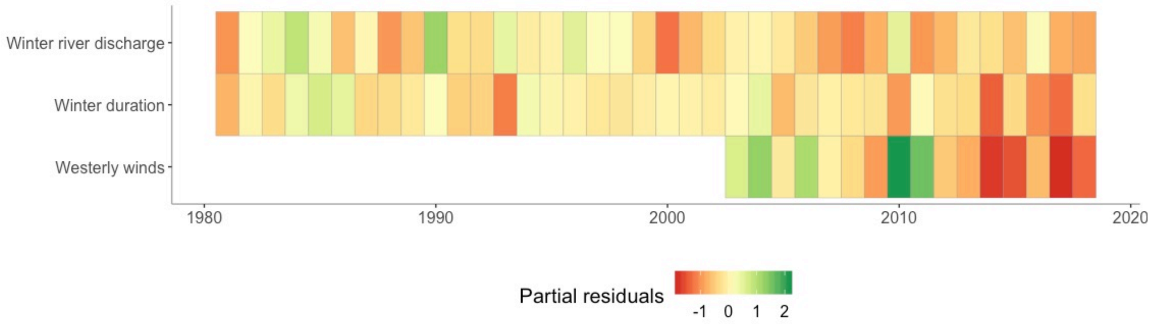

Figure 6. Mean annual partial residuals showing the temporal influence of significant environmental covariates on juvenile Southern Flounder abundance from 1981 – 2018. Partial residuals for winter river discharge and winter duration were drawn from the winter model in the long-term (38-year) Mobile Bay analysis. Partial residuals for westerly winter winds were drawn from the winter model in the short-term (16-year) Mobile Bay analysis. Green tiles represent positive effects on juvenile abundance. Red tiles represent negative effects on juvenile abundance.

CHAPTER TWO

EFFECTS OF AGE-SPECIFIC CONTINGENT TYPE ON SOUTHERN FLOUNDER (*PARALICHTHYS LETHOSTIGMA*) GROWTH AND CONDITION IN MOBILE BAY, ALABAMA

1. Introduction

Estuaries are dynamic environments that provide habitats for many economically important juvenile and adult fishes, including flatfish. Juvenile and adult flatfishes tend to occupy distinct habitats within estuaries based on their needs during specific life stages and seasons. Flatfish exhibit partial migration, a phenomenon where a single population comprises both resident and transient, migratory members (Jonsson & Jonsson 1993, Kerr et al. 2009, Chapman et al. 2011, Gillanders et al. 2015). The term “contingent” refers to a group of individuals who have similar migration behaviors over phases of life or across their entire lifetimes (Secor 2015). Specific contingents of a population have distinct patterns in habitat use within single estuary systems (Gillanders et al. 2015).

Understanding partial migration of flatfish species is important for fisheries scientists to gain insight into recruitment and population dynamics as it relates to the costs and benefits of staying within or moving from a particular habitat (Jonsson & Jonsson 1993, Skov et al. 2013). These partial migration patterns can be largely explained by abiotic factors (e.g., salinity, temperature, dissolved oxygen), which in turn likely serve as proxies for biotic factors like predation and food availability (Able & Fodrie 2015). Abiotic and biotic factors can have lasting effects on the growth and condition of estuarine fishes.

Growth and condition integrate the aggregate effects of many physical and biological processes that together determine habitat quality. Growth and condition have been considered effective indicators of estuarine habitat quality for juvenile flatfish in a number of previous studies (Meng et al. 2000, Phelan et al. 2000, Amara et al. 2009). Increases in growth and condition under optimal conditions in high quality estuarine habitats may ultimately confer survival advantages since smaller individuals are less tolerant of extreme physical conditions compared to their larger counterparts (Lasker 1981, Smith et al. 1999, O'Connor et al. 2007) and are exposed to greater rates of mortality due to starvation and predation (Anderson 1988, Cushing 1990). However, when flatfish encounter suboptimal abiotic conditions or low prey availability in low-quality habitats, stress hormones may be released, followed by the production of glucose to try to account for the lost energy where growth and condition could be negatively impacted (Iwama et al. 1999). Stress increases cortisol levels, which can lead to sex reversal for Paralichthyd flounder, where females differentiate to become males (Yamaguchi et al. 2010). This likely happens because it is energetically less expensive to be male as they produce sperm instead of eggs, grow slower, and reach a smaller size as adults (GSMFC 2015).

Fish otoliths and other calcified structures keep record of slow and fast annual growth as incremental growth rings are laid down (Pannella 1971), and reflect ambient environments that fishes were exposed to during each year of life (Campana 1999). In most fish species, including flatfish, otolith growth correlates with somatic growth (Reichert et al. 2000, Gilliers et al. 2006). Hence, otolith increment widths and lengths at capture can be used to estimate fish lengths during each year of life using back-calculation methods. There are many widely used back-calculation methods that have been developed over the last century to estimate fish sizes-at-age (reviewed by Francis 1990). Incorporating age, growth, and year effects can improve growth estimates by accounting for factors acting on growth variability (Weisberg et al. 2010). Elements, such as strontium, taken up by the fish through the gills are permanently retained in otoliths (Campana 1999). Strontium reflects the chemistry of the water, and strontium: calcium (Sr:Ca) ratios serve as tracers of fish movement as they differ among freshwater and estuarine habitats with low levels indicating freshwater habitat use and high levels indicating estuarine habitat use (Campana 1999, Kraus & Secor 2004). Elemental signatures within sectioned otoliths can be detected using laser ablation inductively coupled plasma mass spectrometry, energy-dispersive electron microphobes, wavelength-dispersive electron microphobes, and proton-induced x-ray emission (Campana 1999). Changes in elemental concentrations across an otolith may indicate shifts in habitat use, and these shifts can be related to increment widths to understand linkages between age-specific growth and habitat use.

While otoliths provide a long-term record of growth and habitat use, condition provides a measure of energetic reserves at the time of collection, which could provide insight into understanding habitat quality within estuaries. Weight increases exponentially with length, and relative condition indices (weight-length relationships) assume that fish with greater body mass at a given length and those that exhibit positive allometric growth are in better condition (Froese 2006). Condition measures fish physiological status (Champion et al. 2020), and therefore, high condition reflects good physical health and nutritional benefit due to increased energy storage.

Southern Flounder (*Paralichthys lethostigma*) is an economically important species that exhibits sexually dimorphic growth where females grow larger and faster than males, consequently being the target for commercial and recreational catches (GSMFC 2015). The species uses a variety of habitats across salinity gradients in and along the Atlantic Ocean and Gulf of Mexico. Southern Flounder are distributed from North Carolina to Texas, but is absent from waters off the southern tip of Florida (GSMFC 2015). During winter, adult Southern Flounder spawn offshore, and larvae migrate to estuarine nurseries where they will grow, settle, and metamorphose into juveniles (Burke et al. 1991, Fischer & Thompson 2004). Furey et al. (2013) found that juvenile Southern Flounder moved up to 2 km day^{-1} and used a variety of habitats within a Texas estuary. While larvae have a zero tolerance of freshwater, juveniles and adults appear to use a variety of habitats across salinity gradients, from tidal freshwater to polyhaline habitats (Smith et al. 1999, Lowe et al. 2011, Farmer et al. 2013, Nims & Walther 2014). Southern Flounder can tolerate temperatures from 0 – 35°C and salinities from 0 – 36‰, but historically have been found in salinities up to 60‰ in Texas (GSMFC 2015). During the late fall, reproductively mature adults will begin moving offshore to begin the process again (Burke et al. 1991, Fischer & Thompson 2004). This presumed life history indicates Southern Flounder is a marine estuarine dependent species (Elliott et al. 2007).

The habitats that Southern Flounder encounter as they go from pelagic to benthic and offshore to inshore environments ultimately impact their growth rates and condition as a result of changing environmental conditions and new suites of prey and competitors (Van der Veer 1986, Chambers & Leggett 1992). Due to the many habitat types that they encounter within or outside of the estuary, it is not surprising that previous studies have found Southern Flounder growth rates and condition to be highly variable across time and space (Fitzhugh et al. 1996, Midway et al. 2015). A recent meta-analysis of Southern Flounder size-at-age data in Texas, Alabama, South Carolina, and North Carolina estuaries found that variability in male and female growth was as high within estuaries as it was among them, suggesting that differing environmental conditions within single estuary systems may be driving highly variable growth rates (Midway et al. 2015). In a recent laboratory study, Howson & Targett (2019) found that optimal linear growth rates (length gain for the duration of the experiment) occurred at 25 – 28° C and 14 – 22‰ for juvenile (45 – 100 mm TL) Southern Flounder collected from North Carolina and fed the same type and amount of food. They also found that optimal specific growth rates (% body weight growth per day) occurred at 25 – 26° C and 10 – 30‰ for these young-of-the-year (Howson & Targett 2019). Therefore, growth and condition of various Southern Flounder contingents (migratory and resident) could be explained by distinct abiotic and biotic factors of the habitats they encounter.

Previous work on Southern Flounder along the Gulf of Mexico has identified individuals that almost completely use freshwater regions or higher salinity regions of the estuary, as well as transient individuals that appear to move between salinity regions

(Farmer et al. 2013, Nims & Walther 2014). These differences may help to explain high variability in growth in single estuary systems. To understand the ecological importance of certain habitat types within estuaries, further research is needed to explore relationships between contingent types, growth, and condition. The potential roles of age-specific contingent type on growth and condition of Southern Flounder has not yet been investigated in estuaries along the northern Gulf of Mexico. This work aims to investigate relationships between habitat-specific markers and back-calculated growth rates and condition (residuals from the weight-length relationships) of Southern Flounder in the northern Gulf of Mexico. Specifically, I hypothesized that:

H1: Age-0, first year, and second year Southern Flounder classified as estuarine residents will have faster growth rates than freshwater or transient contingents in response to optimal abiotic characteristics of estuarine habitats.

H2: Age-0, age-1, and age-2 Southern Flounder classified as estuarine residents would be in higher condition for reasons indicated above.

The primary objective of this work is to test the above hypotheses using mixed effects linear models to investigate how observed patterns in growth and condition relate to patterns in habitat use. Many previous growth studies had limitations as they used caging methods or considered habitat-specific effects only within the area of collection (Guindon & Miller 1995, Meng et al. 2000, Phelan et al. 2000). Our study used Southern Flounder otoliths from fishery-dependent and fishery-independent collections to determine back-calculated lengths-at-age and otolith elemental composition to determine age-specific contingent types. With improved understanding of these relationships, our work seeks to identify high-quality estuarine habitats by relating growth and condition to lifetime patterns of habitat use, as described by otolith chemistry.

2. Methods

2.1 Study area

Mobile Bay, Alabama is an estuary along the northern Gulf of Mexico that has many different habitats and has historically supported large harvests of Southern Flounder (GSMFC 2015). Mobile Bay has the fourth largest river system in the United States, and receives the sixth largest volume of freshwater discharge in North America (mean daily discharge rate: 1850 m^3/s; Morisawa 1968, Park et al. 2007). This large amount of freshwater input promotes a distinct salinity gradient, and influences salinities in the lower estuary during the high discharge period in winter and spring. The upper Mobile Bay is known as the Mobile-Tensaw River Delta (hereafter referred to as "the Delta;" Figure 1), which begins at the confluence of the Alabama and Tombigbee Rivers and is a freshwater region with salinities less than 1‰ for most of the year. The middle and lower Mobile Bay is characterized by estuarine habitats south of I-10 with salinities greater than 1‰ for most of the year (hereafter referred to as "Mobile Bay;" Figure 1). During the summer and fall when the freshwater input is considerably lower, the Gulf of Mexico has a greater influence on the estuary's thermohaline dynamics and stratification occurs with large vertical and horizontal ranges of salinities and temperatures in Mobile Bay (Coogan et al. 2019).

2.2 Flounder collections

We used 313 right sagittal otoliths from Southern Flounder (ages 0 – 4) collected in Alabama coastal waters in 2004 – 2007 and 2018 – 2019 to determine how back-calculated growth rates and condition indices differ among age-specific contingents. Southern Flounder were collected by field researchers from Auburn University (2005 – 2007), the Alabama Department of Conservation and Natural Resources, Marine Resources Division (ADCNR/MRD; 2004 – 2007, 2018 – 2019), and Clemson University (2018 – 2019), as well as from commercial and recreational fishermen.

2.2.1 Fishery-independent collections

Auburn University collected juvenile and adult Southern Flounder from five sites in the Delta and one just south of I-10 (Figure 1). Sampling occurred monthly in the summer and fall of 2005 – 2007 using pulsed-DC electrofishing (7.5 GPP, Smith-Root, Vancouver, Washington). Electrofishing transects were 10 – 15 minutes long, and the minimum total effort per sampling event was one hour. Southern Flounder were placed on ice and brought to the laboratory where they were measured. Sex was determined by macroscopic inspection of gonads when possible, and otoliths were removed for aging and elemental analysis.

ADCNR/MRD’s Fisheries Assessment and Monitoring Program (FAMP) used 4.88 m bottom trawls with 30.48 m of towline (more towline was used if the depth was greater than 9.14 m) to target benthic fishes, including juvenile and adult Southern Flounder, across Alabama coastal and estuarine waters. The trawls were pulled for 10 minutes at 2 – 2.5 knots with 0.36 m head rope. The bottom trawl consisted of a two-seam net with the innermost one having a 4.76 mm mesh. Sampling occurred monthly in

2018 – 2019 at 24 stations in Mississippi Sound, Mobile Bay, Little Lagoon, and Perdido Bay. Southern Flounder were collected at six of the total 24 stations (Figure 1). When flounder were caught, they were measured and placed in ziploc bags that were put on ice and later frozen. In the laboratory, sex was determined by macroscopic inspection of gonads when possible, and otoliths were removed for aging and elemental analysis.

Juvenile and adult Southern Flounder were also collected by Clemson University in 2018 – 2019 at nine of the 12 total surveyed sites that spanned from the Delta to the barrier islands of Mobile Bay to quantify abiotic and biotic conditions across the salinity gradient (Figure 1). Stations were selected across the Delta and Mobile Bay to represent both freshwater and estuarine conditions. There were 1 – 2 sampling events each month in May – July 2018, and March, May – July 2019. The gear types used were boat electrofishing, beam trawls, and gillnets, which depended on salinity and habitat at each site.

Pulsed DC boat electrofishing (Midwest Lake Electrofishing Systems Infinity Box) was used to target juvenile and adult Southern Flounder along the shorelines at oligohaline sites. Delta stations (north of I-10; Figure 1) were oligohaline in all months, while mesohaline stations (middle Mobile Bay along the eastern and western shore) were oligohaline in the spring, but were not sampled with electrofishing during summer due to elevated salinities. During each sampling event, six, 15-minute electrofishing transects were conducted at each site. A 1 m beam trawl with 2 mm mesh was towed for two minutes by boat along shallow shorelines and marsh edges to target small juveniles. At Delta stations, we completed a minimum of three beam trawl transects, and at Mobile

Bay sites (south of I-10; Figure 1), we completed a minimum of eight beam trawl transects. Gillnets (30 by 2.4 m with 127 mm stretch mesh) were used to target large juveniles and adults at Mobile Bay stations. During each sampling event, at least two gillnets had minimum soak times of 2 hours each, and they were set parallel to shore with one end forming a C-shaped “hook” toward the shore. The date, site, gear type, transect number, start and end time, start and end GPS coordinates, and start and end depth was recorded for each transect. All Southern Flounder were measured and placed on ice before returning to the laboratory where they were frozen until processing took place. During sample processing, sex was determined by macroscopic inspection of gonads when possible, and otoliths were removed for aging and elemental analysis.

2.2.2 Fishery-dependent collections

ADCNR/MRD collected adult Southern Flounder from commercial fish houses and recreation fishermen in 2004 – 2007. ADCNR/MRD collected from recreational anglers while conducting creel surveys by using protocols from NOAA Fisheries Marine Recreational Information Program (MRIP) and Access Point Angler Intercept Survey (APAIS) to randomly select public access locations across Alabama coastal waters. Clemson University also collected adult Southern Flounder in 2018 – 2019 from two commercial fish houses, opportunistic recreational fishermen at boat access points, and two major fishing tournaments (Alabama Deep Sea Fishing Rodeo 2018 – 2019; FloraBama Fishing Rodeo 2019). We used opportunistic hook-and-line sampling to target adult Southern Flounder, and we used both artificial (red jig heads and striped mullet Gulps) and live bait (spot, croaker, pinfish).

2.3 Back-calculated growth

Right sagittal otoliths were removed, embedded in epoxy resin, sectioned with an Isomet low speed saw (Buehler), and polished using a MetaServ 250 grinder-polisher (Buehler). We consistently used right otoliths in this analysis since they were easier to read and left and right flounder otoliths are asymmetrical in regard to the core position and weight (Fischer & Thompson 2004). Sipe & Chittenden (2001) found that sectioned right otoliths of summer flounder (*Paralichthys dentatus*) had the clearest structure, as well as the highest confidence scores, lowest reading times, and highest agreement among readers. Farmer et al. (2013) also consistently used sectioned right otoliths of Southern Flounder for aging and otolith chemistry. The sectioned otoliths were placed under a compound microscope (Meiji) and photographed with a digital camera (Cannon Rebel). Two independent readers estimated age from these images by counting the annuli on each otolith. If disagreement occurred, a third reader aged the otolith at question. Transects were drawn on digital images along the ventral sides of the sulcal grooves using iSolution lite software (IMT i-Solution Inc., Stokie, Illinois). Growth increments were measured (mm) from the core to the end of each annulus, and from the core to the edge along these transects (Figure 2). A Dahl-Lea proportional method was used to back-calculate growth rates of Southern Flounder (Lea 1910).

2.4 Determining age-specific contingent type

We used laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) to determine Southern Flounder residencies from otolith elemental signatures. Strontium: calcium (Sr:Ca) ratios were used as a marker for salinity exposures. Details of

LA-ICPMS processing can be found in Chrisp et al. (*in preparation*). Briefly, sectioned and polished otoliths were processed at the Dauphin Island Sea Lab (DISL) instrumentation lab using an Agilent 7700x quadrupole inductively coupled plasma mass spectrometer (ICPMS) coupled to a 213 nm Nd:YAG NWR laser. Mounted otoliths were rinsed with deionized water and cleaned using low power cleaning pre-ablation (40 µm spot, 100 µm/sec, 20% laser power, 5 Hz) to remove contaminants on the otolith surface along the same transect as the chemistry analysis ablation. Otolith Sr:Ca was quantified from the core to the distal edge along a straight transect parallel to the sulcal groove, with an elemental reading collected every 0.6 s. Standard methods were used to assess analytical precision, quantify detection limits, and correct for instrument drift (Longerich et al. 1996, Farmer et al. 2013). To summarize time series of otolith Sr:Ca values, a regime shift detection algorithm was used to detect significant shifts in otolith Sr:Ca values along the laser ablation transects (Rodionov 2004).

Analysis of ambient water chemistry, salinity, and otolith edge chemistry showed that a threshold of 1.71 mmol/mol Sr:Ca could be used to indicate habitat use above or below 1 psu (Chrisp et al. *in preparation*). Any Sr:Ca value above this value was considered to be estuarine habitat use and anything below, tidal freshwater habitat use. The proportion of values above and below this threshold value was quantified for each year of growth (proportion of the laser ablation transect between each otolith annuli). We created three age-specific contingency classes and defined them as freshwater resident, estuarine resident, or transient to group individuals with similar habitat-use patterns during each year of life (Chrisp et al. *in preparation*). The individuals that spent 90% or more of the year in freshwater habitats were classified as freshwater residents. The individuals that spent 90% or more of the year in estuarine habitats were classified as estuarine residents. The individuals that spent less than 90% of the year in either habitat were classified as transients. Our age-specific contingent classes (freshwater resident, transient, estuarine resident) are similar to previously described Southern Flounder contingent types observed in Alabama (Farmer et al. 2013) and Texas (Nims and Walther 2014), and should provide insight into the ecological consequences of these general patterns in habitat use.

2.5 Statistical analyses

2.5.1 Growth

We used linear mixed effects models using package lme4 in R version 3.6.1 (R Development Core Team 2019) to investigate how age-specific contingent types impacted age-specific back-calculated growth rates of Southern Flounder. We accounted for any age, year and individual fish growth effects by incorporating random effects of sex, age at capture, and/or cohort into the models (Weisberg 2010). We conducted these analyses for age-0, first-year of life (hereafter referred to as "first-year"), and second-year of life (hereafter referred to as "second-year"). Southern Flounder included in the age-0 and first-year growth analyses were collected from March – December, and those included in the second-year growth analysis were collected from May – December. We assumed January 1 to be the date of birth and April 1 to be the date of otolith annuli formation (Glass et al. 2008, Corey et al. 2017). For the age-0 growth analysis, the response variable was growth rate (mm d^{-1}), which allowed for comparisons of fish collected at different times throughout the year. Contingent type was used as a fixed effect, and cohort was used as a random intercept to account for any intrinsic differences in growth rates among year-classes. Typically, sex cannot be macroscopically identified in juveniles and was not included as a random intercept in the age-0 growth analysis.

The age-0 analysis quantified growth rates of flounder whose otoliths had zero annuli, while the first-year growth analysis quantified annual growth of flounder whose otoliths had at least one annulus. Southern Flounder that were ages 1 – 4 and 2 – 4 were used for the first-year growth analysis and second-year growth analysis, respectfully. The response variable, growth (mm), was back-calculated using the total length at capture and otolith width from the core to the end of the first annulus for first-year growth, and the otolith width from the end of the first annulus to the end of the second annulus for second-year growth. Contingent type was modeled as a fixed effect. The random effect structures for these analyses were determined with model selection fitted with restricted maximum likelihood (REML) and compared based on AICc. Burnham & Anderson (2002) suggested using AICc with small sample sizes (the number of observations divided by the number of parameters is less than 40), and any difference between AIC and AICc for larger sample sizes would be negligible. The best model was selected according to the least value of AICc and highest weight value. Models were significantly different from one another when the ΔAICc values differed by two or more. For the first-year growth analysis, seven models with different random effect structures were considered that included cohort, age at capture, and sex. Models included one random intercept, two random intercepts, or all three random intercepts. If a model did not converge, the 'L-BFGS-B' optimizer (package optimix) was applied. For the second-year growth analysis, two models included individual intercepts of sex and age at capture, and one model included both of these random intercepts. Cohort was not included as a random intercept in the second-year growth analysis because there were not enough unique observations for the older cohorts, and we wanted to maintain the highest possible sample size within the analysis. For all growth and condition analyses, a Shapiro-Wilk test was used to test the normality of the residuals, and assumptions for linearity and homoscedasticity were verified by examining diagnostic residual plots. *P*-values from post-hoc multiple comparisons among contingent types were adjusted for multiple comparisons using Tukey’s post-hoc test for each age-specific growth and condition analysis (package multcomp; normal if $p > 0.05$).

2.5.2 Condition

Flounder with weight data (g) available were used to assess if condition differed among age-specific contingent types. Condition indices were measured using the residuals of the $\log_{10}$ weight versus $\log_{10}$ total length relationship (Figure 3). Forty-three outliers were removed from the condition analyses if lengths and weights did not follow this positive, linear relationship and were assumed to have errors in weight measurements. To investigate if the condition of Southern Flounder differed among age-specific contingent types, we used linear mixed effects models using package lme4 in R while accounting for intrinsic factors affecting growth (Weisberg 2010). We conducted these analyses for age-0, age-1, and age-2 Southern Flounder. Southern Flounder included in the age-0 and age-1 condition analyses were collected from March –

December, and those included in the age-2 condition analysis were collected from May – December. January 1 was assumed to be the date of birth and April 1 was assumed to be the date of otolith annuli formation (Nieland et al. 2002, Corey et al. 2017) . We used a fixed effect of contingent type and a random intercept for cohort in the age-0 condition analysis. Sex was not included as a random intercept in the age-0 condition analysis due to unidentified sex for most individuals. For the age-1 condition analysis, the random effect structure was determined with model selection fitted with REML and compared based on AICc metrics as described above for the growth analyses. Two models included random intercepts of cohort and sex, one model included both of these random intercepts, and the best model was selected according to the least value of AICc along with the examination of AICc weights and ΔAICc values. For the age-2 condition analysis, we used a fixed effect of contingent type and a random intercept for sex. Cohort was not included in the age-2 condition analysis since there were not enough unique observations for the oldest fish, and we wanted to maintain the highest possible sample size within the analysis.

3. Results

3.1 Back-calculated growth among age-specific contingents

Twenty-six age-0 Southern Flounder were included in our analysis that related growth rate to contingent type. Mean growth rates of age-0 Southern Flounder were 1.061 mm d^{-1} (range 0.705 – 1.525 mm d^{-1}) for estuarine residents, 0.907 mm d^{-1} (range 0.499 – 1.411 mm d^{-1}) for transient contingents, and 0.722 mm d^{-1} (range 0.527 – 0.979 mm d^{-1}) for freshwater residents. Highest age-0 growth rates occurred in transient and estuarine contingents (Figure 4a). According to the multiple comparisons test, growth rates of age-0 transient and estuarine flounder were statistically similar ($p = 0.677$). Age-0 freshwater flounder had significantly lower growth rates than transient ($p < 0.001$) and estuarine ($p < 0.001$) age-0 Southern Flounder.

Two hundred eighty-seven Southern Flounder were used in the first-year growth analysis (30 males, 257 females). The model containing random intercepts for sex, age at capture, and cohort was selected as the best model to explain intrinsic variability in Southern Flounder growth rates during the first year of life (Table 1). The random intercepts were highest for females, age-1 flounder, and the 2018 year-class (Figure 5). Growth rates of transient and estuarine Southern Flounder were statistically similar ($p = 0.913$), and significantly higher ($p < 0.001$; $p < 0.001$, respectively) than freshwater residents during the first year of life (Figure 4b).

Seventy-two Southern Flounder were used in the second-year growth analysis (3 males, 69 females). The model that contained random intercepts for sex and cohort was selected as best to explain Southern Flounder growth rates during the second year of life (Table 2). Random intercepts were highest for females and the 2006 year-class (Figure 6). Growth rates did not differ among contingent types during the second year of life (Figure 4c).

3.2 Condition among age-specific contingents

Twenty-six age-0 Southern Flounder were included in the analysis, and transient and estuarine contingents had higher condition than freshwater contingents (Figure 7a). Condition indices of estuarine and transient flounder were statistically similar ($p =$

0.391), and condition indices of transient and freshwater flounder were statistically similar (*p* = 0.158). However, the condition of age-0 estuarine flounder was significantly higher than the condition of age-0 freshwater flounder (*p* = 0.004).

One hundred sixty Southern Flounder were used in the age-1 condition analysis (27 males, 133 females). The model that contained a random intercept for sex was selected as best to explain age-1 Southern Flounder condition (Table 3). The random intercepts were highest for females (Figure 8). Condition indices of estuarine and transient flounder were statistically similar (*p* = 0.651), and condition indices of transient and freshwater flounder were statistically similar (*p* = 0.651). However, the condition of age-1 estuarine flounder was significantly higher than the condition of age-1 freshwater flounder (*p* = 0.007; Figure 7b).

Thirty-nine Southern Flounder were used in the age-2 condition analysis (3 males, 36 females). The condition of age-2 Southern Flounder did not differ between contingent types (Figure 7c).

4. Discussion

Physiological and behavioral responses (e.g. metabolic rates, movement patterns, feeding rates) resulting from dynamic abiotic factors within estuaries impact growth rates and condition of flatfish (Brett & Groves 1979, Iwama et al. 1999, Taylor & Miller 2001). Our results support previous work (e.g., Malloy & Targett 1991, Henne & Watanabe 2003, Glass et al. 2008, O'Neill et al. 2011, Howson & Targett 2019) that found salinity to be an important factor for growth and condition of Southern Flounder and other flatfish, especially during early life. The distinct salinity gradient and observed differences in growth rates and condition among Southern Flounder contingent types during the first year of life in Mobile Bay suggests the estuary may vary spatially in habitat value (Lankford & Targett 1994, Glass et al. 2008, Midway et al. 2015). This study expanded knowledge on flatfish growth rates and condition because it led to understanding differences among age-specific resident and migratory contingents across salinity gradients in single estuary systems without the caging limitations presented in previous studies (Guindon & Miller 1995, Meng et al. 2000, Phelan et al. 2000).

Our results indicated that contingent type is an important factor used to determine Southern Flounder growth rates and condition in Mobile Bay during the first year of life. We found that optimal growth occurred for age-0 and first-year Southern Flounder classified as estuarine contingents in Mobile Bay (salinities > 1 psu), which is consistent with our hypothesis (*H1*), as well as the results of Henne & Watanabe (2003) and Howson & Targett (2019). Growth rates and condition of age-0, first-year, and age-1 transient contingents were not significantly different than estuarine residents, suggesting there may be nutritional benefits of moving that outweigh the costs of energy expenditure and predation risk. These responses may be associated with life-history characteristics as larvae are spawned offshore in high salinity waters and migrate to estuaries. Juveniles may grow faster as transient or estuarine contingents during the first year of life since more time and energy would likely be required to reach the freshwater habitats in the Delta. Since freshwater contingents spent at least 90% of their short lives in the Delta, energy allocated to growth may have instead been used for migration, buoyancy maintenance, and osmoregulation during the larval and juvenile stages (Brett 1979, Moustakas et al. 2004, Howson & Targett 2019). Sampio and Bianchini (2002) found that growth rates of another juvenile Paralichthyd flounder (Brazillian flounder, *Paralichthys* orbinyanus) were lower in freshwater possibly due to energy expenditure involved in osmoregulation. Additionally, freshwater habitats within estuaries are associated with maximum turbidity, which could impair visibility when searching for food (Schubel 1968).

River-dominated estuaries like Mobile Bay are highly productive ecosystems where nutrients are incorporated into coastal food webs (Abrantes et al. 2015). Mobile Bay has extremely high rates of river discharge, suggesting that nutrients can be transferred to estuarine habitats during periods of high flow. High nutrient concentrations and peak phytoplankton production can also be found in mesohaline regions as they are regenerated from particulate decomposition in the summer after periods of high river flow in winter and spring (Kemp & Boynton 1984). Therefore, the observed patterns in early life growth and condition of Southern Flounder may also be explained by spatial trends in estuarine primary production. This primary production in estuarine habitats can fuel more energetically dense prey for Southern Flounder.

In our Mobile Bay study, mean growth rates of age-0 Southern Flounder were 1.06 mm d^{-1} (range 0.71 – 1.53 mm d^{-1}) for estuarine residents, 0.91 mm d^{-1} (range 0.50 – 1.41 mm d^{-1}) for transient contingents, and 0.72 mm d^{-1} (range 0.53 – 0.980 mm d^{-1}) for freshwater residents. Our values were estimates since daily growth rings were not counted and hatch dates were assumed to be January 1st. Age-0 Southern Flounder ranged from 52 – 307 mm in this study, which is a broad size-range and these larger juveniles could be growing faster than smaller juveniles as in other studies (Glass et al. 2008). Nevertheless, mean age-0 Southern Flounder growth rates in our study fell in the ranges of other age-0 *Paralichthys* species including Southern Flounder (1.20 – 1.40 mm d^{-1}, Reichert & van der Veer 1991; 0.21 – 0.76 mm d^{-1}, Glass et al. 2008; 0.40 – 1. 50 mm d^{-1}, Howson & Targett 2019), Summer Flounder (*Paralichthys dentatus*; 0.50 – 1.30 mm d^{-1}, Reichert & van der Veer 1991), and Japanese Flounder (*Paralichthys olivaceus*; 0.34 – 0.94 mm d^{-1}, Gwak et al. 2003). High growth results found in our study and Howson & Targett (2019), in conjunction with the largest observed random intercepts of recent cohorts in our first-year growth analysis (2015 – 2018; Figure 4a), suggest that juvenile Southern Flounder growth rates may have accelerated in recent years. Potential reasons for this include decreased competition and density-dependence due to high mortality rates leading to declining juvenile abundance (see Chapter 1), variable environmental conditions, or fishing-induced evolution of adults, which could select for younger age-at-maturity and faster growth (Enberg et al. 2012).

Although larger individuals have advantages over smaller individuals (e.g., size-dependent predation and greater ability to escape), habitats that promote higher growth rates are often associated with higher predation risk (Werner & Anholttt 1993). In Mobile Bay, Southern Flounder appear to have higher growth rates and condition within estuarine habitats during their first year of life, but a behavioral tradeoff may be made since they could be more susceptible to mortality (Sogard 1997). Future studies that aim to quantify juvenile Southern Flounder mortality rates across salinity gradients would be useful to see if higher predation was occurring in estuarine habitats that promote fast growth in Mobile Bay.

We also found that optimal condition occurred for age-1 Southern Flounder classified as transient and estuarine contingents in Mobile Bay. Males had the highest random intercept for sex in the age-1 condition analysis, suggesting that age-1 males may have higher condition and energetic reserves than age-1 females (Figure 7). Although males had higher condition, females had the highest random intercepts for annual growth in the first- and second-year annual growth analyses (Figure 4b, Figure 5). Age-1 female Southern Flounder may be putting more energy toward growth, while males may be allocating their energy toward fat reserves, resulting in elevated condition.

Results differed from our hypothesis (*H2*) since growth rates and condition did not differ among Southern Flounder contingent types for older individuals in the age-2 condition and second-year growth analysis. Nelson (1969) found that salinity influenced the distribution and growth rates of juvenile Atlantic croaker (*Micropogonias undulatus*), another economically important estuarine fish, more than adults. The only other Paralichthyd flounder found in Mobile Bay is the Gulf Flounder (*Paralichthys albiguttata*). Adult Gulf Flounder are found in high salinity waters so a lack of co-occurrence could allow age-2 Southern Flounder to use and benefit from habitats across the salinity gradient in Mobile Bay (Glass et al. 2008).

Sustainable management of the declining species along the Gulf of Mexico is crucial in the face of climate change. Over the next one hundred years, the Gulf of Mexico region is expected to see increased durations of dry conditions and increased intensity of precipitation events, as well as increased durations of heat waves and decreased cold snaps (Diffenbaugh et al. 2005, Biasutti et al. 2012). Increased periods of dry conditions or intense rainfall could alter the amount of freshwater input that enters each estuary, thus altering growth rates and condition of Southern Flounder, especially for juveniles. Because human activity is typically highest within close proximity to the coasts, estuarine environments are strongly influenced by anthropogenic stressors and fishing pressure, which could exacerbate these negative effects of climate change. This is concerning for estuarine species, especially those that use estuaries for nurseries or experience ontogenetic habitat shifts throughout their lifetimes (Ong et al. 2015).

Growth and condition were highest for young-of-the-year Southern Flounder that were classified as transient or estuarine contingents, and it is important to protect habitats so these individuals can survive to the harvestable stage. Therefore, these habitats could also be productive for estuarine fishes that serve as prey and predators of Southern Flounder. Our work can assist managers in setting user group expectations for the productivity of Southern Flounder populations along the northeastern Gulf of Mexico. Additionally, ADCNR/MRD recently developed a stock enhancement program, and the results of this study could help in selecting locations to stock new recruits so they may have the best chances of growing rapidly and surviving at higher rates. Ultimately, these results may assist with ongoing habitat conservation and restoration efforts to support high quality habitats of estuarine fishes.

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TABLES

Table 1. Random effect model structure for first-year growth analysis. The models were listed in order from most to least optimal, and were fitted using restricted maximum likelihood estimation. *df* = degrees of freedom. *LL* = log likelihood.

Random effect growth covariates	**df**	**LL**	**AICc**	**ΔAICc**	**Weight**
Cohort + Age at capture + Sex	7	-1485.7	2985.9	0.0	0.949
Cohort + Sex	6	-1489.7	2991.7	5.8	0.051
Age at capture + Sex	6	-1501.8	3015.9	30.0	<0.001
Cohort + Age at capture	6	-1508.9	3030.0	44.1	<0.001
Cohort	5	-1510.6	3031.3	45.5	<0.001
Age at capture	5	-1525.8	3061.9	76.0	<0.001
Sex	5	-1527.7	3065.7	79.8	<0.001

Table 2. Random effect model structure for second-year growth analysis. The models were listed in order from most to least optimal, and were fitted using restricted maximum likelihood estimation. *df* = degrees of freedom. *LL* = log likelihood.

Random effect growth covariates	df	LL	AICc	ΔAICc	Weight
Sex	5	-326.9	664.8	0.0	0.675
Age at capture + Sex	6	-326.5	666.4	1.6	0.306
Age at capture	5	-330.5	671.9	7.1	0.019

Table 3. Random effect model structure for the age-1 condition analysis. The models were listed in order from most to least optimal, and were fitted using restricted maximum likelihood estimation. *df* = degrees of freedom. *LL* = log likelihood.

Random effect growth covariates	**df**	**LL**	**AICc**	**ΔAICc**	**Weight**
Sex	5	314.1	-617.8	0.0	0.670
Cohort + *Sex*	6	314.4	-616.2	1.6	0.300
Cohort	5	311.0	-611.6	6.2	0.030

FIGURES

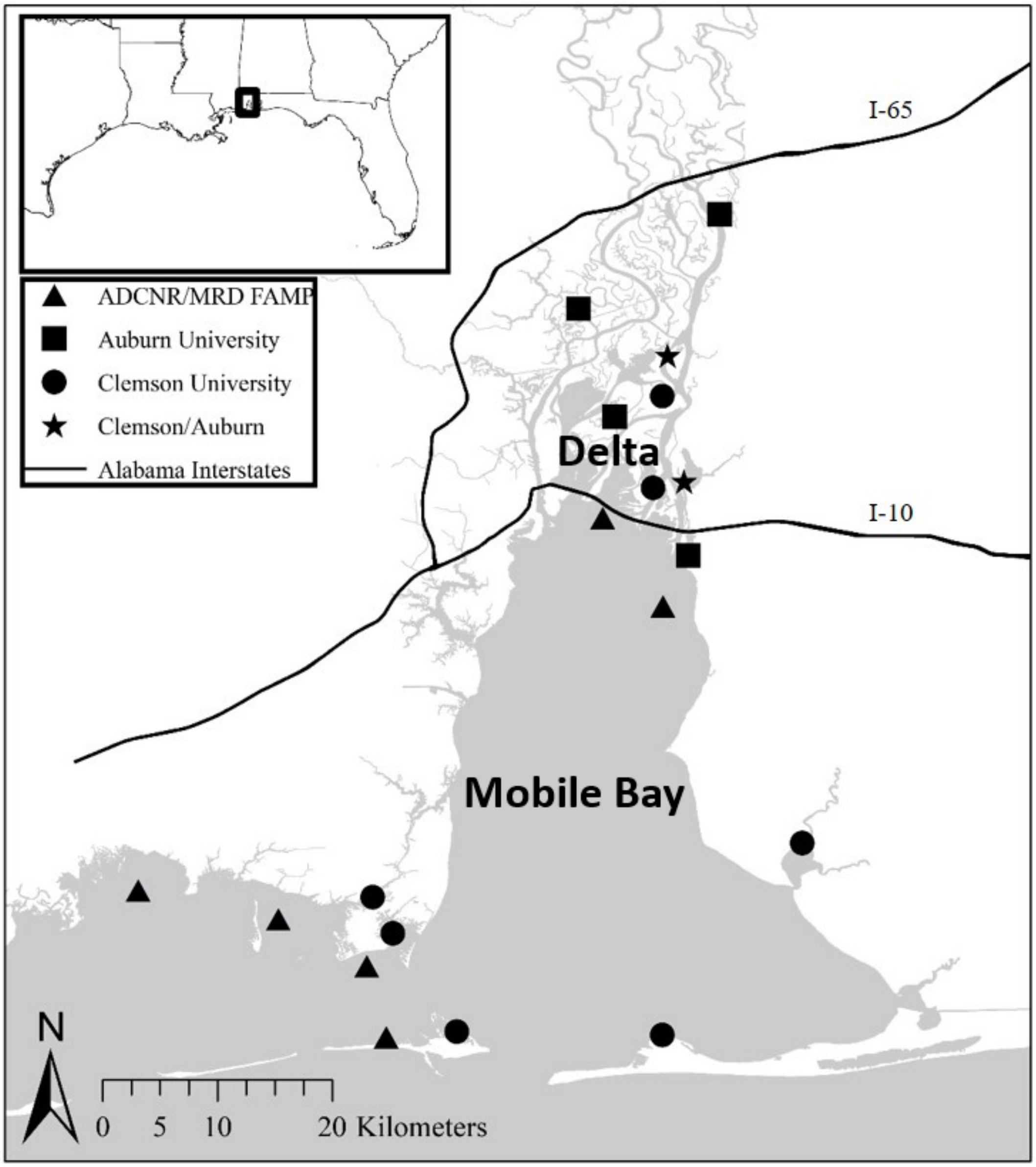

Figure 1. Southern Flounder were collected at twenty stations in Alabama by Alabama Department of Conservation and Natural Resources, Marine Resources Division's (ADCNR/MRD's) Fisheries Assessment and Monitoring Program (FAMP; 2018 – 2019; triangles), Auburn University (2005 – 2007; squares, stars), and Clemson University (2018 – 2019; circles, stars). Southern Flounder harvested in freshwater habitats were collected from the Delta (north of I-10). Southern Flounder harvested in estuarine habitats were collected from Mobile Bay (south of I-10).

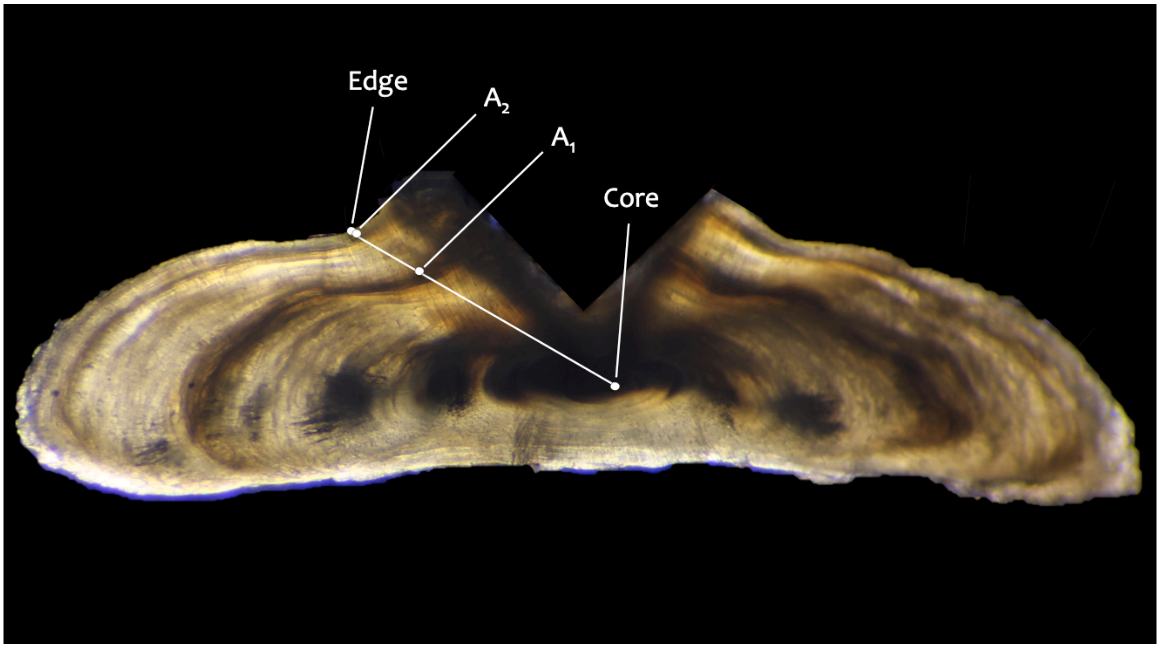

Figure 2. Sectioned right sagittal otolith from an age-2 Southern Flounder. Transects were drawn along the ventral side of the sulcal groove. Growth increments were measured (mm) from the core to the end of the first annulus (A_1), from the first to the second annulus (A_2), and from the core to the edge.

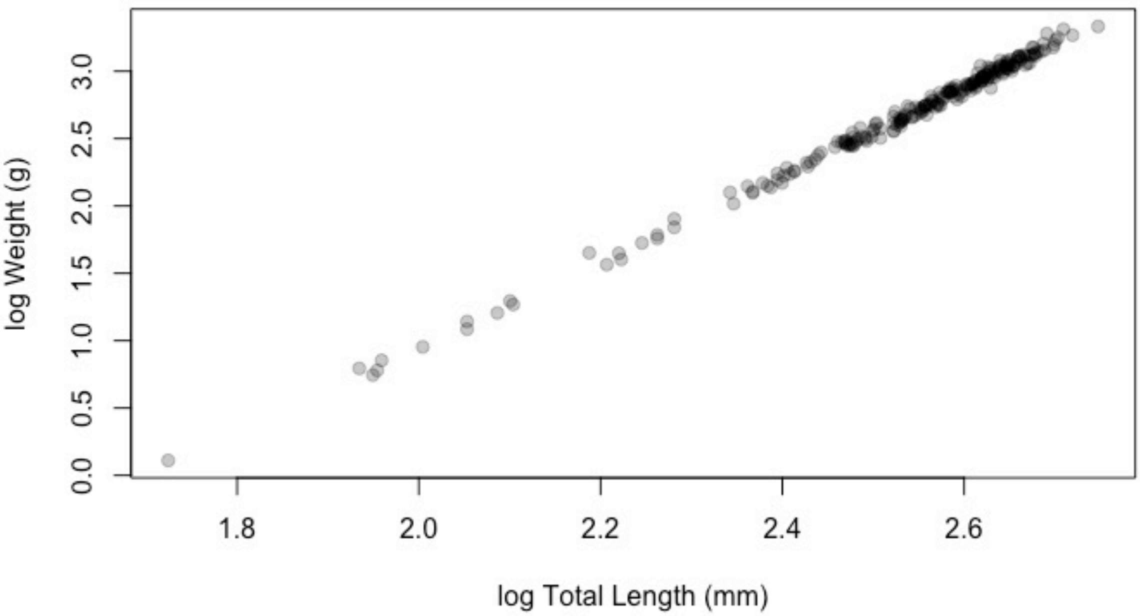

Figure 3. Residuals of the $\log_{10}$ total lengths (mm) fitted against the $\log_{10}$ weights (g) of Southern Flounder (ages 0 – 2) in Mobile Bay, AL.

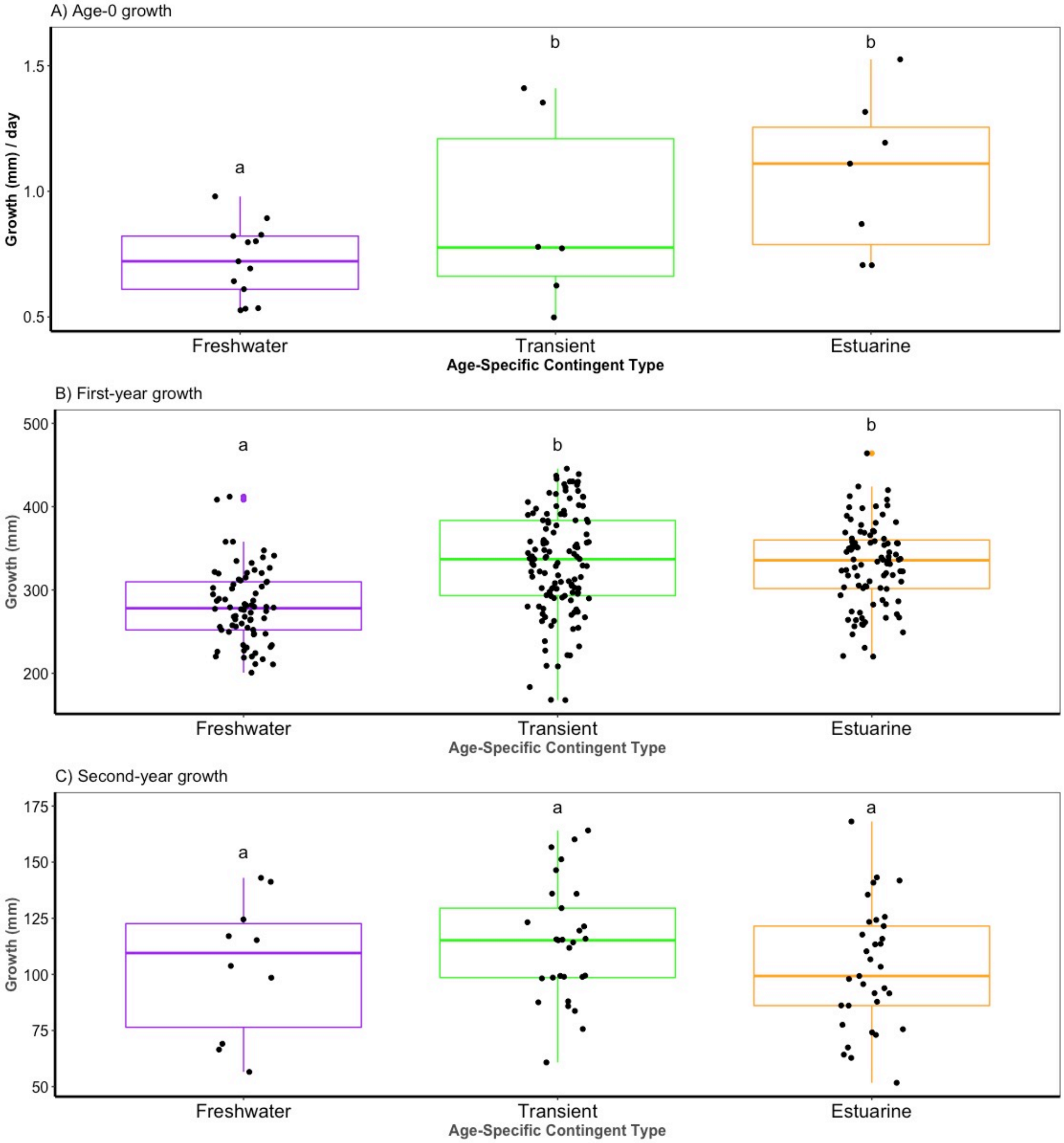

Figure 4. Southern Flounder A) observed age-0 growth rates (size at collection divided by number of days at large [assuming January 1 hatch date]), B) annual back-calculated first-year growth, and C) annual back-calculated second-year growth of freshwater (purple), transient (green), and estuarine (orange) Southern Flounder contingents in Mobile Bay, AL. The lower case letters indicate significant differences ($p < 0.05$) among age-specific contingent types.

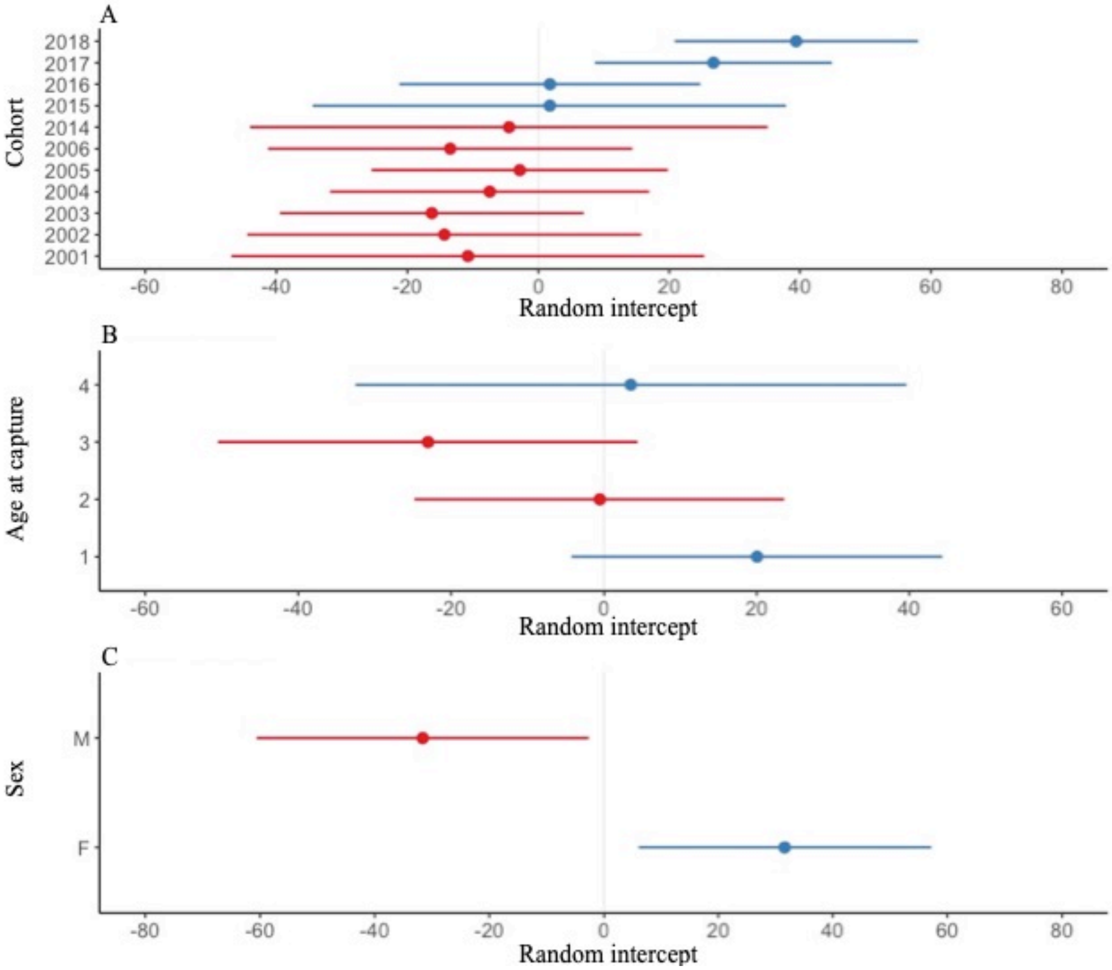

Figure 5. Random intercepts for each A) cohort, B) age at capture, and C) sex derived from the model that best explained growth rates among contingent types in the first-year growth analysis. Blue circles represent values greater than the mean, and red circles represent those less than the mean.

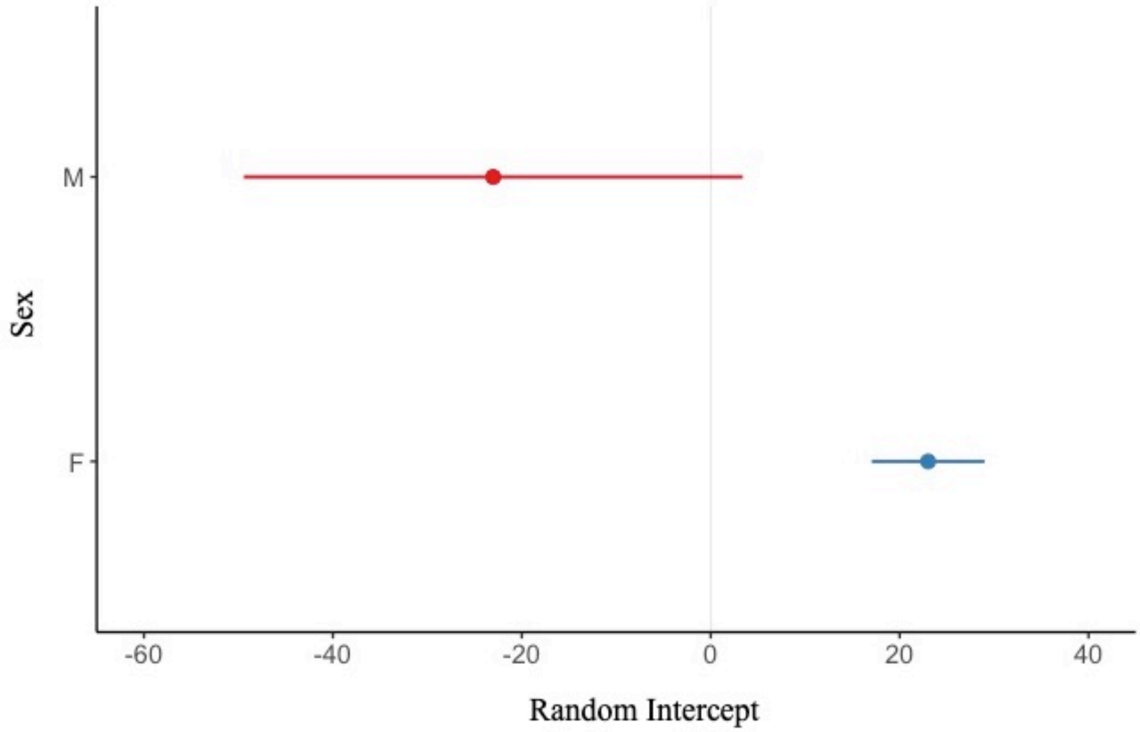

Figure 6. Random intercepts for each sex derived from the model that best explained growth rates among contingent types in the second-year growth analysis. The blue circle represents a value greater than the mean, and the red circle represents a value less than the mean.

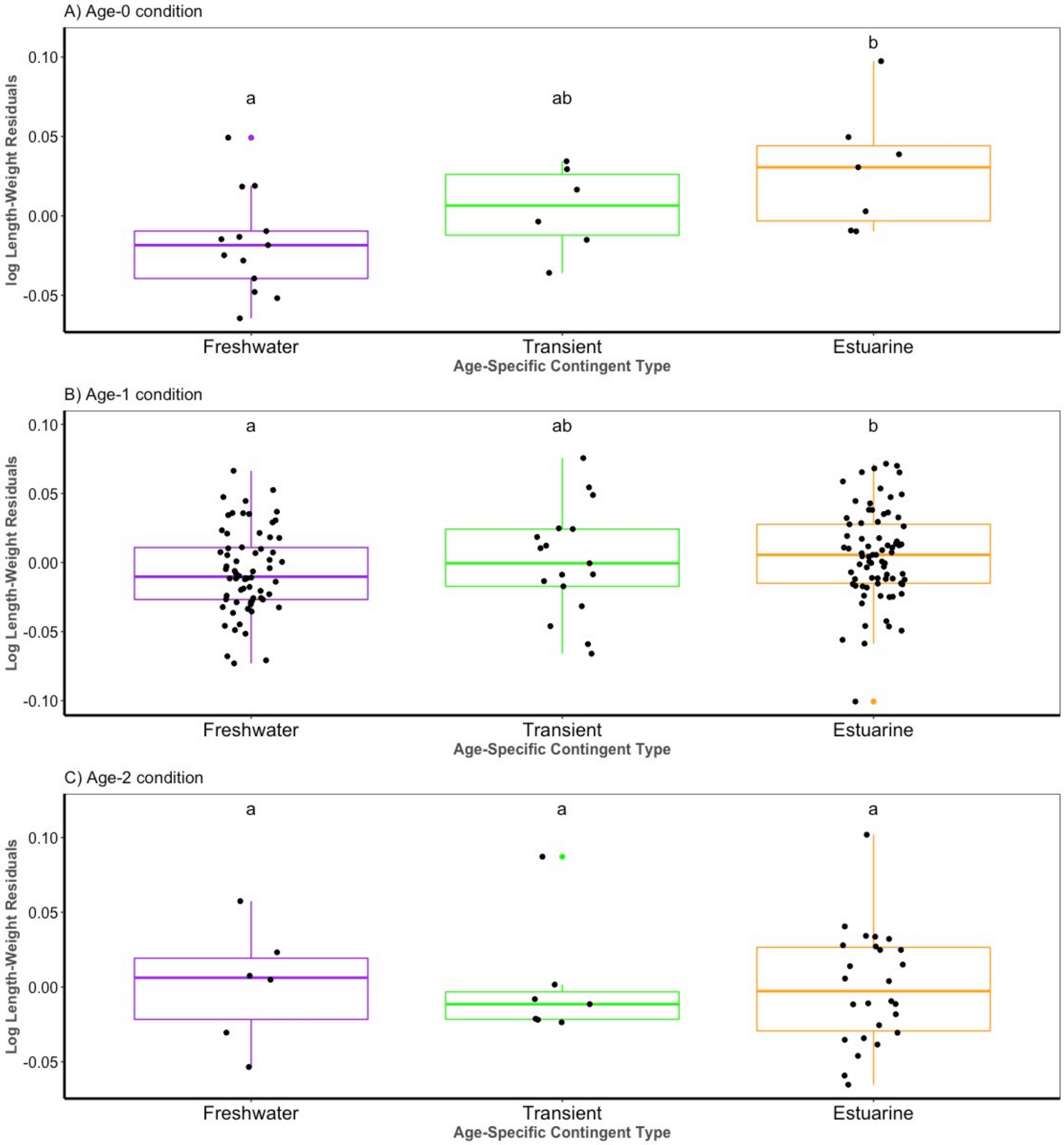

Figure 7. Southern Flounder A) age-0 condition (residuals of the $\log_{10}$ weight versus $\log_{10}$ total length relationship), B) age-1 condition, and C) age-2 condition of freshwater (purple), transient (green), and estuarine (orange) Southern Flounder contingents in Mobile Bay, AL. The lower case letters indicate significant differences ($p < 0.05$) among age-specific contingent types.

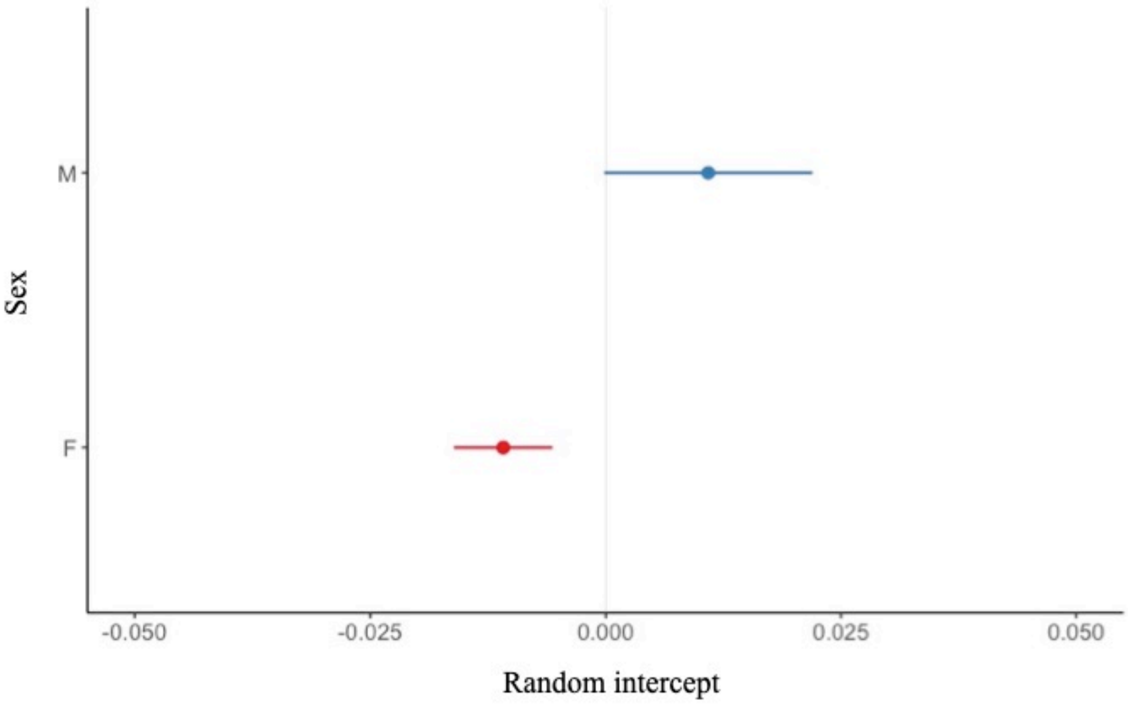

Figure 8. Random intercepts for each sex derived from the model that best explained condition among contingent types in the age-1 condition analysis. The blue circle represents a value greater than the mean, and the red circle represents a value less than the mean.