

THE EFFECTS OF CLIMATE VARIABILITY ON THE TIMING OF ICHTHYOPLANKTON
INGRESS THROUGH BEAUFORT INLET, NC, USA

By

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Climate change has shifted the timing of seasons in many ecosystems worldwide. Species are responding to these shifting seasons with shifts of their own, both in space via migrations and in time via phenology. However, species vary in the direction and magnitude of these spatial and temporal shifts. As the effects of climate change become more pronounced, this variation in the response of species may disrupt interspecific interactions in ecological communities. Research into the responses of species to climate change is therefore critical to understanding how ecosystems may function in the future.

In this thesis I examined one way in which the fall and winter ichthyoplankton community of Beaufort Inlet, North Carolina has responded to environmental variability over the last 27 years. I related changes in sea surface temperature, the Atlantic Multidecadal Oscillation, the North Atlantic Oscillation, offshore wind phenology, nearshore wind strength, and tidal height to the time at which ten species of larval fish ingressed through Beaufort Inlet. I also examined whether any species had exhibited trends in ingress phenology over the last three decades. Species varied in the magnitude of their responses to all of the environmental variables studied, but most shared a common direction of change. Sea surface temperature and northerly wind strength appear to have the largest impact on ingress phenology, with most species advancing their ingress during warm years and delaying ingress during years of strong northerly

winds. As sea surface temperatures warm in the coming decades, the average timing of ingress of some species may advance on the order of weeks to months, assuming temperatures do not exceed a threshold at which species can no longer respond. These shifts in ingress could affect the chances of survival of larvae since environmental conditions in the estuarine and pelagic nursery habitats of fishes also vary seasonally. The extent to which larval survival is affected by their changes in phenology will depend on how climate change shapes conditions in estuarine and coastal habitats.

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INGRESS THROUGH BEAUFORT INLET, NC, USA

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DEDICATION

This thesis is dedicated to my granddaddy, who taught me to bait a hook, drive a boat, clean a fish, and love the coast. You led my first science class on “The Keeper”, and your hot dogs, egg rolls, sausage balls, love, support, and prayers have gotten me through everything since. Thanks for helping me finish strong these last few months.

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TABLE OF CONTENTS

LIST OF TABLES	viii
LIST OF FIGURES	ix
CHAPTER 1: SYSTEM OF STUDY OVERVIEW: CLIMATE CHANGE, EARLY LIFE HISTORY, AND THE SOUTH ATLANTIC BIGHT	1
Section 1.1: Ichthyoplankton phenology and climate change	1
Section 1.2: Oceanography and ichthyoplankton transport in the South Atlantic Bight, Onslow Bay, and Beaufort Inlet.....	7
Section 1.3: The NOAA SWFSC Bridgenet database	13
Section 1.4: Research objectives.....	14
Section 1.5: Literature cited.....	16
CHAPTER 2. HISTORIC CHANGES IN ICHTHYOPLANKTON PHENOLOGY AND RELATIONSHIPS TO ENVIRONMENTAL VARIABLES	22
Section 2.1: Introduction.....	22
Section 2.2: Methods	24
Section 2.2.1: Bridgenet sampling design.....	24
Section 2.2.2: Calculation of phenology indices	25
Section 2.2.3: Phenology changes over time	26
Section 2.2.4: Environmental influences on phenology: Linear regression ..	27
Section 2.2.5: Principle component analysis and regression	27
Section 2.2.6: Environmental metrics.....	28
Section 2.3: Results.....	32
Section 2.3.1: Historic variation and trends in ingress phenology	32

Section 2.3.2: Phenology and the environment: Linear regression	33
Section 2.3.3: Phenology and the environment: Principle component analysis and regression	36
Section 2.4: Discussion.....	38
Section 2.4.1: Temporal changes in ingress phenology.....	38
Section 2.4.2: Community trends in ingress phenology and the environment	39
Section 2.4.3: Species level trends in ingress phenology and the environment	44
Section 2.4.4: Conclusions.....	46
Section 2.5: Literature cited.....	79
CHAPTER 3: MANAGEMENT IMPLICATIONS, FUTURE RESEARCH DIRECTIONS, AND CONCLUSIONS	87
Section 3.1: Management implications.....	87
Section 3.2: Future research directions.....	89
Section 3.3: Conclusions.....	92
Section 3.4: Literature Cited	94

LIST OF TABLES

Table 2.1a. Taxonomy and basic life history of species studied	50
Table 2.1b. Life history of species.....	51
Table 2.1c. Transport of species and relationships to the environment.....	52
Table 2.2: Linear mixed models of community changes in larval fish ingress phenology over time	53
Table 2.3: Linear mixed models of environmental effects on community changes in larval fish ingress phenology	54
Table 2.4: Principle component analysis of environmental variables	55
Table 2.5: Principle component regressions of environmental effects on community ingress phenology.....	56
Table 2.6: Principle component regressions of environmental effects on ingress phenology of species.....	57
Table S2.1: Phenology metrics removed for each species and the reason for their removal	63
Table S2.2: Results from linear models of temporal changes in ingress phenology of species.....	66
Table S2.3: Results of the best fitting linear models of ingress phenology of species as a response to the environment.....	67

LIST OF FIGURES

Figure 1: Map of study site	15
Figure 2.1: Temporal change in ingress phenology	58
Figure 2.2: Boxplots of temporal trend in each species' phenology metrics	59
Figure 2.3: Added-variable plots of environmental metrics included in best models of ingress of the community	60
Figure 2.4: Boxplots of effects of environmental factors on species' phenology metrics.....	61
Figure 2.5: Biplots of principle components.....	62
Figure S2.1: Cumulative density of <i>Brevoortia tyrannus</i> caught over time during the 2009 Bridgenet season	69
Figure S2.2: Correlation plots of sea surface temperature anomalies measured by buoys, weather stations, and satellite observations	70
Figure S2.3: Correlation plots of daily east and north wind vector observations from buoys, weather stations, and satellite	71
Figure S2.4: Wind climatology of weather stations and satellite observations in the South Atlantic Bight.....	72
Figure S2.5: Cumulative wind stress in the northwest direction observed in Onslow Bay during the fall/winter of 1990 and spring of 1991.....	73
Figure S2.6: Added-variable plots of environmental metrics included in best models of ingress of species	74

CHAPTER 1: SYSTEM OF STUDY OVERVIEW: CLIMATE CHANGE, EARLY LIFE HISTORY, AND THE SOUTH ATLANTIC BIGHT

Section 1.1: Ichthyoplankton phenology and climate change

Many organisms rely on the environment to signal the timing of life history events, such as metamorphosis, migration, or reproduction (Visser & Both 2005). The seasonal timing of these events is referred to as phenology. The specific cues responsible for the phenology of an organism must be detectable, predictable, and capable of producing a response in the organism. Oftentimes, these cues have evolved due to their link to the success of the life history event they trigger (Pankhurst & Porter 2003). The result of this is often a direct connection between an individual's fitness and its environment, or, in the case of reproduction, the environment of its parents.

Fish reproductive phenology is an example of how species have evolved to breed during conditions that can maximize the chance of survival of their offspring. Many species of fishes utilize estuaries or other nursery areas during the larval and juvenile stages, and spawn at times that coincide with prey abundance in these nursery areas (Cushing 1990, Fortier & Cagne 1990). Fish reproduction takes place over an extended period of time with gonadal maturation and gamete development taking weeks to months (Lowerre-Barbieri et al. 2011). Due to this, most fishes do not use food abundance itself as a cue to reproduce, but rather rely on a suite of environmental cues that, though temporally separated from the arrival of their offspring to nurseries, have evolutionarily correlated with optimal nursery conditions at this time of arrival (Pankhurst & Porter 2003). These cues may also be spatially separated from the nurseries of fish whose larvae are transported through advection by currents far from the spawning and feeding grounds of the adult population (Cushing 1990).

For the majority of fishes that have been studied, these cues are often photoperiod and temperature (Pankhurst & Munday 2011). Though the mechanisms by which these cues are transduced into hormonal responses is not entirely understood, their general effects on the behavior and reproductive biology of many species is known. For example, temperature's interaction with the hypothalamo-pituitary-axis has been shown to influence the rate of embryogenesis and hatching time in females and reproductive hormone synthesis in both sexes (Pankhurst & Munday 2011). Fish pineal glands are sensitive to photoperiod, with annual changes in photoperiod resulting in changes in melatonin levels (Pankhurst & Porter 2003). Photoperiod, the annual pattern of which remains mostly unchanged from year to year, is responsible for signaling the beginning of gonadal development; whereas temperature, which has higher interannual variability, is thought to synchronize the final stages of reproductive maturation with optimal environmental conditions for offspring (Pankhurst & Porter 2003). Generally, increased temperatures are believed to advance and shorten the spawning duration of spring-spawning fishes; delay maturation, ovulation, and spawning of fall spawners; and advance the spawning of summer spawners (Pankhurst & Munday 2011). These effects on spawning may be confounded by temperature effect on offspring, though, as warmer water can also accelerate embryonic and larval development on the scale of hours to days (Pankhurst & Munday 2011).

Other biological events that depend on temperature cues, such as bird and butterfly migrations, bird nesting, plant flowering, and frog breeding have responded to climate change with shifts in phenology over the past century (Parmesan & Yohe 2003, Cohen et al. 2018). The intimate link between fish reproduction and temperature makes fishes especially sensitive to climate change as well. Over the past century, sea surface temperature (SST) has risen at a global average rate of 0.13°C per decade, a rate that is increasing (IPCC 2014). Changes in reproductive

phenology have been observed for fishes in the North Sea, California Current, and Bay of Biscay (Edwards & Richardson 2004, Genner et al. 2010, Asch 2015, Chevillot et al. 2017). These changes have been correlated to variation in physical processes, such as SST, stratification, and upwelling events.

Variations in phenology occur most often in populations that already experience a wide range of thermal conditions, and thus already possess the genetic variation to adapt to changing temperatures (Pankhurst & Munday 2011, Anderson et al. 2013). Individual shifts in phenology, therefore, display organisms' adaptability to climate change and climate variability, which at face value might seem positive. When shifts in phenology across different species do not occur synchronously there is potential for ecosystem function and structure to be disrupted. Long-term studies have shown that trophic levels are differentially sensitive to climate change in grasslands (Voigt et al. 2003), many shifts in bird reproductive phenology are lagging behind phenology shifts in the food sources of their offspring (Visser et al. 2012), and disrupted plant-pollinator relationships are partially due to and increased frequency of phenology mismatches (Burkle et al. 2013). Similarly, differences in climate sensitivity have been seen across trophic levels in marine pelagic systems (Edwards & Richardson 2004). Coupled with the fact that the effects of climate change are occurring faster in marine than terrestrial systems (Poloczanska et al. 2013), this highlights the need for further research into what specific phenology shifts we can expect climate change to cause in the ocean (Burrows et al. 2011).

One possible result of climate change is a reduction in the seasonal overlap between the abundance of larval fish in nurseries and the abundance of prey. As mentioned earlier, fish spawning is initiated by environmental cues that are evolutionarily associated with an abundance of prey for their offspring, primarily mesozooplankton (Pankhurst & Porter 2003). Primary

production and subsequent zooplankton abundance are inherently variable from year to year, so these environmental cues correlate with the highest probability of matching phenology between larvae and prey rather than a guaranteed match between the two (Anderson 1988). The Match-Mismatch Hypothesis proposes the frequency of “matches” between offspring and prey can be related to recruitment in populations, with the likelihood of higher recruitment greater for larvae born into productive waters with an abundance of food (Cushing 1969, Cushing 1990).

The rationale behind the Match-Mismatch Hypothesis is based on the idea that larval fish survival is dependent on them reaching a critical size, at which the risk of mortality steeply declines (Anderson 1988). Whether this mortality is primarily due to direct starvation or to increased predation is subject of debate (Anderson 1988). It is generally accepted that recruitment is the result of both density-independent and density-dependent survival of larval and juvenile fishes, which results from the influence of food availability on growth rates and subsequently how quickly fishes can reach critical size (Shepherd & Cushing 1980). Density-dependent growth moderates some of the interannual variability in recruitment that arises from variability in prey abundances (Reed et al. 2013), but for the most part recruitment fluctuates greatly from year to year (Shepherd & Cushing 1980). Due to this, many fish populations rely on the infrequent “good year” of recruitment to maintain population size rather than depend on steady levels of recruitment each year (Anderson 1988; Tolimieri & Levin 2005). It is worth noting, though, that fishes display a diversity of life-history strategies, and no recruitment hypothesis can encapsulate this diversity and be relevant for all fish species (Winemiller & Rose 1992).

Though Cushing’s hypothesis was initially focused on the match between temperate marine populations and the system’s typical spring phytoplankton bloom, the Match-Mismatch

Hypothesis can be applied to many predator-prey relationships and provides a theoretical framework for assessing how phenology shifts may affect recruitment in fish populations globally. It was traditionally thought that fish reproduction was relatively constant compared to variability in primary and secondary production in the ocean and that this variability in production was, therefore, the driver behind matches and mismatches (Cushing 1990). It is now acknowledged that the timing of both fish spawning and plankton productivity are variable and subject to shift with climate change (Durant et al. 2007). Zooplankton phenology, like that of fish, has been shown to vary with environmental cues, specifically water temperature, wind patterns, water column stratification, chlorophyll concentrations, and predation (Mackas et al. 2012). Zooplankton and fish reproductive phenology may differ in the cues to which they respond, or they may respond to similar cues in different ways. If fishes and zooplankton respond differentially to climate change, correlations between environmental cues and favorable nursery conditions may deteriorate, likely resulting in less frequent matches, increased starvation and predation on larval fishes in nurseries, and poor recruitment in populations. Shifts in phenology may also lead to increased (decreased) overlap in the abundance of larvae and that of their predators, which would also result in increased (decreased) predation on larval fish and poor (better) recruitment. For example, the spatial and temporal overlap between post-settlement juvenile *Pseudopleuronectes americanus* (winter flounder) and their predator *Crangon septemspinosus* (sand shrimp) has been related to significant predation mortality of the fish in Narragansett Bay and the Niantic River (Taylor 2005). Cnidarians and ctenophores are also known predators of fish larvae and eggs (Purcell 1985). Evidence suggests that the spatiotemporal distribution of one species of cnidarian, *Chrysaora quinquecirrha*, in the Neuse River Estuary in North Carolina relates to environmental variables, such as wind (Kaneshiro-

Pineiro & Kimmel 2015). Environmental effects on the phenology of both the fish and their predators may drive rates of predation on ichthyoplankton.

This increase in mismatches is likely to coincide with an increased metabolic demand for prey among larval fishes. Water temperature directly influences the growth rates and basic metabolic needs of most poikilothermic organisms (Ricker 1979). Even small temperature changes can greatly increase both of these rates among fishes (Anderson 1988). Though a combination of warmer waters and abundant food can result in higher-than-average recruitment years, increased metabolic demands can lead to increased starvation in years where mismatches occur (Pankhurst & Munday 2011). This increase in starvation may be further exacerbated by other consequences of climate change, such as ocean acidification and deoxygenation. Moderate increases in ocean acidity have been shown to affect fish olfaction, resulting in decreased foraging efficiency and increased predation (Munday et al. 2009). Climate-related expansion of oxygen minimum zones reduce suitable habitat for organisms across trophic levels (Prince et al. 2010, Netburn & Koslow 2015). Earth system models project that changes in ocean temperature, stratification, and biogeochemistry may result in global declines in primary and secondary production, which will have cascading effects on fisheries production (Bopp et al. 2013, Stock et al. 2014, Stock et al. 2017). In summary, mismatches between larval fishes and their prey due to climate-related shifts in phenology may be occurring at a time when matches are especially critical to recruitment.

This highlights the need for an increase in the understanding of phenology shifts expected to occur in both ichthyoplankton and zooplankton abundances worldwide. Management tactics can be adjusted to account for declines in recruitment due to increasing mismatches, but regional-specific studies need to be conducted to assess the magnitude of phenology shifts and

the severity of potential mismatches (Asch 2015). The ability to study these phenology shifts is often limited by historical knowledge of the timing of their occurrences (Visser & Both 2005). Long-term time series of the temporal distribution of ichthyoplankton offer the best look at how reproductive phenology has varied over time, but comparisons between current ichthyoplankton phenology and studies from past decades also offer some insight (Koslow & Wright 2016).

Section 1.2: Oceanography and ichthyoplankton transport in the South Atlantic Bight, Onslow Bay, and Beaufort Inlet

The longest-running, continuous time series of ichthyoplankton collections on the United States' East Coast has been recorded in Beaufort Inlet, North Carolina (Ortner et al. 1999). Since 1986, the National Oceanic and Atmospheric Administration's (NOAA's) Southeast Fisheries Science Center "Bridgenet" program has made late fall to early spring collections of larvae from Beaufort Inlet, *en route* to estuarine nursery habitat. This time series, which is described in detail in *Section 1.3*, offers insight into the interannual variation of ichthyoplankton phenology in this estuarine nursery habitat.

The ichthyoplankton community of Beaufort Inlet was well-studied in the 1980s and 1990s as both a precursor to, and a part of, NOAA's South Atlantic Bight Recruitment Experiment (SABRE). The goal of SABRE was to understand the relationship between environmental variation and recruitment variability of fishes in the South Atlantic Bight (Ortner et al. 1999). These studies included characterizations of ichthyoplankton temporal abundance, age, and size (Hettler & Chester 1990, Warlen & Burke 1990); the implications of the inlet flow dynamics on larval fish transport (Hettler & Hare 1998, Churchill et al. 1999a, Churchill et al. 1999b, Forward et al. 1999); influence of hydrodynamics along the continental shelf on larval

fish transport (Hare et al. 1999, Quinlan et al. 1999, Rice et al. 1999, Werner et al. 1999); daily variability in larval fish ingress (Hettler et al. 1997, Forward et al. 1999, Joyeux 1999); and comparisons of Beaufort's ichthyoplankton community to that of nearby inlets (Hettler & Barker 1993).

The southern-facing Beaufort Inlet is the primary route of larval fish ingress to the estuarine nurseries of Newport River and Bogue Sound to the west, and North River and Back Sound to the east, which are connected via Core Sound to the much larger Albemarle-Pamlico Estuarine System (Figure 1). A regularly-dredged navigation channel beginning at the Morehead City port and running 3.5 km offshore links the inlet to the estuarine systems located west of the inlet (Churchill et al. 1999a). Three other channels, the Shackleford Channel, Bird Shoal Channel, and Bulkhead Channel (Radio Island Channel), branch from the Morehead City Channel and direct water northward and eastward from the inlet (Figure 1; Churchill et al. 1999a). These channels are responsible for the tidal exchange of the system's estuaries. Studies of the water circulation of the inlet have found that the majority of flow entering the inlet on flood tide passes to the east through Shackleford Channel, and most flow leaving the inlet comes from the west via Morehead City Channel (Churchill et al. 1999a). Consequently, the greatest densities of larval fishes entering the inlet pass through its east side, with their concentrations decreasing moving westward (Hettler & Hare 1998, Churchill et al. 1999b). The relative species composition of larval fishes is mostly consistent throughout the inlet, such that sampling in any of the channels is mostly representative of the community that entered the inlet (Hettler & Hare 1998). Concurrent ichthyoplankton collections inside and outside the inlet have found larval densities in the two locations to be correlated, suggesting that sampling within the inlet may also

be representative of the ichthyoplankton community retained at the inlet mouth (Hettler & Hare 1998).

Since larvae can be retained outside of the inlet for several tidal cycles before entering, it is likely that ingress measured on any given day is more of an average of the larvae that arrived to the inlet over the course of several past days than an indication of those larvae recently arrived to the inlet (Hettler & Hare 1998). There is consensus that most species of larvae enter the inlet by ascending in the water column during flood tides (known as selective tidal stream transport), and the greatest number of fish larvae routinely have been caught during nighttime flood tides (Hettler et al. 1997, Forward et al. 1999). However, this is not the case for *Brevoortia tyrannus* larvae, which seem to rely on especially strong flood tides rather than selective tidal stream transport to drive them far enough into the inlet so that they are not washed out on the following ebb tide (Joyeux 1999). Sampling for ichthyoplankton is most effective when conducted at night during the peak flow of flood tide, since this optimizes the likelihood of catching both larvae that use selective tidal stream transport and those that do not.

Unlike many other areas of the ocean, no long-term trends in SST have been observed off the coast of the southeastern United States (Shearman & Lentz 2010). However, barring major reductions in greenhouse gas emissions, winter bottom temperatures in the region are projected to increase by 2-3°C by the end of the century (Grieve et al. 2016). Therefore, an understanding of possible relationships between water temperature and the life histories of fishes in the area is critical to assessing potential climate change impacts. Historic relationships between variations in temperature, ichthyoplankton ingress phenology, and species composition in of Beaufort Inlet can offer insight into how the community may respond to future temperature increases.

Water temperature may account for some interannual variation in when larvae are spawned, but the time when larvae are captured in Bridgenet sampling is not likely to be perfectly coupled with adult reproduction times. Both local inlet hydrology and offshore hydrodynamic flow play important roles in transporting larvae to estuarine nursery grounds. Beaufort Inlet is located near the northern boundary of the South Atlantic Bight (SAB), which encompasses the continental shelf from West Palm Beach, Florida to Cape Hatteras, North Carolina (Figure 1). The majority of the Newport Estuary ichthyoplankton community originates from spawning in and around Onslow Bay, an embayment bounded by Cape Fear, Cape Lookout, and the shelf break (Epifanio & Garvine 2001; Figure 1). Though the exact spawning areas of most species collected by Bridgenet are largely unknown, many of the climatic and oceanographic processes thought to be responsible for larval transport in the SAB have been explored. Variations in these transport processes could potentially contribute just as greatly as temperature to interannual variation in ingress phenology (Hettler et al. 1997, Quinlan et al. 1999, Rice et al. 1999).

Previous work on the hydrographic dynamics of the SAB and Beaufort Inlet has suggested that ocean surface wind stress to be an important driver of ichthyoplankton transport (Hare et al. 1999, Quinlan et al. 1999). Specifically, north-northeast (NNE) winds along the continental shelf drive surface ocean water against the shore, causing both water and plankton to be funneled into inlets along the coast (Luettich et al. 1999, Quinlan et al. 1999, Werner et al. 1999). Winds local to the inlet also play an important role in larval transport (Luettich et al. 1999, Logan et al. 2000). Local hydrology results in larvae being more concentrated on the eastern side of the inlet, therefore easterly winds tend to drive larvae into the main channel of the inlet, aiding ingress (Luettich et al. 1999). Southerly winds also increase larval ingress by forcing

water through the inlet, whereas northerly winds tend to hinder larval ingress (Luettich et al. 1999, Logan et al. 2000).

Sea level changes in Onslow Bay may also affect larval ingress, as sea level influences tidal stream strength in Beaufort Inlet. Whereas local winds may affect tidal stream strength on a weekly time scale, interannual variation in the sea level of Onslow Bay may influence tidal stream strength across months or seasons. The sea level of Onslow Bay varies with changes in barometric pressure, predominate wind direction and strength, and Gulf Stream activity (Atkinson et al. 2013). Changes in sea level due to these factors affect tidal amplitude in North Carolina's estuaries (Pope 1993). Though the exact effects vary spatially, increases in sea level generally seem to relate to both larger tidal amplitude and greater tidal stream strengths (Giese et al. 1985, Pope 1993). Increases in sea level due to anthropogenic sea level rise are also predicted to slightly increase tidal amplitude across the SAB (Pickering et al. 2017). Generally, larger tidal amplitudes and subsequently faster tidal currents should aid larval ingress through the inlet, since larvae are more likely to be entrained in the larger volume of water associated with these events.

Gulf Stream intrusion events, such as meanders, filaments, and eddies, have also been hypothesized as a viable transport mechanism for fish larvae, but have historically been difficult to detect and quantify, especially before the satellite era (Govoni & Spach 1999). The recently-released AVISO+ (Archiving, Validation, and Interpretation of Satellite Oceanography) dataset of worldwide mesoscale eddy trajectories from 1993-2016 includes satellite observations of warm core eddies generated by the Gulf Stream (Mason et al. 2014, Faghmous et al. 2015). This could prove a useful tool for exploring how Gulf Stream intrusions influence ecology across the Southeast US.

Internal pressure waves formed when the surface tide moves up the continental shelf also have the potential to push larvae toward the shore (Miller et al. 1984). The overall effect of these waves on the interannual variability of larval ingress phenology is likely minimal, however, since there is little temporal variability in their magnitude (Werner et al. 1999). Furthermore, there is little vertical shear in the portion of the water column where larvae are typically found in the SAB (i.e., the upper 15m), indicating that pressure waves do not regularly travel through the area of the water column where larvae exist (Werner et al. 1999).

Two large-scale modes of climate variability, the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO), may also influence the phenology of larval fish ingress. Both of these modes of climate variability affect water temperature and wind stress across the SAB (Hurrell et al. 2003, Visbeck et al. 2003, Knight et al. 2006). The NAO results from changing atmospheric pressure over the Arctic and subtropical Atlantic, which subsequently produces large changes in wind speed and direction, heat and moisture transfer between the land and sea, and storm intensity and path (Hurrell et al. 2003). Positive (negative) phases of the NAO are associated with warmer (colder) winters across the east coast of the United States (particularly the northeast), strong (weak) mid-latitude westerlies, and strong (weak) easterly trade winds. Phase changes of the NAO are highly variable over time, sometimes changing from month-to-month (Hurrell et al. 2003). The amplitude of variation in SST is typically on the order of 0.5 – 2.0°C between NAO phases, with regional variation in the specific temperature fluctuations (0.3 – 0.7°C in western subtropical gyre, which is located to the east of the SAB; Visbeck et al. 2003).

The AMO is a climate cycle that affects SST in the North Atlantic Ocean, consisting of warm and cool phases that alternate every 55 – 70 years (Knudsen et al. 2011). The AMO index

itself is calculated from SST across the North Atlantic, with positive phases corresponding to warmer temperatures (Knight et al. 2006). Average temperature differences between extremes are $\sim 0.5^{\circ}\text{C}$; the cycle has been in its warm phase since 1995 (Knudsen et al. 2011). Variation in AMO phase has also been correlated to regional climate anomalies beyond SST, such as hurricane frequency (positive relationship) and rainfall across the US (negative relationship) (Knight et al. 2006). These warmer temperatures and increased hurricane frequency associated with the positive phase of the AMO may resemble aspects of projected conditions under climate change. Analyzing how the ingress phenology of fishes varies between the phases of the NAO and AMO may give insight into how species will respond to the large-scale shifts in environmental conditions associated with climate change.

Section 1.3: The NOAA SWFSC Bridgenet database

Since 1986, NOAA has collected ichthyoplankton samples from Pivers Island bridge as part of the Beaufort Inlet Ichthyoplankton Sampling Program (Bridgenet) (Figure 1). Previous research has found that $\sim 10\%$ of the water entering Beaufort Inlet passes through the 40-m channel from which NOAA's Beaufort Bridgenet samples are taken (Churchill et al. 1999a). The Bridgenet collections from this section of the inlet have been found to underestimate the absolute abundance of species entering the inlet (i.e., extrapolating the densities of larvae found in Bridgenet samples to the total volume of water entering the inlet would not give an accurate representation of the number of larvae entering the inlet). However, Bridgenet collections have been shown to provide an accurate representation of the relative abundances of species to one another (Forward et al. 1999).

The Bridgenet program was initially designed to study *B. tyrannus*. As a result, the “core” season of Bridgenet sampling occurs from October/November – April/May, the usual window of *B. tyrannus* ingress. In 1999, 2005, 2007, 2008, and 2009 NOAA extended their core collection of Bridgenet samples through the summer. These samples were not processed, however, and have been stored in 70-90% ethanol since their collection. The Bridgenet sampling methodology is explained in greater detail in Chapter 2 of this thesis.

Section 1.4: Research objectives

The second chapter of this thesis examines the interannual variability of the Beaufort Inlet ichthyoplankton community’s ingress phenology during late fall through early spring using data collected from the core season of Bridgenet. The following specific questions are addressed:

- How much interannual variability is there in the ingress phenology of common species in the winter and early spring ichthyoplankton community?
- Has there been a long-term trend in ingress phenology since Bridgenet sampling began?
- Does variability in ingress phenology relate to potential environmental variables influencing the timing of fish reproduction (temperature, AMO, and NAO) or the pathway of larval transport (offshore wind, nearshore wind, tidal height, AMO, and NAO)?

The final chapter summarizes the main findings and implications of this thesis and presents suggestions for future research.

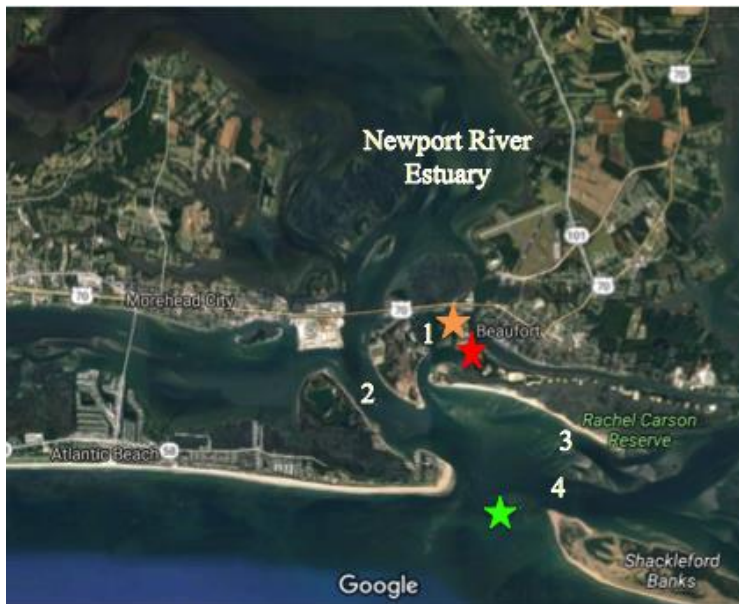
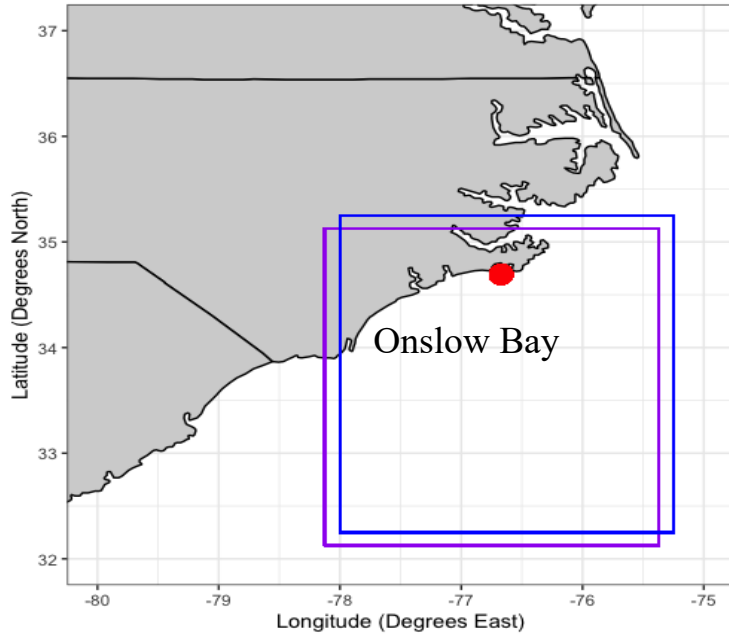


Figure 1: Map of study site. Top: The purple and blue polygons indicate the areas of Optimum Interpolation Sea Surface Temperature and Blended Sea Winds observations, respectively. The red circle indicates Beaufort Inlet, which is magnified in the bottom panel. The embayment to the south of Beaufort Inlet is Onslow Bay. Bottom: Beaufort Inlet (green star) and the four major channels branching from the inlet (1: Bulkhead Channel, 2: Morehead City Channel, 3: Bird Shoal Channel, and 4: Shackleford Channel) are pictured. The orange star at the top of the map indicates the location of weekly Bridgenet sampling from November to April. The red star indicates NOAA’s National Data Buoy Center Station BFTN7, from which local wind and tide data were obtained.

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CHAPTER 2. HISTORIC CHANGES IN ICHTHYOPLANKTON PHENOLOGY AND RELATIONSHIPS TO ENVIRONMENTAL VARIABLES

Section 2.1: Introduction

Many organisms rely on their environment to signal the seasonal timing of life history events, which is also called phenology. Examples of phenological events include metamorphosis, migration, and reproduction (Visser & Both 2005). Seasonal temperature change is one of the most common environmental drivers of phenology across taxa; interannual variations in temperature have been linked to the timing of bird and butterfly migrations, bird nesting, plant flowering, and frog breeding (Parmesan & Yohe 2003). Temperature, as well as water column stratification and upwelling events, has been correlated to changes in fish reproductive phenology in the North Sea, California Current, and Bay of Biscay (Edwards & Richardson 2004, Greve et al. 2005, Genner et al. 2010, Pankhurst & Munday 2011, Asch 2015, Chevillot et al. 2017). The timing of reproduction and subsequent transport of fish offspring has been hypothesized to link to be linked to recruitment success in several fish taxa, emphasizing the importance of reproductive phenology in fishes (Cushing 1990). Given that sea surface temperature (SST) has risen globally at an average rate of $0.13^{\circ}\text{C decade}^{-1}$ and is expected to continue to increase into the next century (IPCC 2014), it is critically important that we continue to study how changes to the ocean may affect the phenology of fish reproduction and larval transport processes.

The ability to study environmental-phenology relationships is limited by historical knowledge of phenology (Visser & Both 2005). In the case of fish reproduction, long-term times series of ichthyoplankton abundance and occurrence offer the best look at how reproductive phenology has varied over time (Koslow & Wright 2016). The longest-running, continuous time

series of ichthyoplankton collections on the United States' East Coast is located in Beaufort Inlet, North Carolina (Ortner et al. 1999). Since 1986, the National Oceanic and Atmospheric Administration's (NOAA's) Southeast Fisheries Science Center "Bridgenet" program has collected winter-spawned larvae from Beaufort Inlet en route to their estuarine nursery habitat. This time series offers insight into the interannual variation of ichthyoplankton phenology in their estuarine nursery habitat.

The southern-facing Beaufort Inlet is located in Onslow Bay, an embayment near the northern extreme of the South Atlantic Bight (SAB), bounded by Cape Fear, Cape Lookout, and the shelf break (Epifanio & Garvine 2001; Figure 1). During the fall and winter, millions of larvae spawned across Onslow Bay ingress Beaufort Inlet while traveling to the estuarine nursery habitats of Bogue Sound, Back Sound, and the Newport and North Rivers (Figure 1). Though the exact spawning areas of most species collected by Bridgenet are largely unknown, many of the SAB's and Onslow Bay's climatic and oceanographic processes thought to be responsible for larval transport were explored as a part of NOAA's South Atlantic Bight Recruitment Experiment (SABRE). Products of and precursors to SABRE included studies of: ichthyoplankton temporal abundance, age, and size (Hettler & Chester 1990, Warlen & Burke 1990); comparisons of Beaufort's ichthyoplankton community to that of nearby inlets (Hettler & Barker 1993); daily variability in larval fish ingress (Hettler et al. 1997, Forward et al. 1999, Joyeux 1999); the implications of the inlet's flow dynamics on larval fish transport (Hettler & Hare 1998, Churchill et al. 1999a, Churchill et al. 1999b, Forward et al. 1999); and the influence of hydrodynamics along the continental shelf on larval fish transport (Hare et al. 1999, Quinlan et al. 1999, Rice et al. 1999, Werner et al. 1999). Variations in these transport processes may contribute just as greatly as temperature to interannual variation in ingress phenology.

I used 27 years of the Bridgenet time series to explore the historic variability in ichthyoplankton ingress phenology through Beaufort Inlet. Ten species' beginning, peak, end, and duration of ingress through the Inlet were examined both individually (species-by-species) and collectively as a community. I then attempted to relate variability in larval ingress phenology to the variability in potential environmental variables influencing fish reproduction in Onslow Bay and larval transport both across the Bay into Beaufort Inlet. Relationships between ingress phenology and SST, winds across the Bay, winds local to the Inlet, tidal strength, the Atlantic Multidecadal Oscillation (AMO), and the North Atlantic Oscillation (NAO) were examined. Though processes besides these influence reproduction and larval transport, these factors are highly variable from year-to-year, accounted for in long-term datasets, and susceptible to change as the climate changes (Saba et al. 2016, Yuan et al. 2017).

Section 2.2: Methods

Section 2.2.1: Bridgenet sampling design

Since 1986 NOAA has collected ichthyoplankton samples from Pivers Island Bridge as part of the Beaufort Inlet Ichthyoplankton Sampling Program (Bridgenet) (Figure 1). These samples are taken from a 40-m wide channel located 1.5 km upstream of the inlet. The sampling protocol has changed slightly over time, but the experimental design has remained consistent. Larvae are collected with a 2 m² rectangular plankton net with 1-mm stretch mesh that is equipped with an analog (pre-1998, 2016-present) or digital (1998-2016) flowmeter. All samples are collected just below the water's surface during nighttime flood tides, approximately 2.5 hours before the predicted high tide. Three (1986-1988) or four (1988-present) replicate tows are conducted during each sampling event, which occur weekly from October/November to

April/May. Samples have been preserved in 95% ethanol and enumerated to species either at the NOAA Beaufort Laboratory (pre-2001) or the Sea Fisheries Institute, Plankton Sorting and Identification Center in Gdynia, Poland (2001-present). At the time of data analysis (fall and winter of 2018), only the samples collected from the fall of 1986 to the spring of 2013 had been processed. Note that henceforth, “sampling season”, “season”, and “year” refers to the year sampling ended (i.e., the “season” 1987 was from Nov. 1986 – Apr. 1987).

Section 2.2.2: Calculation of phenology indices

The cumulative catch of each species was plotted over time for each sampling season. A loess smoothed average function (span = 0.75, degrees = 2) was fitted to each of these plots. This function was then used to calculate the date when 15%, 50%, and 85% of individuals were captured in a given season (Figure S2.1). These dates were referred to as the “beginning”, “peak”, and “end” of each species’ ingress season. These 15%, 50%, and 85% metrics have been used in previous scientific literature and are preferred to the actual first and last occurrence of a given species, since first and last occurrence can vary greatly with sampling effort (Greve et al. 2005, Batten and Mackas 2009, Mackas et al. 2012). Relatedly, the loess approximation was used rather than each metric’s actual date-of-occurrence to account for the effect Bridgenet’s weekly sampling frequency may have on when these catch thresholds were reached. Ingress duration was defined as the difference (in days) between the 85% and 15% metrics.

Bridgenet usually captured the entirety of selected species’ ingress, but there were exceptions. The beginning and end metrics were excluded if they occurred within two weeks of the respective start or end date of a sampling season. If either the beginning or end metric was removed in a given season, that season’s peak and duration metrics were also removed. Entire

seasons were excluded when species were captured on fewer than 13 weeks of the sampling season, since such seasons did not show a distinct ingress pattern. Lastly, peak ingress metrics were removed for years that demonstrated a bimodal ingress pattern. See supplemental information for a table of metrics removed for each species (Table S2.1).

Of the ~150 taxa collected by Bridgenet, ten species met the criteria for inclusion in this study (Table 2.1). Species were selected based on whether: 1) their identifications were accurately resolved to species level; 2) the Bridgenet sampling season captured their entire ingress phenology for more than 10 years based on the above criteria, and; 3) they were abundant enough in samples to demonstrate a clear beginning, peak, and end of ingress.

Section 2.2.3: Phenology changes over time

Temporal changes in each of the four phenological metrics were assessed for both individual species and the community as a whole. Species' phenology trends, their uncertainty, and correlations with year were calculated from standard linear regressions. A mixed effect linear modeling incorporating species as a random effect was used to assess the community's phenology trends. The four phenological metrics of each species were analyzed for temporal autocorrelations at 1 – 5 year lags. Approximately 5% of these 200 autocorrelation tests were significant at a classical significance threshold of $p < 0.05$, which is the amount that one would expect to be significant based solely on spurious results associated with multiple testing. There was no pattern in the species, metric, or lag in which significance occurred, therefore, autocorrelation was not considered a relevant factor when designing subsequent analyses.

Section 2.2.4: Environmental influences on phenology: Linear regression

Linear regressions were used to statistically test for relationships between ingress phenology and environmental variables (i.e., SST, offshore wind shifts to the southwest and southeast, northerly wind strength local to the inlet, tidal height, AMO, and NAO; each described in Section 2.2.6). Separate multiple linear regressions were calculated for each of the four phenological metrics of the ten species of interest for a total of forty species-level analyses. Community-level relationships were analyzed similarly, but with a mixed effects modeling approach in which species were included as a random effect. The best models of each species' and the community's phenology metrics were chosen by reverse-stepwise Akaike Information Criteria (AIC) comparisons. Model fit was assessed by p value, AIC, marginal r-squared, and conditional r-squared comparisons (Nakagawa & Schielzeth 2012). Effect size, standard error, and univariate significance was calculated for each environmental variable included in the models. Added-variable (also called partial regression) plots were used to visualize multivariate models. These plots show the partial regression of an individual environmental variable included in a multivariate model plotted against phenology, after accounting for the variability attributed to the other variables in the model. All analyses were conducted in R v3.3.3 (R Development Core Team 2013).

Section 2.2.5: Principle component analysis and regression

Principle component analysis (PCA) and regression (PCR) were also used to: 1) test for correlations between environmental variables; 2) reduce the dimensionality of the environmental data matrix; and 3) test for relationships between ingress phenology and combinations of environmental variables. To standardize among the different scales and units of the variables, a

correlation matrix of the environmental variables was used as the basis of the PCA. Four separate PCAs were performed since each phenology metric had a unique range of months over which wind and tide data were obtained (November – February, beginning of ingress; January – April, peak ingress; February – May, end of ingress; October – May, duration of ingress). These ranges were chosen because they capture conditions all ten species were likely to encounter in most years. The standard deviation and percent of variance explained by each principle component (PC) was calculated along with the correlations between PCs and the seven original environmental variables.

The first two PCs were included as terms in multiple linear regressions of ingress phenology. Separate multiple linear regressions were calculated for each of the four phenological metrics of the ten species of interest for a total of forty species-level analyses. Community-level relationships were analyzed similarly, but with a mixed effects modeling approach in which species were included as a random effect. Model fit was assessed by *p* value, AIC, marginal *r*-squared, and conditional *r*-squared comparisons (Nakagawa & Schielzeth 2012). Effect size, standard error, and univariate significance was calculated for the individual PCs included in the models.

Section 2.2.6: Environmental metrics

SST: Spatially averaged SST across Onslow Bay (32.125 – 35.125°N, 75.375 – 78.125°W) was obtained from NOAA's Optimum Interpolation Sea Surface Temperature (OISST; <http://www.ncdc.noaa.gov/oisst/data-access>) database (Figure 1). SST anomalies for the average of the month of each species' mean beginning of ingress and the month prior were regressed against all phenology metrics. Note that SST for species-specific spawning grounds

was not used, because the spawning location of many of these fishes is unknown or incompletely known. Nonetheless, the monthly SST anomalies from OISST were highly correlated with those from seven weather stations and buoys across the southeast and were moderately correlated with air temperature anomalies at Cape Lookout (Figure S2.2). This suggests that SST changes in a uniform manner across the region at a monthly scale, implying that the SST index described above should capture temperature variability across most species' spawning grounds.

Offshore wind: Wind vectors were obtained from NOAA's Blended Sea Winds (<https://www.ncdc.noaa.gov/data-access/marineocean-data/blended-global>) database, which was averaged across Onslow Bay (32.25 – 35.35°N, 75.25 – 78.0°W). Research-quality data from Sea Winds was only available from 1987 – 2011, so data from the Cape Lookout weather station (National Buoy Data Center (NBDC) station CLKN7) was used during 1986 and 2011 – 2013. Monthly average north and east wind vectors from Sea Winds, NBDC weather stations (BFTN7 and CLKN7), and five NBDC buoys (41025, 41037, 41013, 41004, and 41008) across the southeast US were highly correlated across space (Figure S2.3). This suggests that the annual wind pattern is moderately uniform across the region, and that winds from Cape Lookout are a reasonable supplement to the missing seasons from Sea Winds.

Along the southeast US winds blow predominately to the north in the spring and summer, then blow towards the south during the fall and winter (Figure S2.4). Wind-driven currents have been hypothesized to be the main transport mechanism for larval advection. Due to Ekman transport, winds to the SW drive surface and mid-depth water to the NW, which could funnel ichthyoplankton into southern-facing inlets along the coast (Luettich et al. 1999, Quinlan et al. 1999, Werner et al. 1999). Therefore, the timing of the shift from spring/summer southerly (northward) winds to fall/winter northerly (southward) winds could be a driver of

ichthyoplankton phenology along coastal estuaries, with an earlier shift in winds leading to an earlier entrance of larvae into the inlet. Similarly, the time at which winds shift to blowing to the SE may be related to the end of ichthyoplankton ingress, as this wind direction results primarily in currents moving offshore and away from the inlet.

To determine the timing of these shifts, I plotted each season's cumulative offshore wind stress to the NW (SW) from July 1st – June 30th of each year and fitted a loess function to this relationship (span = 0.75, degrees = 2) (Figure S2.5). The date at which the cumulative NW (SW) wind stress begins to decrease (the maximum of the loess function) corresponds to winds moving counterclockwise past the SW (SE) direction. This SW wind phenology was hypothesized to relate to the beginning, peak, and duration of ichthyoplankton ingress. The SE wind phenology was hypothesized to relate to the end and duration of ichthyoplankton ingress.

Local Northerly Wind Strength: Wind vectors were obtained from the NBDC CLKN7 weather station at Cape Lookout, NC. Winds local to the inlet may affect ingress by influencing inter-weekly tidal stream strength. Winds near Beaufort typically blow to the south during the Bridgenet season. Modeling studies have shown these northerly (southward) winds may hinder particle ingress through the inlet (Luettich et al. 1999, Logan et al. 2000). To determine northerly wind strength's effect on ingress phenology, I averaged daily northerly wind stress for the month of and month prior to each species' typical beginning, peak, and end of ingress, and regressed these wind strengths against the respective ingress phenology metrics (Table 2.1).

Tidal height: Tide level was obtained from NBDC BFTN7 at the Duke Marine Lab in Beaufort, NC. Whereas local wind strength on a given night may affect tidal stream strength in the short term, interannual variation in the sea level of Onslow Bay may influence tidal stream strength across months or seasons. Sea level may, like winds, indirectly drive ichthyoplankton

ingress patterns through these effects on tidal stream strength (Churchill et al. 1999). To examine this potential relationship, I calculated the cumulative sum of maximum daily tidal height for the two months prior to each species' typical beginning, peak, and end of ingress (Table 2.1a). These tidal height metrics were then regressed against their respective ingress phenology metrics. The cumulative tidal height from October – May was also regressed against ingress duration.

AMO and NAO: Data on the AMO index were obtained from the National Center for Atmospheric Research (Trenbeth and Shea 2006; <https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo>), while the NAO index was obtained from the NOAA National Weather Service Climate Prediction Center (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>). Both of these modes of climate variability affect water temperatures and wind stress across the SAB, with positive phases of both corresponding to warmer temperatures (Hurrell et al. 2003, Visbeck et al. 2003, Knight et al. 2006). The NAO is variable from month-to-month (Hurrell et al. 2003) and associated with temperature fluctuations on the order of 0.3 – 0.7°C in the region around the SAB (Visbeck et al. 2003), whereas the periodicity of the AMO is on the order of decades and associated with temperature fluctuations of ~0.5°C (Knudsen et al. 2011). A similar climate oscillation, the El-Niño Southern Oscillation (ENSO), has been shown to influence both ichthyoplankton and zooplankton phenology (Mackas et al. 2012, Asch 2015), so it is likely that the NAO and AMO may also influence larval fish phenology. Both the NAO and AMO are correlated with variations in the abundance and composition of the larval fish community in Roanoke River, North Carolina (McCulloch 2017). Winter (December – February) averages of the monthly, unsmoothed, detrended Hadley AMO and monthly NAO indices were regressed against all ingress metrics.

Section 2.3: Results

Section 2.3.1: Historic variation and trends in ingress phenology

Linear modeling revealed the ichthyoplankton community of Beaufort Inlet has advanced the beginning of its arrival, on average, by three weeks over the past 27 years, with the peak of larval ingress advancing by two weeks (Table 2.2). There is no evidence that the end of ingress has shifted, however, which has resulted in an increase in ingress duration by approximately one week decade⁻¹. For all four phenology metrics, interspecific differences explained more variability in the community-level model than did temporal shifts in phenology. This can be seen in the difference between the marginal r-squared (R^2m), which represents the variance explained by fixed effects (i.e., year) in the models, and the conditional r-squared (R^2c), which represents variance explained by both fixed and random effects (Table 2.2). Inclusion of “species” as a random effect greatly reduced unexplained variance in all community-level models.

Although species varied in the magnitude and significance of their temporal shifts in ingress, most showed similarities in the direction of their shifts (Figures 2.1 & 2.2). The beginning of ingress advanced in all species with the exception of *Anguilla rostrata*; the peak advanced in all species but *Micropogonias undulatus*; and ingress duration lengthened in all species but *Lagodon rhomboides*. There was no common trend in the direction of shifts in the end of species’ ingress, though. Some species shifts in ingress were particularly drastic (Table S2.3). *Mugil cephalus* (-14.47 days decade⁻¹; p = 0.051), *Myrophis punctatus* (-14.41 days decade⁻¹; p = 0.0031), *M. undulatus* (-9.13 days decade⁻¹; p = 0.054), and *Paralichthys albigutta* (-13.39 days decade⁻¹; p=0.016) have all had significant advances in their arrival to the inlet. The peak ingress of *Brevoortia tyrannus* (-12.44 days decade⁻¹; p = 0.030) has also significantly advanced and the ingress duration has lengthened in *M. cephalus* (27.96 days decade⁻¹, p =

0.0023) and *P. albigutta* (16.81 days decade⁻¹, $p = 0.020$). No significant changes were seen among any species for the end of ingress.

Section 2.3.2: Phenology and the environment: Linear regression

The relationships between phenology and environmental variability were examined at both the community and species level using linear mixed effect modeling and multiple regression, respectively. Interspecific differences in phenology accounted for more variability than any combination of environmental factors in all community-level models, as seen in the difference between the R^2m and R^2c of each (Table 2.3). The environmental factors included in the best community-level model for each metric are plotted as added-variable (AV) plots (Figure 2.3). The factors included in each species-level model are visualized in a box-and-whisker plot (Figure 2.4). The specifics of each species-level model can be found in Table S2.3, and model visualizations in Figure S2.6.

Beginning of ingress: At the community-level, interannual variance in the initial arrival of fall-winter ichthyoplankton was best explained by a combination of southward wind strength, the winter NAO index, maximum tidal height across the ingress season, and a random species effect (Table 2.3). Stronger northerly winds related to a delay in ingress by 8.47 +/- 1.90 (standard error) days for each meter second⁻¹ increase in average wind strength across the ingress season. Positive winter NAO index values and greater tidal heights correlated to earlier ingress by -5.32 +/- 1.98 days NAO⁻¹ and -0.69 +/- 0.32 days m⁻¹ of cumulative high tide height, respectively.

Environmental factors outperformed a null model of start-of-ingress phenology for all species but *M. undulatus*, as determined by AIC comparisons. Offshore wind phenology to the

southwest, southward wind strength local to the inlet, AMO, NAO, and tidal height all had consistent effect directions across species. Delayed phenology of offshore winds to the southwest and stronger southward local winds related to delayed ingress among two and four species, respectively. Positive AMO, NAO, and higher tidal height were related to earlier ingress among two, five, and one of the species studied, respectively (Figure 2.4). These effect directions were consistent with those of the three terms included in the community-level model (i.e., local winds, NAO, and tidal height). SST was generally associated with advances in ingress affecting four species. The exception was *L. rhomboides*, which ingressed later in warm years.

Peak ingress: SST, AMO, NAO, tidal height, and a random species effect best explained community-level variability in peak ingress phenology (Table 2.3). Greater tidal heights correlated to delays in peak ingress by 0.91 ± 0.41 days m^{-1} of cumulative high tide height. Increases in SST and positive AMO & NAO indices correlated with earlier peak ingress phenology, with effect sizes of -6.46 ± 1.78 days C^{-1} , -35.63 ± 9.15 days AMO^{-1} , and -2.94 ± 2.00 days NAO^{-1} .

As determined by AIC comparisons, environmental factors outperformed a null model of peak ingress phenology for all species, except *M. punctatus* and *P. lethostigma*. SST, offshore wind phenology to the southwest, local southward wind strength, AMO, and NAO all had consistent effect directions across species. Delayed offshore wind phenology to the southwest and stronger southward winds local to the inlet related to delayed ingress in three and four species, respectively. Warmer SST and positive AMO and NAO were associated with earlier ingress among five, three, and two species, respectively (Figure 2.4). These species-level effect directions of SST, AMO, and NAO were consistent with those of the community-level model. The effect of tidal height on peak ingress phenology varied between the two species for which it

was included; higher tidal height correlated with earlier ingress for *B. tyrannus* and later ingress for *A. rostrata*.

End of ingress: Community-level variability in end-of-ingress phenology was best explained by SST, offshore wind phenology to the southeast, AMO, NAO, tide, and species as a random effect (Table 2.3). Offshore winds to the southeast and greater tidal heights correlated with delays in ingress' end by 0.049 ± 0.023 days wind day⁻¹ and 0.64 ± 0.37 days m⁻¹ of cumulative high tide height. Warmer SST and positive AMO and NAO indices were associated with advances in phenology by 6.09 ± 1.52 days °C⁻¹, 16.25 ± 7.55 days AMO⁻¹, and 2.85 ± 1.63 days NAO⁻¹, respectively.

All species' end-of-ingress was better explained by some combination of environmental factors than by a null model. SST, offshore wind phenology to the southeast, local wind strength, and tide all had consistent effect directions across species. Delays in offshore wind phenology and higher tidal height delayed the end of ingress in three and two species, respectively. Warmer SST and stronger southward winds advanced the end of ingress in seven and one species, respectively. These effect directions were consistent with community-level model results for offshore wind phenology, tidal height, and SST. Species-level relationships between the AMO index and end-of-ingress was also mostly consistent with that seen at the community level (4 species advanced ingress as AMO increased), with the exception of *L. rhomboides*. The NAO index, however, had varying effects on the species for which it was important; *M. undulatus* and *L. xanthurus* had an earlier end of ingress as NAO increased, whereas *M. cephalus* and *P. dentatus* had a delayed end of ingress.

Ingress duration: Ingress duration at the community level was best explained by SST, NAO, tidal height, and species as a random effect (Table 2.3). Warmer SST related to shortened

duration by 5.16 +/- 2.18 days °C⁻¹. Increases in the NAO index and greater tidal heights correlated with increases in duration by 4.03 +/- 2.55 days NAO⁻¹ and 0.40 +/- 0.15 days m⁻¹ of cumulative high tide height.

A half of the species' ingress durations were better explained by a combination of environmental factors than by a null model. Warmer SST (*L. rhomboides* & *L. xanthurus*) and delayed offshore wind phenology to the southwest (*P. lethostigma*) correlated with shortened ingress duration, whereas increasing AMO (*P. albigutta*), NAO (*M. cephalus*), and tidal height (*M. cephalus* and *P. lethostigma*) were related to longer ingress duration. Changes in offshore wind phenology to the southeast had varying effects on species, with delays in the wind phenology related to shortened ingress duration in *M. cephalus* and longer duration in *L. rhomboides* and *P. lethostigma*.

Section 2.3.3: Phenology and the environment: Principle component analysis and regression

The PC1 and PC2 calculated for the environmental datasets associated with each of the four phenology metrics were very similar. In all four PCAs, PC1 captured 32.09% – 33.01% of the environmental variance and PC2 captured 25.82% – 31.06% (Table 2.4; Figure 2.5). PC1 was primarily associated with SST and the AMO and NAO indices and PC2 was primarily associated with the timing of when offshore wind shifts to the southeast, northerly wind strength near Beaufort Inlet, and cumulative tide height (Table 2.4; Figure 2.5). The timing of offshore wind shifts to the southeast were generally positively correlated with the strength of northerly winds near Beaufort Inlet (Figure 2.5). The AMO and NAO indices were generally negatively correlated (Figure 2.5).

Beginning of ingress: PCs 1 and 2 explained a significant amount of variability in the beginning of ingress phenology for the community as a whole (Table 2.5). Strong trends were seen for both PCs. PC1 was negatively correlated with the ingress phenology of the community, and PC2 was positively associated with ingress phenology. The trend was slightly larger for PC1, which is associated with cooler SST, a lower AMO index, and a higher NAO index (Table 2.5). Interspecific differences in phenology accounted for more variability than any combination of environmental factors in the community-level model, as seen in the difference between the R^2m and R^2c of each (Table 2.5). This was consistent across all phenological metrics. Neither PC nor a combination of the two explained a significant amount of variability in the timing of ingress for any individual species (Table 2.6).

Peak ingress: PCs 1 and 2 were not significantly related to the peak ingress phenology of the community (Table 2.5). PC2, which is associated with a delay in the timing of offshore wind shifts to the southeast, stronger northerly wind strength near Beaufort Inlet, and a greater cumulative tide height, had significant positive correlations with the peak ingress phenology of *L. rhomboides* and *P. dentatus* (Table 2.6).

End of ingress: PCs 1 and 2 were not significantly related to the end of ingress phenology of the community (Table 2.5). PC1, which is associated with cooler SST, a lower AMO index, and a higher NAO index, had a significant positive correlation with the phenology of the end of *L. xanthurus* ingress (Table 2.6). PC2, which is associated with a delay in the timing of offshore wind shifts to the southeast, stronger northerly wind strength near Beaufort Inlet, and a greater cumulative tide height, had significant positive correlations with the phenology of the end of ingress of *L. rhomboides* and *P. lethostigma* (Table 2.6).

Ingress duration: A model including PCs 1 and 2 explained a significant amount of variability in the duration of ingress for the community as a whole (Table 2.5). The positive correlation between ingress duration and PC1, which is associated with a lower AMO and higher NAO index, was much larger than the negative correlation with PC2, which is associated with delays in the timing of offshore wind shifts to the southeast and stronger northerly wind strength near Beaufort Inlet (Table 2.5). PC1 also had a significant positive correlation with the duration of *P. albigutta* ingress, and PC2 had a significant positive correlation with the duration of *P. lethostigma* ingress (Table 2.6).

Section 2.4: Discussion

Overall, my findings suggest that the phenology of ichthyoplankton ingress through Beaufort Inlet, NC has been variable between years, changed over time, and is influenced by the environment. I examined ten taxonomically diverse species that utilized a breadth of life-history strategies (Table 2.1). The direction of observed phenology shifts over time and of phenology responses to the environment were, in many cases, consistent across these diverse species.

Section 2.4.1: Temporal changes in ingress phenology

Over the past three decades, the ichthyoplankton community as a whole has changed its phenology to enter Beaufort Inlet earlier in the year. Though the level of significance varied between species, I found the beginning of ingress has advanced for all fishes examined. However, temporal changes in the peak and end of ingress were not as consistent across species or as statistically significant. This may suggest that the beginning of ingress is more directly linked to particular aspects of the environment, whereas variation in the peak and end of ingress

phenology are mediated by compounding abiotic and biotic factors across the months-long ingress season. The direction of these temporal shifts in phenology are consistent with SST's effect on ingress, even though SST has not warmed in the SAB during recent decades (Shearman & Lentz 2010, Morley et al. 2016). Alternatively, changes in fish population abundance, age structure, and size structure could be a driver of these shifts. Spawning behaviors vary across ages and sizes of fishes, with older fishes spawning earlier in certain species, such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Gadus chalcogrammus*) (McQueen & Marshall 2017, Rogers & Dougherty 2019). Changes to the size and age structure of cod stocks have also been linked to variations in the abundance and distribution of cod eggs in the Barents Sea (Stige et al. 2016).

The October to May sampling season of the Bridgenet program captured the majority of most species' ingress, but there were years when part of some species' ingress phenology fell outside of this range. I excluded species' beginning and end of ingress for years in which they occurred within two weeks of the respective start or end date of a sampling season. It is possible that these exclusions dampened some of the trends in species' phenology over time. For example, if the removed years in which ingress began especially early were recent, then the inclusion of these years would have strengthened the advance observed in the beginning of ingress. This was the case for *M. cephalus*, *M. punctatus*, *P. dentatus*, and *P. lethostigma* (Table S2.1).

Section 2.4.2: Community trends in ingress phenology and the environment

SST was the most frequent metric found to be significant in environmental models of species' ingress. With the exception of *L. rhomboides*, warmer SST were consistently related to

earlier ingress phenology. As temperatures cool in the fall and winter, six of the ten species examined move offshore to spawn (Table 2.1). Research from other ecosystems indicates that in warmer years, the preferred thermal habitat of many fishes with offshore winter migrations occurs nearer to shore (Myers 1998, Sims 2004). This pattern may also occur in the SAB. As a result, their offspring may reach Beaufort Inlet earlier in warmer years, since they have less distance to travel. It is also possible that for some species, warmer SST leads to quicker reproductive maturation (Pankhurst & Munday 2011). Temperature and photoperiod have both been linked to fishes' gonadal development, with temperature primarily involved in the finalization of the process (Pankhurst & Porter 2003, Pankhurst & Munday 2011). The exact role temperature plays in reproductive development varies between species and is poorly understood for most species though, making it difficult to say for certain how SST relates to the ingress phenology of the ten fishes examined here. Lastly, temperature affects the stage duration of larvae during development. In the presence of adequate resources, larvae grow faster in warmer waters (Houde 1989, Meekan et al. 2003, Laurel et al. 2008). For larvae with the capability of actively swimming (and especially for the leptocephali larvae of *A. rostrata* and *M. punctatus*), this accelerated growth may result in larvae arriving earlier to the inlet based on increases in swimming speed with faster development. The effect of temperature on metabolic processes will have a stronger influence on species that are older by the time that they ingress in the inlet, because the effect of temperature on development will have been compounded over a longer period. Ultimately, temperature's impact on larval ingress phenology is an integration of effects spanning many life history stages that occur over days (i.e., larval stage duration and changes in swimming travel time) to months (i.e., spawning time, location, and overall transport distance).

The AMO and NAO integrate temperatures across a wide spatial and temporal area that may be more representative of the conditions that fishes experience as they migrate over time. As a result, these climate indices may be a better predictor of ingress phenology than SST for some species. Although PCA revealed the AMO and NAO to be negatively correlated, I mostly found consistency between the effect directions of SST, the AMO, and the NAO. This consistency is expected given that SST is used in the calculation of the AMO (albeit from a broader spatial area than Onslow Bay) and is affected by the processes that define the NAO (Hurrell et al. 2003). The discrepancies between *P. dentatus*' and *M. cephalus*' relationships to the NAO and temperature compared to other species could be a result of other climatological factors that are also influenced by the NAO, such as wind strength and direction.

Winds local to Beaufort Inlet also exhibited the hypothesized effects on larval ingress phenology. Stronger southward winds always delayed the beginning and peak timing of ingress in cases when local winds were included in environmental ingress models. Given that Beaufort Inlet opens to the south, this is likely due to these southward winds weakening the northward tidal stream that larvae use to enter the inlet. Offshore wind phenology also had the expected effect on several species, with delayed wind phenology causing delays in ingress. The phenology of wind shift may influence the strength of southward winds near Beaufort Inlet, as PCA revealed these two environmental variables were correlated. However, offshore winds were not a common variable included in species-level models. It is possible that interannual variability in offshore wind strength, in addition to wind phenology, contributes to the timing of larval ingress. I focused on the timing of wind shifts to the southwest and southeast, but other wind directions could also be important depending on where species spawn and their trajectory of larval dispersal. For instance, Taylor et al. (2010) found winds to the west and northwest partially

explain recruitment of juvenile *P. lethostigma* in estuaries along North Carolina's coast. Another explanation for the weaker influence of offshore winds is that their effect may be diluted by other climatic, hydrographical, or biotic factors that influence larval fish phenology in between the time when fishes are spawned offshore and when they reach estuaries.

Of the seven environmental metrics examined, cumulative tidal height had the least influence on ingress phenology. While tidal height and corresponding tidal stream strength affect larval ingress on a given night, the integration of cumulative tidal height across a season does not translate to appreciable interannual differences in ingress phenology. PCA found variability in tide height was associated with offshore wind phenology and the strength of southward winds near Beaufort Inlet. It is possible that the few observed relationships between tide and ingress phenology are artifacts of this covariance between winds and tides near Beaufort Inlet. I attempted to use seasonal tidal height in the estuary as a proxy for changes in sea surface height in Onslow Bay. It is possible that the sea levels of the estuary and the Bay are not closely related. As satellite altimetry improves in coastal areas, altimetry products could be used to reexamine this relationship (Mason et al. 2014, Faghmous et al. 2015).

Aspects of the environment besides those examined can also impact the early life history of fishes. In some fishes, spawning seasonality is affected by river flow (Trépanier et al. 1996, Todd et al. 2012), population age structure (Stige et al. 2016, McQueen & Marshall 2017, Rogers & Dougherty 2019), lunar cycle (Taylor 1984), and potentially prey abundance for income breeders (McBride et al. 2013). After spawning, Gulf Stream eddies, meanders, and filaments have been hypothesized to influence larval transport of fishes in the SAB (Govoni & Pietrafesa 1994, Govoni & Spach 1999). Tropical storms could also play a role in the transport of larval

fishes, and have been related to the settlement of *Callinectes sapidus* (blue crab) larvae in North Carolina estuaries (Eggleston et al. 2010).

Processes local to Beaufort Inlet can affect larval ingress on a short time scale. River discharge has been related to recruitment and distribution of *P. lethostigma* in North Carolina estuaries (Taylor et al. 2010). Strong river flow may also impede ingress by weakening the strength of the incoming tidal stream, similar to northerly wind stress. River discharge impacts the salinity of the water in and around the inlet, as well (Churchill et al. 1999). These changes in salinity may affect the ability of larvae to detect the tidal stream that transports them through the inlet (Forward et al. 1999). The shape and size of the inlets of North Carolina also change over time due to both natural sedimentation, erosion, and anthropogenic dredging (Cleary & FitzGerald 2003). Though changes in inlet hydrography unlikely to have an effect on ingress timing, they could affect the distribution of fish within the inlet from year to year.

Tidal stream strength is intrinsically related to the lunar cycle (Churchill et al. 1999). The greatest tidal amplitude and corresponding strongest tidal stream strength occur during new and full moons. The weekly sampling resolution of the Bridgenet program alternatively samples strong and weak flows every other week. We accounted for this in our analysis by analyzing the density rather than abundance of fish caught each week, since less water passes through plankton nets during weeks of low flow. Lastly, the Bridgenet program aims to sample 2.5 hours before high tide, since this is when the incoming tidal stream is usually strongest (Churchill et al. 1999). Sampling times are based on the predicted timing of lunar tides rather than the actual high tide, which varies as a function of wind strength and direction. As a result, sampling may not have always occurred during the absolute peak in tidal stream strength. Samples were likely representative of the ingressing ichthyoplankton community regardless (Hettler & Hare 1998).

Issues such as this may have added noise to the phenology dataset, therefore the “actual” relationships between ingress phenology and the environment may be stronger than my analysis suggests.

Section 2.4.3: Species level trends in ingress phenology and the environment

There is some consistency between my results and what has been previously described about certain species’ spawning behaviors. Temperature and the AMO and NAO indices were related to the phenology of several species in ways that are intuitive given what is known about their life histories. The larvae of *A. rostrata* grow and transform into long, ribbon-like leptocephali while in the Sargasso Sea, then travel hundreds of miles to reach Beaufort Inlet, NC (Smith 1968, Power & McCleave 1983). It is hypothesized that the transport of these larvae is augmented by active swimming, which is made possible by this ribbon-like shape (Wuenschel & Able 2008). I found *A. rostrata* larvae arrive to Beaufort Inlet sooner in warm years. In warmer waters and with adequate food, these larvae may grow faster, transform into leptocephali sooner, and reach the inlet earlier. *M. punctatus* also have leptocephali larvae, but the majority of their growth does not occur until after they leave the Gulf Stream (Able et al. 2011). This may explain why *M. punctatus* ingress was not correlated with water temperature.

The ingress of *P. dentatus*, and to a slightly lesser extent *P. albigutta* and *P. lethostigma*, had the strongest relationships with environmental variables out of all the species studied. It is known that *P. dentatus* travels offshore to spawn as water temperatures cool in the winter, and that *P. albigutta* moves shoreward post-spawning as water temperatures warm (Stokes 1977, Able & Fahay 2010) (Table 2.1c). Recent work also suggests that *P. lethostigma* disperse along the coast during their shoreward migration post-spawning rather than return to a native estuary,

which means individuals' spawning grounds may vary widely between years (Wang et al. 2018). Though the complete life history is not known for any of these three Paralichthyid flounders, it is plausible that all three species share these traits. Warmer temperatures and positive AMO or NAO indices were related to advances in either the beginning, middle, or end of ingress for all three species. It is possible that these flounders spawn nearer to shore during warmer years due to less cooling of the shallow coastal waters that they typically leave during the winter. These fishes' offspring subsequently may have a shorter journey to the estuary in warm years and thus arrive earlier. Rising water temperatures may also signal an earlier shoreward migration during warm years, which would explain why warmer temperatures were associated with ingress ending earlier for all three Paralichthyids.

Though many species exhibited intuitive responses to the environment, some did not. For instance, the relationship between water temperature and ingress phenology was the opposite of what expectations were for *B. tyrannus*. *B. tyrannus* migrates south from New England as temperatures cool in the winter, spawning along the way (Able & Fahay 2010). The center of this migration has been reported to follow the 10°C isotherm, which would imply their migration would be delayed during warmer years (Able & Fahay 2010). However, I found that *B. tyrannus* larvae ingress earlier in warmer years. The spawning habitat of other fishes in this family is influenced by temperature, typically in a non-linear fashion (Lluch-Belda et al. 1991; Reiss et al. 2008; Takasuka et al. 2008; Weber & McClatchie 2010; Zwolinski et al. 2011; Asch & Checkley 2013). As a result, a nonlinear model may be needed to better explain how *B. tyrannus* phenology relates to temperature. Alternatively, an aspect of the species' life history besides the timing of their migration may be related to temperature. Due to temperature's role in finalizing reproductive development (Pankhurst & Munday 2011), it is possible that spawning occurs

earlier in warm years across the entire range of *B. tyrannus*. Prior to migration, larger and older *B. tyrannus* are typically found in the northern half of the population's range, but smaller adults are ubiquitous across the MAB and SAB throughout most of the year (Able & Fahay 2010). The offspring of these smaller individuals that are already in the proximity of Beaufort Inlet may ingress ahead of those from the larger migrating cohort. Overall, species, such as *B. tyrannus*, where the environmental effects on phenology were unexpected based on prior knowledge of their life histories demonstrate the diversity of behavioral responses to climate. More research is needed to understand the root causes of these exceptions.

Section 2.4.4: Conclusions

Sustained warming of SST has not yet been seen off the coast of North Carolina although this is expected to occur in the future (Morley et al. 2016). This study provides insight on how species may be expected to respond when warming does occur. Extrapolation of the trends observed here with the potential 2°C global average of SST change projected by the IPCC would result in substantial changes to the average ingress phenology of some of the species I studied (IPCC 2014). For example, this would result in a 30-day delay in the beginning of *L. rhomboides* ingress, a 27-day advance in the peak ingress of *M. undulatus*, and a 55-day advance in the end of *P. dentatus* ingress. These projections assume linear responses of phenology to temperature, although there may be temperature thresholds beyond which fishes and other organisms can no longer adapt to changes by altering their phenology (Sparks et al. 2000, Neuheimer et al. 2011). These future changes in phenology could have negative ecological consequences for these fishes, depending on how their estuarine and pelagic prey and predators respond to climate change. Previous research has shown responses to climate change vary across trophic levels (Beaugrand

et al. 2003, Voigt et al. 2003, Edwards & Richardson 2004, Visser et al. 2012, Burkle et al. 2013), so it is possible that shifts in larval ingress phenology will not match with shifts the phenology of their zooplankton prey.

The observed relationship between SST and larval ingress phenology is consistent with similar studies of the environment's effect on fish reproduction and early life history. Select fish species have been found to spawn earlier during warmer years in Alaska, the North Sea, and the California Current (Asch 2015, McQueen & Marshall 2017, Rogers & Dougherty 2019). This “earlier when warmer” trend is common among marine species that spawn or bloom in spring and summer and has also been observed in other marine taxa, such as lobster migrations in Maine, plankton blooms in the North Sea, and egg-laying in seabirds (Poloczanska et al. 2016, Mills et al. 2017). The “later when warmer” trend observed for several of the species I studied is also common among fall and winter spawners/bloomers (Poloczanska et al. 2016). Some species studied also had specific life history characteristics that could be connected to this response to temperature.

This study expands upon previous work on climate change and fish phenology by examining factors beyond SST. I explored how larval transport processes relate to ingress phenology and found evidence that at least some species studied are influenced by wind-driven currents. Larval transport mechanisms such as these need further study. I used winds as a proxy for current-facilitated larval drift, whereas a more direct measurement of currents may better elucidate why the timing of larval transport varies between years. As we continue to improve our ability to observe and quantify these phenomena, we should examine how they relate to the movement of larvae in the SAB. Similarly, larval transport processes in other ecosystems need attention to better understand how they impact the phenology of fishes' early life history.

PCAs were able to reduce the dimensionality of the environmental datasets associated with four phenology metrics such that the first two PCs for each phenology metric consistently explained approximately 60% of the datasets' variability. PCA also revealed correlations between environmental variables that may be mechanistically linked, such as SST, the AMO, and the NAO, as well as wind strength, wind phenology, and tide height. However, regressions of these two PCs against ingress phenology explained less variance and were less significant than regressions based on the original environmental variables. This suggests that the variability in the phenology metrics was associated more closely with variability in the original environmental variables than with the variability captured in PC1 and PC2.

In conclusion, I found interesting and often intuitive relationships between phenology and environmental variables that were consistent across taxa. I also found evidence that the ingress phenology of specific species relates to the environment in ways are sometimes congruent and other times in contrast to prior knowledge of their life histories. The Beaufort Bridgenet time series and similar ichthyoplankton time series offer opportunities for further study of relationships between the environment and ingress phenology. Comparisons across similar time series in New Jersey (Wuenschel & Able 2008) and South Carolina (Allen & Barker 1990) could provide insight on the future of certain fishes as they migrate or expand their range with changing ocean conditions and would also elucidate whether environmental influences on phenology are consistent across a species' range. Egg collections across the continental shelf can also help elucidate how different life-history stages are impacted by the environment, since spawning time and location are particularly apparent in egg collections. Continuous Underway Fish Egg Sampler (CUFES) surveys could be used to achieve this goal (Checkley et al. 2000).

Lastly, factors besides the environment, such as the effects of population size and age structure, may influence phenology and are worthy of study.

Table 2.1a: Taxonomy and basic life history of species studied. “Start”, “peak”, and “end” months refer to the time ranges over which SST, local wind strength, and cumulative high tide height were calculated when modeling the environment’s effect on each species’ ingress phenology. “?” indicates an unknown aspect of a species’ life history. Species are ordered by taxonomic relation. This order is conserved in subsequent tables and figures throughout this paper.

	Family	Start months	Peak months	End months	Age at maturity (years)	Spawning strategy	Eggs
	<i>Anguilla rostrata</i>	Anguillidae	Jan – Feb	Mar – Apr	Apr – May	5 – 19 ^a	? ?
	<i>Myrophis punctatus</i>	Ophichthidae	Dec – Jan	Jan – Feb	Mar – Apr	? ?	? ?
	<i>Brevoortia tyrannus</i>	Clupeidae	Jan – Feb	Mar – Apr	Apr – May	2 – 3 ^b	Batch ^a Pelagic ^a
	<i>Mugil cephalus</i>	Mugilidae	Jan – Feb	Feb – Mar	Mar – Apr	1 – 3 ^a	Isochronal ^d Pelagic ^a
	<i>Lagodon rhomboides</i>	Sparidae	Dec – Jan	Feb – Mar	Mar – Apr	1 – 2 ^c	? Pelagic ^a
	<i>Leisotomus xanthurus</i>	Sciaenidae	Jan – Feb	Feb – Mar	Mar – Apr	2 – 3 ^a	Batch ^a Pelagic ^a
50	<i>Micropogonias undulatus</i>	Sciaenidae	Nov – Dec	Jan – Feb	Mar – Apr	1 – 2 ^e	Batch ^e ?
	<i>Paralichthys albigutta</i>	Paralichthyidae	Dec – Jan	Feb – Mar	Apr – May	? ?	? ?
	<i>Paralichthys dentatus</i>	Paralichthyidae	Jan – Feb	Feb – Mar	Mar – Apr	2 ^f	Batch ^a Pelagic ^a
	<i>Paralichthys lethostigma</i>	Paralichthyidae	Jan – Feb	Feb – Mar	Mar – Apr	1 – 3 ^g	? ?

^aAble and Fahay 2010, ^bLewis et al. 1987, ^cDarcy 1985, ^dRender et al. 1995, ^eBarbieri et al. 1994, ^fMorse 1981, ^gMidway and Scharf 2012

Table 2.1b: Species' life histories. Approximate area and time where species spawn, the migration they take to spawning grounds, and the age (size) of species' larvae upon ingress. For species ubiquitous across the Atlantic, information refers to spawning in/near the South Atlantic Bight (SAB) or studies specific to Beaufort Inlet. Age (size) at ingress is given in either a range or mean. “?” indicates an unknown aspect of a species' life history.

	Spawning area	Spawning time	Spawning migration	Age (size) at ingress
<i>Anguilla rostrata</i>	Sargasso Sea ^a	Feb – Apr ^a	2 – 3 months from rivers to Sargasso sea ^a	175.4 days (55.9 mm) ^a
<i>Myrophis punctatus</i>	Largely unknown: SAB*, off Florida, or in Bahamas ^a	Fall ^a	Presumed to move offshore (adults usually found in estuaries) ^a	53 - 110 days (60 - 75 mm) ^d
<i>Brevoortia tyrannus</i>	MAB** & SAB*, mainly inner-shelf ^a	Oct – Apr ^a	From northern MAB** to SAB*, spawning en route ^a	25 – 100 days (10 - 20 mm) ^b
<i>Mugil cephalus</i>	MAB** & SAB* mid- and outer-shelf & into Gulf Stream ^a	Oct – Feb ^a	Move offshore ^a	? (18 - 25 mm) ^a
<i>Lagodon rhomboides</i>	SAB* shelf, smallest larvae mainly inner-shelf but some farther offshore ^a	Oct - Mar; later to south ^a	Move offshore ^a	? (10 - 15 mm) ^a
<i>Leisotomus xanthurus</i>	NC outer-shelf near Gulf Stream front ^a	Winter - early spring ^a	Move offshore ^a	82 days (17.2 mm) ^c
<i>Micropogonias undulatus</i>	MAB** & SAB* shelf, likely inner- to mid-shelf based on captures ^a	Fall – early winter ^a	Move offshore; some may move south from MAB** ^a	30 - 60 days (8 - 20 mm) ^c
<i>Paralichthys albigutta</i>	Largely unknown: Offshore ^f	Fall – winter; Later moving south ^f	?	?
<i>Paralichthys dentatus</i>	MAB** & SAB* shelf, moving offshore as migration progresses ^a	Oct – Mar ^g	Move offshore to deeper water, spawning en route ^a	? (8 – 15 mm) ^a
<i>Paralichthys lethostigma</i>	Outer-shelf, south of resident estuary ^h	Fall – winter ^h	Move offshore and southward during winter ^h	~30 days ⁱ (?)

^aAble and Fahay 2010, ^bRice et al. 1999, ^cFlores-Coto and Warlen 1993, ^dAble et al. 2011, ^eWarlen 1980, ^fStokes 1977, ^gWenner et al. 1990, ^hCraig et al. 2015, ⁱTaylor et al. 2010; *South Atlantic Bight; **Middle Atlantic Bight

Table 2.1c: Species’ transport and relationships to the environment. Hypothesized larval transport mechanisms/directions and environmental factors that have been hypothesized to affect spawning or larval transport phenology. “?” indicates an unknown aspect of a species’ life history.

	Larval transport	Suggested environmental impacts
<i>Anguilla rostrata</i>	Use Gulf Stream to travel north from Sargasso Sea ^a	Increased temperature and precipitation in and around rivers and estuaries from which adults migrate correlate with earlier spawning migrations ^b . Higher abundance of ingressing glass eels when precipitation is above average ^c .
<i>Myrophis punctatus</i>	Use Gulf Stream to travel north from spawning grounds ^h	Water temperature in the estuary found to correlate to delays in first and last occurrence at Beaufort Inlet ^h .
<i>Brevoortia tyrannus</i>	North to south along inner-shelf ^d	Temperature influences time and rate of north to south spawning migration. Reported to move coincident with the position of the 10°C isotherm and spawn most intensely at 15 – 18°C ^a .
<i>Mugil cephalus</i>	Wind-driven drift facilitates shoreward movement ^a	Falling temperatures are involved in finalizing gonadal development. 21°C is optimal temperature for quick development in captive fish, with warmer temperatures slowing development and cooler temperatures leading to incomplete development ^e .
<i>Lagodon rhomboides</i>	?	Temperature contributes to depth at which fish spawn after moving offshore ^c . Similarity among Sparids in low latitudes spawning in the coldest month of the year ^f .
<i>Leisotomus xanthurus</i>	?	?
<i>Micropogonias undulatus</i>	?	?
<i>Paralichthys albigutta</i>	?	Warming temperatures relate to phenology of shoreward adult migration post-spawning ⁱ .
<i>Paralichthys dentatus</i>	?	Cooling temperatures influence phenology of offshore spawning migration ^a .
<i>Paralichthys lethostigma</i>	?	?

^aAble and Fahay 2010, ^b Verreault et al 2012, ^c Sullivan et al. 2006, ^dSimpson et al. 2017, ^eDarcy 1985, ^fSheaves 2006, ^gKuo et al. 1974, ^hAble et al. 2011, ⁱStokes 1977

Table 2.2: Linear mixed models of community changes in larval fish ingress phenology over time. The fit of all models improved with the addition of species as a random effect. $\chi^2(1)$ refers to the difference in deviance between the full and null models. R^2_m refers to variance explained solely by the fixed effects. R^2_c refers to variance explained by the full model. $dAIC_{null}$ refers to the difference between each full and null models. p and $\chi^2(year)$ refers to the significance of the “year” term in each model, and reduction in deviance attributable to the “year” term.

Model	$\chi^2(1)$	$R^2_m^*$	$R^2_c^*$	$dAIC_{null}$	df	Intercept (day)	Trend +/- S.E. (days year⁻¹)	p	$\chi^2(year)$
Start ~ Year + (1 Species)	103.37	0.0498	0.488	102.9	204	1703.0	-0.75 +/- 0.17	<0.0001	18.978
Peak ~ Year + (1 Species)	69.248	0.0188	0.405	68.4	187	1158.8	-0.40 +/- 0.17	0.016	5.8366
End ~ Year + (1 Species)	74.083	0.0032	0.395	72.6	216	573.0	-0.15 +/- 0.14	0.282	1.1571
Duration ~ Year + (1 Species)	45.425	0.0410	0.311	44.9	187	-1278.9	0.67 +/- 0.20	0.001	10.791

Table 2.3: Linear mixed models of environmental effects on community changes in larval fish ingress phenology. The fit of all models improved with the addition of species as a random effect. $\chi^2(I)$ refers to the difference in deviance between the full and null models. R^2m refers to variance explained solely by the fixed effects. R^2c refers to variance explained by the full model. ΔAIC_{null} refers to the difference between each metric's best model and the null model. p and $\chi^2(I)$ refers to the significance of the best model and difference in deviance between the best and null models. The effect size and standard error is given for all terms included in each metric's best model.

Model	$\chi^2(I)$	p	R^2m	R^2c	ΔAIC_{null}	df	Terms*	Trend +/- S.E.
Start ~ LW + NAO + Tide + (1 Species)	107.04	<0.0001	0.0733	0.431	99.0	201	LW	8.47 +/- 1.90
							NAO	-5.32 +/- 1.98
							Tide	-0.69 +/- 0.32
End ~ SST + AMO + NAO + Tide + (1 Species)	89.652	<0.0001	0.100	0.402	79.7	183	SST	-6.46 +/- 1.78
							AMO	-35.63 +/- 9.15
							NAO	-2.94 +/- 2.00
							Tide	0.91 +/- 0.41
Peak ~ SST + OWSE + AMO + NAO + Tide + (1 Species)	100.57	<0.0001	0.0794	0.427	88.5	211	SST	-6.09 +/- 1.52
							OWSE	0.049 +/- 0.023
							AMO	-16.25 +/- 7.55
							NAO	-2.85 +/- 1.63
							Tide	0.64 +/- 0.37
Duration ~ SST + NAO + Tide + (1 Species)	46.217	<0.0001	0.0449	0.298	38.3	184	SST	-5.16 +/- 2.18
							NAO	4.03 +/- 2.55
							Tide	0.40 +/- 0.15

*AMO units: days AMO^{-1} ; LW = strength of southward winds local to the inlet, units: days $(m\ s^{-1})^{-1}$; NAO units: day NAO^{-1} ; OWSE = phenology of offshore winds to the southeast, units: days $(wind\ day)^{-1}$; SST units: days $^{\circ}C^{-1}$; Tide units: days m^{-1}

Table 2.4: Principle component analysis (PCA) of environmental variables. The standard deviation and percent of variation explained (% Var) by each principle component (PC) are shown. The correlation between the original variables and each PC are also shown. Correlations with an absolute value greater than 0.4 are bolded and highlighted to emphasize the variables primarily associated with each PC.

		PC1	PC2	PC3	PC4	PC5	PC6	PC7
Beginning on ingress	STDEV	1.5150	1.4746	0.8919	0.8487	0.7415	0.5042	0.4580
	% Var	32.80	31.06	11.37	10.29	7.85	3.63	3.00
	SST	-0.400	0.221	-0.287	0.688	-0.453	0.146	0.096
	OWSW	-0.325	-0.308	0.663	-0.205	-0.551	0.108	0.047
	OWSE	-0.228	0.568	0.164	-0.221	0.108	-0.239	0.693
	AMO	-0.487	-0.087	0.384	0.379	0.590	-0.246	-0.235
	NAO	0.536	0.102	0.313	0.374	-0.263	-0.627	-0.038
	LW	-0.230	0.555	-0.051	-0.335	-0.209	-0.204	-0.663
Tide	0.324	0.455	0.450	0.200	0.139	0.644	-0.109	
Peak ingress	STDEV	1.5000	1.3900	0.9540	0.9140	0.7520	0.5691	0.4280
	% Var	32.14	27.60	13.00	11.93	8.08	4.63	2.62
	SST	-0.403	0.137	0.586	-0.320	-0.573	0.202	-0.054
	OWSW	-0.323	-0.262	-0.717	-0.136	-0.495	0.050	0.214
	OWSE	-0.255	0.615	-0.028	-0.035	0.154	-0.283	0.672
	AMO	-0.481	-0.145	-0.064	-0.556	0.461	-0.337	-0.329
	NAO	0.537	0.108	-0.020	-0.364	-0.385	-0.640	-0.096
	LW	-0.241	0.553	-0.246	0.399	-0.165	-0.138	-0.608
Tide	0.300	0.443	-0.275	-0.526	0.121	0.578	-0.114	
End of ingress	STDEV	1.4987	1.3444	0.9311	0.9010	0.7534	0.6597	0.5149
	% Var	32.09	25.82	12.38	11.60	8.11	6.22	3.79
	SST	-0.400	0.218	-0.315	0.574	-0.584	0.099	-0.112
	OWSW	-0.332	-0.320	0.656	-0.220	-0.461	-0.226	-0.212
	OWSE	-0.249	0.573	-0.031	-0.095	0.229	-0.707	-0.217
	AMO	-0.484	-0.096	0.351	0.457	0.476	0.034	0.443
	NAO	0.539	0.116	0.221	0.289	-0.333	-0.415	0.530
	LW	-0.222	0.549	0.125	-0.480	-0.210	0.368	0.472
Tide	0.307	0.445	0.530	0.299	0.110	0.360	-0.443	
Ingress duration	STDEV	1.5201	1.4048	0.9728	0.8541	0.7402	0.5539	0.4307
	% Var	33.01	28.19	13.52	10.42	7.83	4.38	2.65
	SST	-0.393	0.216	0.250	-0.717	0.444	-0.153	-0.023
	OWSW	-0.302	-0.393	0.245	0.537	0.620	-0.112	0.089
	OWSE	-0.235	0.581	0.168	0.354	0.003	0.152	-0.656
	AMO	-0.458	-0.147	0.541	-0.004	-0.491	0.408	0.263
	NAO	0.543	0.079	0.289	-0.082	0.384	0.676	0.063
	LW	-0.236	0.564	-0.353	0.207	0.139	0.160	0.644
Tide	0.371	0.339	0.591	0.148	-0.102	-0.541	0.272	

* LW = strength of southward winds local to the inlet, units; OWSW and OWSE = phenology of offshore winds to the southwest and southeast; SST = sea surface temperature

Table 2.5: Principle component regressions of environmental effects on community changes in larval fish ingress phenology.

The fit of all models improved with the addition of species as a random effect. $\chi^2(1)$ refers to the difference in deviance between the full and null models. R^2m refers to variance explained solely by the principle components. R^2c refers to variance explained by the full model. ΔAIC_{null} refers to the difference between each full and null models. The effect size and standard error is given for both principle components. *Indicates 95% confidence intervals do not overlap with zero.

Model	$\chi^2(1)$	<i>p</i>	R^2m	R^2c	ΔAIC_{null}	df	Terms	Trend +/- S.E.*
Start ~ PC1 + PC2 + (1 Species)	10.171	<0.01	0.0270	0.469	6.1	202	PC1	-2.26 +/- 0.92 *
							PC2	1.87 +/- 0.97
Peak ~ PC1 + PC2 + (1 Species)	1.945	0.378	0.0062	0.402	-2.0	185	PC1	-0.58 +/- 0.90
							PC2	1.12 +/- 0.95
End ~ PC1 + PC2 + (1 Species)	3.022	0.221	0.0083	0.403	-1	214	PC1	0.69 +/- 0.73
							PC2	1.15 +/- 0.78
Duration ~ PC1 + PC2 + (1 Species)	9.055	0.011	0.0344	0.297	5	185	PC1	3.18 +/- 1.09 *
							PC2	-0.70 +/- 1.14

Table. 2.6: Principle component regressions of environmental effects on species-level changes in larval fish ingress phenology. The overall model fit is shown alongside the effect sizes and significance levels of the two principle components included in each model. *P* values of each principle component refer to the significance of their relationship with phenology. Models and principle components that explain a significant amount of variance in phenology (*p* < 0.05) are emphasized in bold and highlight.

	Species	R ²	<i>p</i>	df	PC1		PC2	
					Trend +/- S.E.	<i>p</i>	Trend +/- S.E.	<i>p</i>
Beginning of ingress	<i>A. rostrata</i>	0.101	0.558	11	2.66 +/- 2.53	0.315	-0.82 +/- 2.40	0.739
	<i>B. tyrannus</i>	0.026	0.749	22	-1.86 +/- 4.14	0.657	2.60 +/- 4.23	0.545
	<i>L. rhomboides</i>	0.050	0.555	23	-0.46 +/- 2.51	0.856	2.84 +/- 2.68	0.301
	<i>L. xanthurus</i>	0.145	0.153	24	-0.26 +/- 2.00	0.900	4.13 +/- 2.05	0.056
	<i>M. undulatus</i>	0.125	0.280	19	-2.24 +/- 2.57	0.395	3.29 +/- 2.46	0.197
	<i>M. cephalus</i>	0.134	0.316	16	-6.70 +/- 4.52	0.157	0.35 +/- 4.00	0.931
	<i>M. punctatus</i>	0.059	0.526	21	-2.98 +/- 2.75	0.290	-0.90 +/- 2.61	0.734
	<i>P. albigutta</i>	0.175	0.195	17	-5.54 +/- 2.92	0.075	-0.49 +/- 3.10	0.876
	<i>P. dentatus</i>	0.395	0.081	10	-2.85 +/- 2.26	0.236	4.17 +/- 2.36	0.107
	<i>P. lethostigma</i>	0.166	0.281	14	0.52 +/- 1.53	0.739	-2.04 +/- 1.29	0.136
Peak of ingress	<i>A. rostrata</i>	0.108	0.565	10	0.98 +/- 2.58	0.712	2.91 +/- 2.87	0.334
	<i>B. tyrannus</i>	0.066	0.522	19	-2.79 +/- 3.27	0.404	2.57 +/- 3.40	0.459
	<i>L. rhomboides</i>	0.238	0.044	23	-0.17 +/- 2.56	0.947	7.84 +/- 2.95	0.014
	<i>L. xanthurus</i>	0.127	0.209	23	0.69 +/- 1.63	0.675	3.03 +/- 1.71	0.089
	<i>M. undulatus</i>	0.114	0.316	19	2.87 +/- 2.12	0.191	2.00 +/- 2.24	0.382
	<i>M. cephalus</i>	0.116	0.449	13	-4.85 +/- 3.81	0.226	-2.19 +/- 3.99	0.593
	<i>M. punctatus</i>	0.034	0.696	21	-2.34 +/- 2.93	0.434	-0.74 +/- 2.92	0.803
	<i>P. albigutta</i>	0.008	0.951	13	1.43 +/- 4.58	0.759	0.19 +/- 5.38	0.972
	<i>P. dentatus</i>	0.616	0.057	6	0.30 +/- 2.22	0.897	5.47 +/- 1.93	0.030
	<i>P. lethostigma</i>	0.021	0.872	13	0.06 +/- 1.51	0.971	0.72 +/- 1.36	0.607
End of ingress	<i>A. rostrata</i>	0.024	0.877	11	1.11 +/- 2.17	0.617	0.21 +/- 2.71	0.941
	<i>B. tyrannus</i>	0.013	0.876	20	-1.14 +/- 2.21	0.612	-0.19 +/- 2.48	0.940
	<i>L. rhomboides</i>	0.290	0.017	24	3.05 +/- 2.39	0.214	7.60 +/- 2.66	0.009
	<i>L. xanthurus</i>	0.193	0.085	23	4.18 +/- 1.82	0.032	-1.18 +/- 1.98	0.557
	<i>M. undulatus</i>	0.017	0.811	24	-0.43 +/- 2.59	0.869	1.81 +/- 2.88	0.536
	<i>M. cephalus</i>	0.142	0.251	18	2.36 +/- 2.85	0.418	-4.72 +/- 3.22	0.160
	<i>M. punctatus</i>	0.086	0.341	24	-3.15 +/- 2.11	0.149	-0.41 +/- 2.35	0.862
	<i>P. albigutta</i>	0.089	0.433	18	1.95 +/- 1.88	0.313	-1.63 +/- 2.14	0.457
	<i>P. dentatus</i>	0.120	0.564	9	-2.47 +/- 2.98	0.429	1.95 +/- 2.90	0.517
	<i>P. lethostigma</i>	0.219	0.108	18	0.83 +/- 1.46	0.578	3.21 +/- 1.45	0.040
Ingress duration	<i>A. rostrata</i>	0.046	0.789	10	-1.43 +/- 2.99	0.643	1.78 +/- 3.59	0.630
	<i>B. tyrannus</i>	0.069	0.507	19	1.14 +/- 3.40	0.741	-4.00 +/- 3.60	0.280
	<i>L. rhomboides</i>	0.092	0.331	23	3.20 +/- 3.25	0.334	4.49 +/- 3.59	0.224
	<i>L. xanthurus</i>	0.179	0.103	23	3.64 +/- 2.46	0.152	-4.34 +/- 2.57	0.104
	<i>M. undulatus</i>	0.037	0.701	19	1.97 +/- 3.60	0.590	-2.32 +/- 3.65	0.534
	<i>M. cephalus</i>	0.216	0.206	13	10.1 +/- 6.13	0.123	-3.45 +/- 5.68	0.554
	<i>M. punctatus</i>	0.005	0.951	21	0.98 +/- 3.13	0.757	0.06 +/- 3.14	0.984
	<i>P. albigutta</i>	0.321	0.081	13	8.10 +/- 3.33	0.030	-0.55 +/- 3.93	0.891
	<i>P. dentatus</i>	0.059	0.833	6	2.88 +/- 4.70	0.562	1.39 +/- 4.47	0.767
	<i>P. lethostigma</i>	0.362	0.054	13	2.23 +/- 1.93	0.268	4.68 +/- 1.83	0.024

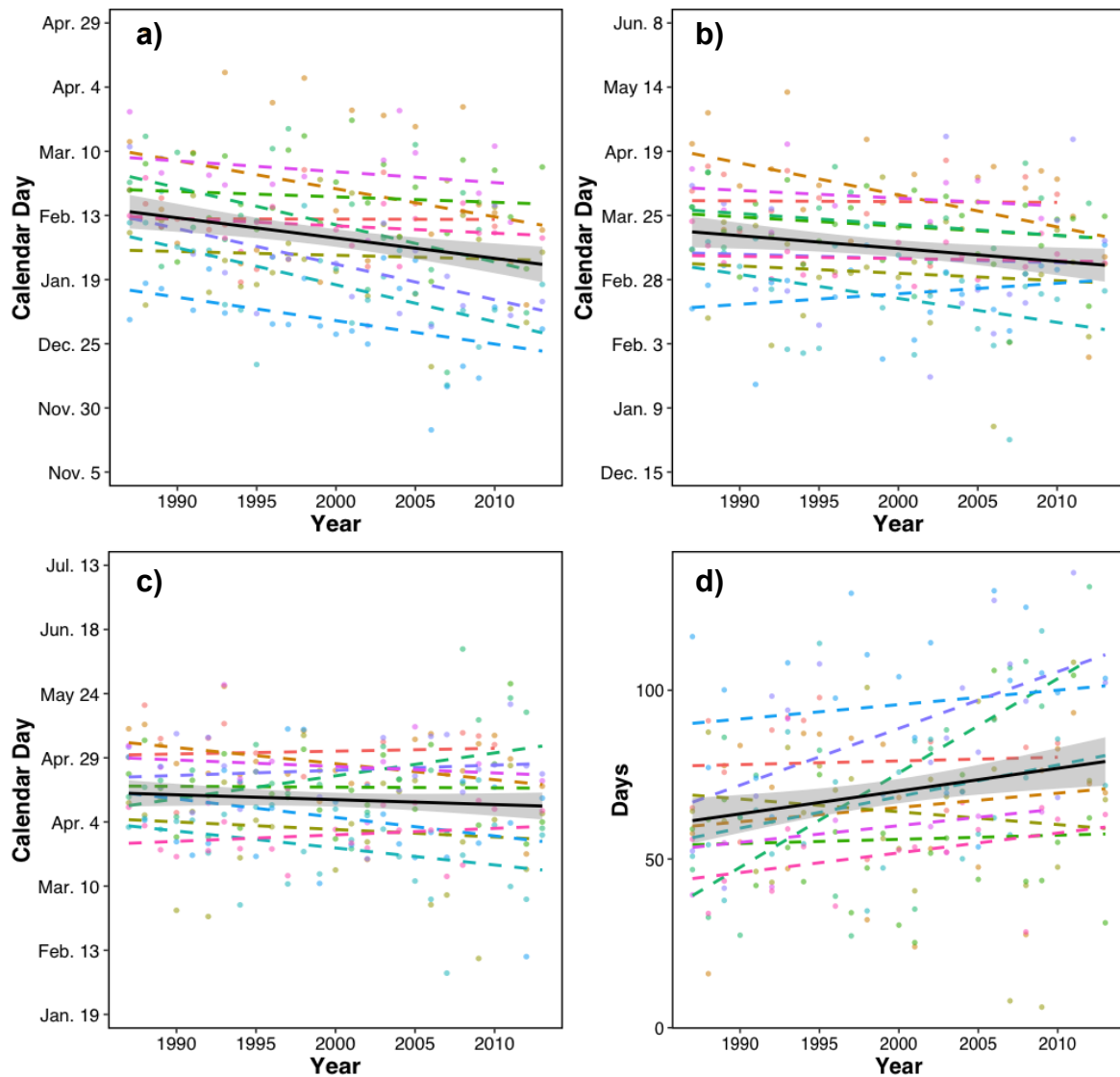


Figure 2.1: Temporal change in ingress phenology. Species are shown by dashed colored lines and the community by a solid black line. Grey shading shows standard error around community's temporal trend. a-d: beginning, peak, end, and duration of phenology, respectively. Species' color coding is consistent with Figure 2.2.

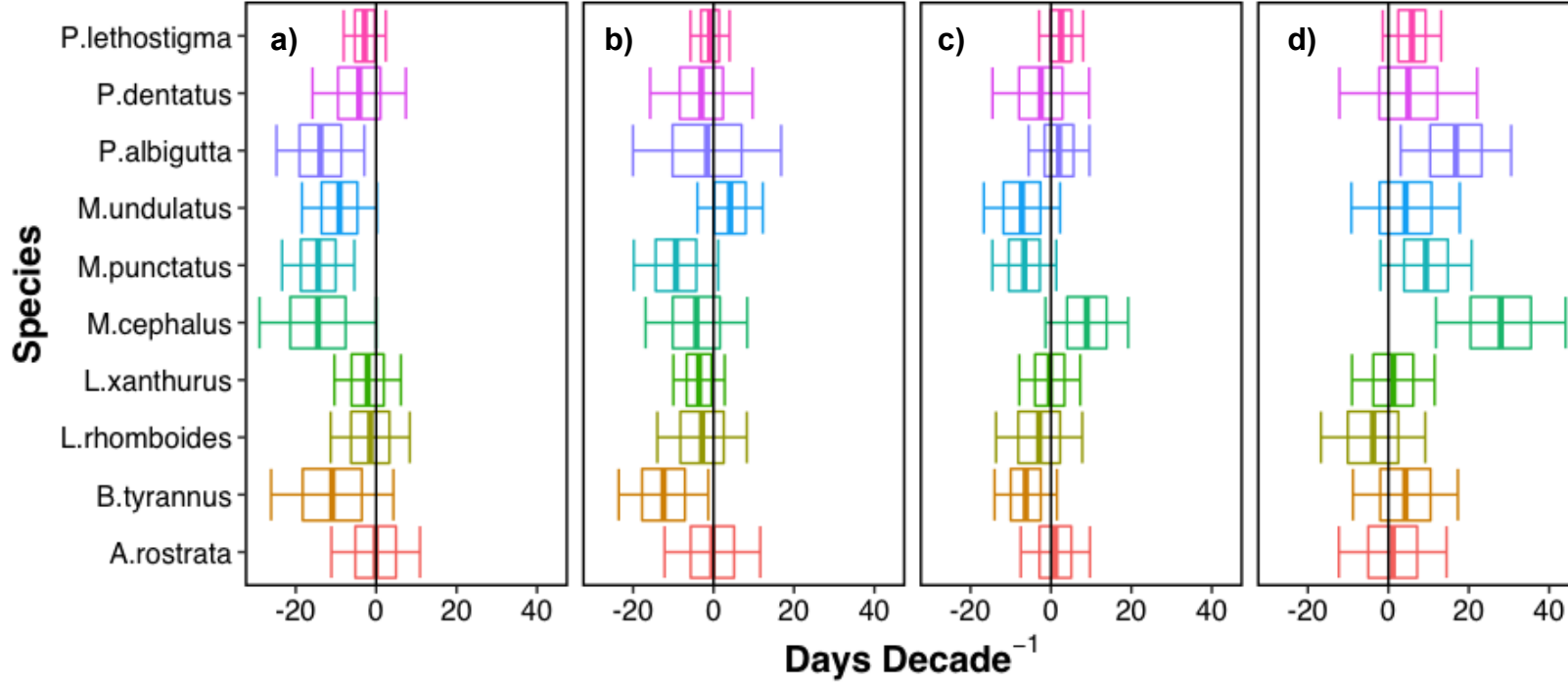


Figure 2.2: Boxplots of temporal trend in each species' phenology metrics. Centerlines, boxes, and whiskers show the trend, standard error, and 95% confidence interval, respectively. Trends with 95% confidence intervals that do not overlap the zero line are significant ($p < 0.05$). Full scientific names are given in Table 2.1. a-d: beginning, peak, end, and duration of phenology, respectively.

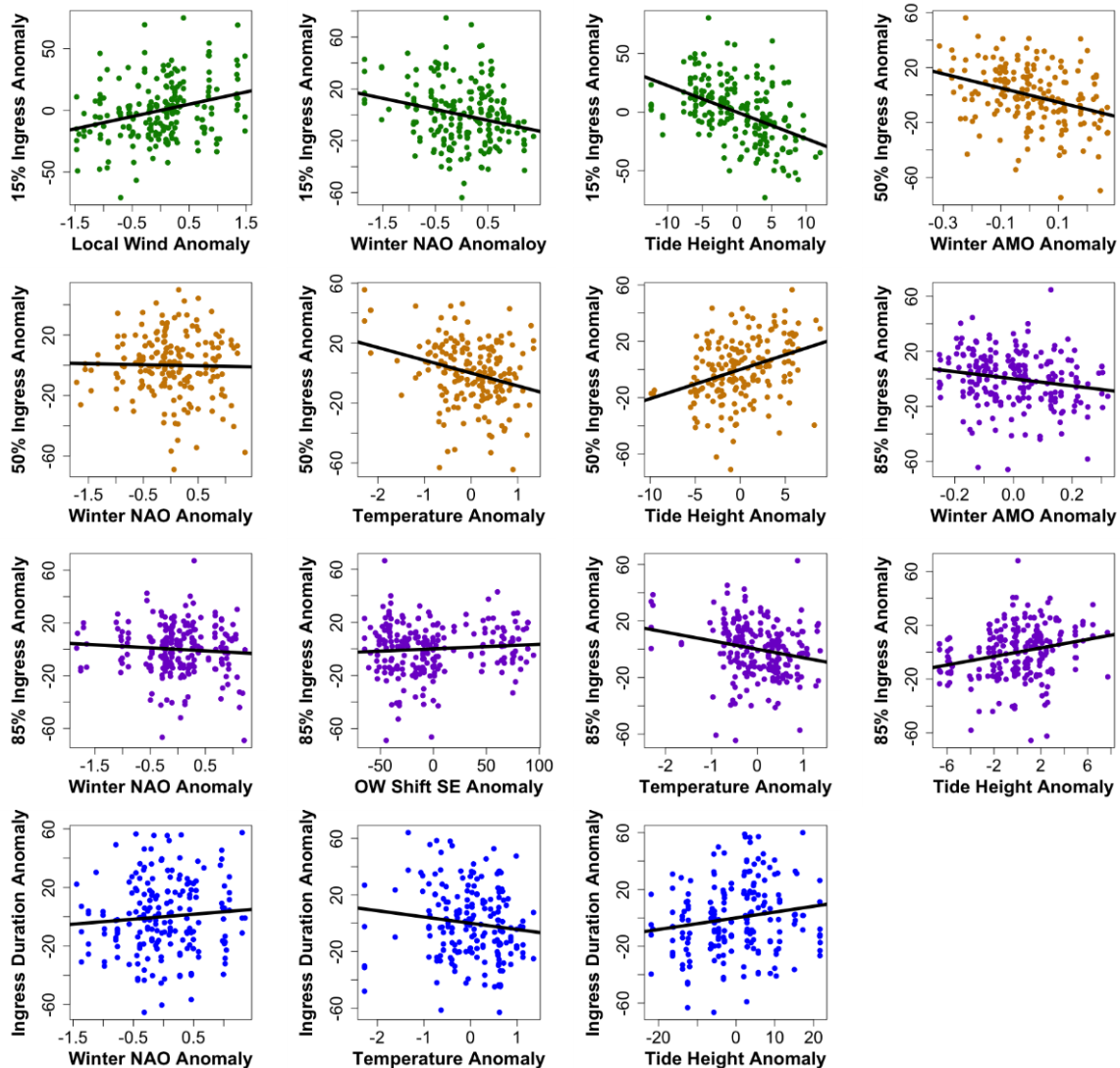


Figure 2.3: Added-variable plots of environmental metrics included in best models of ingress of the community. Green, orange, purple, and blue points represent models of beginning, peak, end, and duration of ingress, respectively. Positive (negative) slopes indicate factors that delay (advance) ingress. Each point represents species' phenology in given year. See Table 2.3 for the specifications of each model.

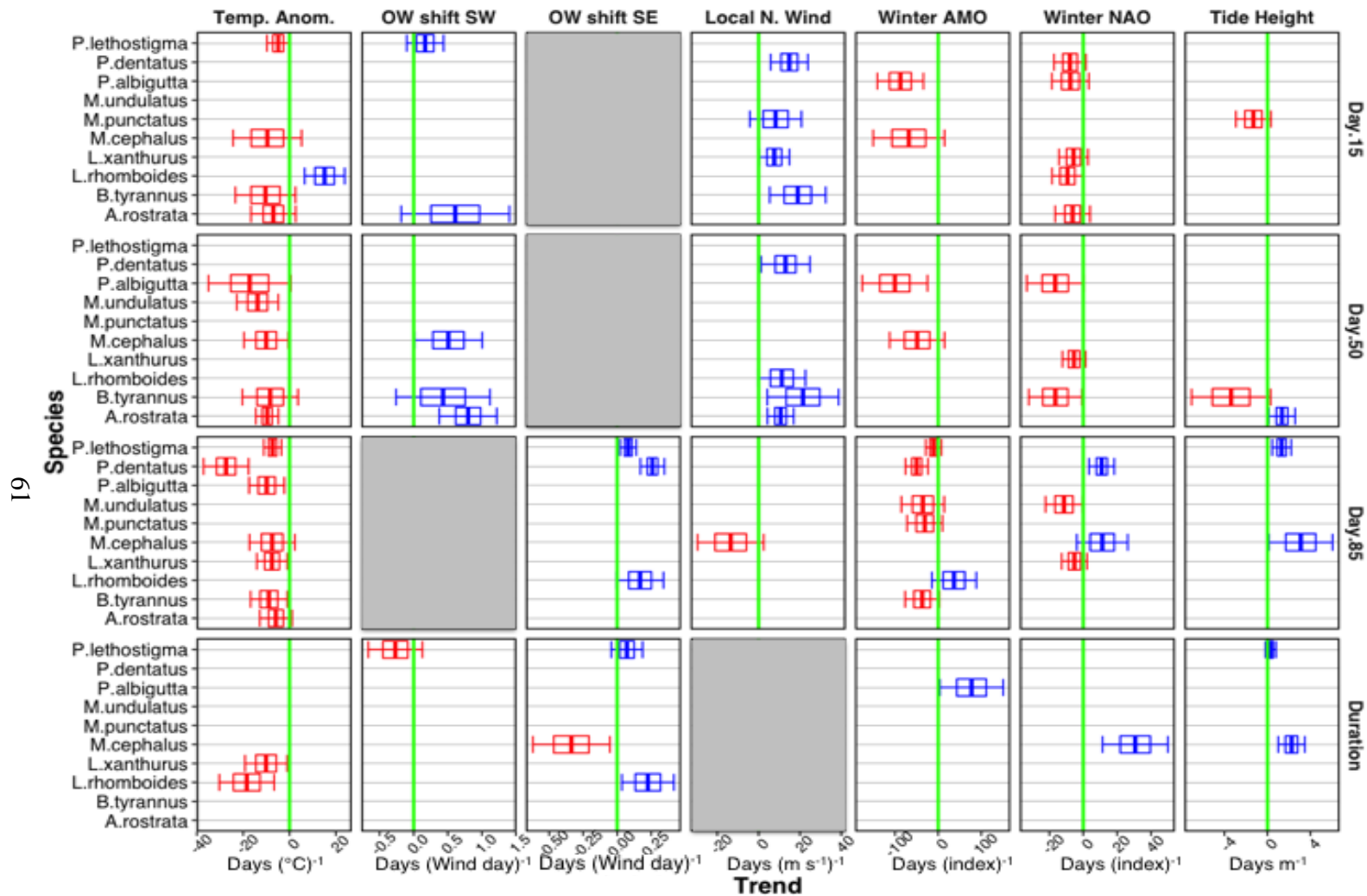


Figure 2.4: Boxplots of effects of environmental factors on species' phenology metrics. Centerlines, boxes, and whiskers show the trend, standard error, and 95% confidence interval, respectively. Trends are color coded by effect direction: red = advancing ingress, blue = delayed ingress. Green lines show an effect size of zero. Grey boxes indicate that an environmental factor was not considered in model of a particular phenology metric. Boxplots are only included for metrics that were included in species' best model of environmental influences on phenology.

Figure 2.5: Biplots of principle components (PCs) 1 and 2 of environmental variables associated with each phenology metric. Vector sizes and directions show the weight of each environmental variable in the two PCs. PC1 was typically associated with sea surface temperature and the AMO and NAO indices. PC2 was typically associated with the timing of wind shifts the southeast, northerly wind strength near Beaufort Inlet, and cumulative tide height. The angle between vectors relates to the correlation between environmental variables. Angles approaching 0° indicate positive correlations, angles approaching 180° indicate negative correlations, and angles approaching 90° indicate no correlation. a-d: beginning, peak, end, and duration of phenology, respectively.

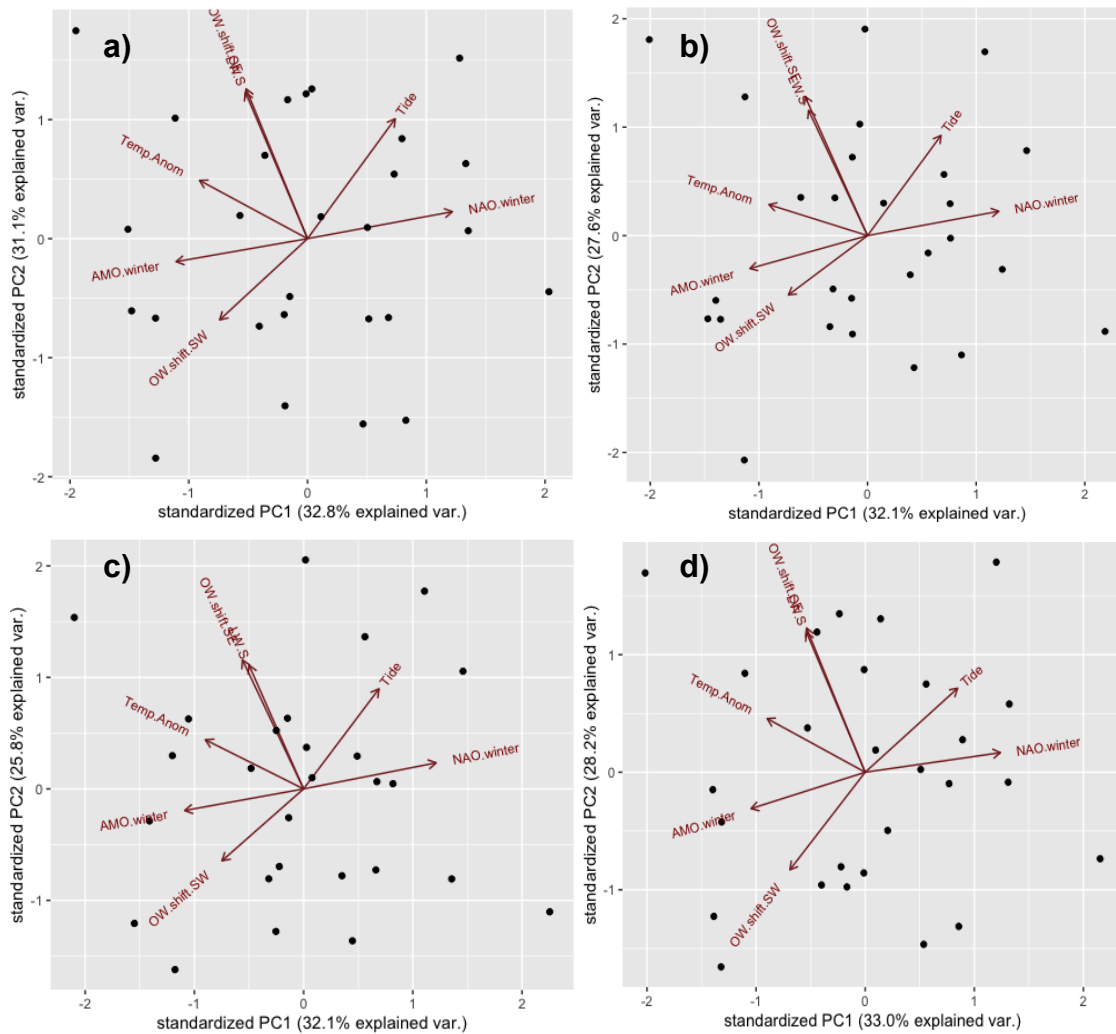


Table S2.1: Phenology metrics removed for each species and the reason for their removal.
 See Section 2.3.2: *Calculation of phenology indices* for further explanation of the criteria for metric removal.

Species	Year	Metrics	Reason
<i>Anguilla rostrata</i>	1991	All	Sample size
	1996	All	Sample size
	1997	All	Sample size
	1999	All	Sample size
	2000	All	Sample size
	2001	All	Sample size
	2004	All	Sample size
	2005	Peak, end, and duration	Metric within 2 weeks of season's end
	2006	All	Sample size
	2009	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Brevoortia tyrannus</i>	2011	All	Sample size
	1991	Peak, end, and duration	Metric within 2 weeks of season's end
	1996	Peak, end, and duration	Metric within 2 weeks of season's end
	2003	Peak, end, and duration	Metric within 2 weeks of season's end
	2004	All	Bimodal ingress
<i>Lagodon rhomboides</i>	2007	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2007	Peak, end, and duration	Metric within 2 weeks of season's end
<i>Leiostomus xanthurus</i>	1992	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Mugil cephalus</i>	1993	Peak, end, and duration	Metric within 2 weeks of season's end
	1994	Peak, end, and duration	Metric within 2 weeks of season's end
	1998	All	Sample size
	1999	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2000	All	Sample size
	2004	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2005	Peak, end, and duration	Metric within 2 weeks of season's end
	2010	All	Sample size

Species	Year	Metrics	Reason
<i>Mugil cephalus</i>	2011	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2013	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Micropogonias undulatus</i>	1990	Beginning, peak, and duration	Metric within 2 weeks of season's start
	1994	Beginning, peak, and duration	Metric within 2 weeks of season's start
	1995	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2011	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2012	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Myrophis punctatus</i>	1997	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2011	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2012	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Paralichthys albigutta</i>	1990	Beginning, peak, and duration	Metric within 2 weeks of season's start
	1994	Beginning, peak, and duration	Metric within 2 weeks of season's start
	1996	Peak, end, and duration	Metric within 2 weeks of season's end
	1997	Peak, end, and duration	Metric within 2 weeks of season's end
	1999	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2000	Peak, end, and duration	Metric within 2 weeks of season's end
	2001	Peak, end, and duration	Metric within 2 weeks of season's end
	2009	Beginning, peak, and duration	Metric within 2 weeks of season's start
	2012	Beginning, peak, and duration	Metric within 2 weeks of season's start
<i>Paralichthys dentatus</i>	1988	All	Sample size
	1990	All	Sample size
	1991	All	Sample size
	1994	Beginning, peak, and duration	Metric within 2 weeks of season's start

Species	Year	Metrics	Reason
<i>Paralichthys dentatus</i>	1995	All	Sample size
	1997	Beginning, peak, and duration	Metric within 2 weeks of season's start
	1998	Peak, end, and duration	Metric within 2 weeks of season's end
	2000	All	Sample size
	2001	All	Sample size
	2004	Peak, end, and duration	Metric within 2 weeks of season's end
	2006	All	Sample size
	2008	All	Sample size
	2010	Peak, end, and duration	Metric within 2 weeks of season's end
	2011	Peak, end, and duration	Metric within 2 weeks of season's end
	2012	All	Sample size
	2013	Beginning, peak, and duration	Metric within 2 weeks of season's start
	<i>Paralichthys lethostigma</i>	1990	Beginning, peak, and duration
1991		All	Sample size
1995		Peak, end, and duration	Metric within 2 weeks of season's end
1997		Beginning, peak, and duration	Metric within 2 weeks of season's start
1999		All	Sample size
2002		Beginning, peak, and duration	Metric within 2 weeks of season's start
2006		Beginning, peak, and duration	Metric within 2 weeks of season's start
2007		Beginning, peak, and duration	Metric within 2 weeks of season's start
2011		All	Sample size
2012		All	Sample size

Table S2.2: Results from linear models of species' temporal changes in larval ingress phenology. * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$; **** $p < 0.001$

	Species	Trend (days year ⁻¹) +/- S.E.	R ²	<i>p</i>	df
Beginning of ingress	<i>A. rostrata</i>	-0.01 +/- 0.51	4.8 x 10 ⁻⁵	0.981	12
	<i>B. tyrannus</i>	-1.09 +/- 0.74	0.087	0.151	23
	<i>L. rhomboides</i>	-0.15 +/- 0.48	0.004	0.760	24
	<i>L. xanthurus</i>	-0.21 +/- 0.40	0.011	0.604	25
	<i>M. undulatus</i>	-0.91 +/- 0.45	0.173	0.054*	20
	<i>M. cephalus</i>	-1.45 +/- 0.69	0.206	0.051*	17
	<i>M. punctatus</i>	-1.44 +/- 0.43	0.335	0.003***	22
	<i>P. albigutta</i>	-1.39 +/- 0.52	0.284	0.016**	18
	<i>P. dentatus</i>	-0.42 +/- 0.53	0.055	0.441	11
	<i>P. lethostigma</i>	-0.28 +/- 0.25	0.082	0.265	15
Peak ingress	<i>A. rostrata</i>	-0.03 +/- 0.54	2.5 x 10 ⁻⁴	0.959	11
	<i>B. tyrannus</i>	-1.24 +/- 0.53	0.214	0.030**	20
	<i>L. rhomboides</i>	-0.29 +/- 0.54	0.012	0.601	24
	<i>L. xanthurus</i>	-0.36 +/- 0.31	0.054	0.254	24
	<i>M. undulatus</i>	0.41 +/- 0.39	0.053	0.305	20
	<i>M. cephalus</i>	-0.43 +/- 0.59	0.036	0.481	14
	<i>M. punctatus</i>	-0.93 +/- 0.51	0.134	0.079*	22
	<i>P. albigutta</i>	-0.16 +/- 0.86	0.003	0.854	14
	<i>P. dentatus</i>	-0.30 +/- 0.54	0.043	0.591	7
	<i>P. lethostigma</i>	-0.09 +/- 0.23	0.011	0.705	14
End of ingress	<i>A. rostrata</i>	0.11 +/- 0.40	0.006	0.786	12
	<i>B. tyrannus</i>	-0.63 +/- 0.37	0.119	0.108	21
	<i>L. rhomboides</i>	-0.29 +/- 0.52	0.013	0.578	25
	<i>L. xanthurus</i>	-0.03 +/- 0.37	2.8 x 10 ⁻⁴	0.935	24
	<i>M. undulatus</i>	-0.72 +/- 0.46	0.089	0.130	25
	<i>M. cephalus</i>	0.89 +/- 0.49	0.148	0.085*	19
	<i>M. punctatus</i>	-0.66 +/- 0.39	0.105	0.099*	25
	<i>P. albigutta</i>	0.20 +/- 0.36	0.016	0.583	19
	<i>P. dentatus</i>	-0.25 +/- 0.54	0.022	0.649	10
	<i>P. lethostigma</i>	0.25 +/- 0.26	0.047	0.346	19
Ingress duration	<i>A. rostrata</i>	0.11 +/- 0.61	0.003	0.861	11
	<i>B. tyrannus</i>	0.42 +/- 0.63	0.022	0.506	20
	<i>L. rhomboides</i>	-0.38 +/- 0.63	0.015	0.552	24
	<i>L. xanthurus</i>	0.12 +/- 0.50	0.003	0.807	24
	<i>M. undulatus</i>	0.43 +/- 0.65	0.021	0.516	20
	<i>M. cephalus</i>	2.80 +/- 0.75	0.497	0.002***	14
	<i>M. punctatus</i>	0.94 +/- 0.55	0.118	0.100*	22
	<i>P. albigutta</i>	1.68 +/- 0.64	0.330	0.020**	14
	<i>P. dentatus</i>	0.50 +/- 0.72	0.063	0.515	7
	<i>P. lethostigma</i>	0.59 +/- 0.34	0.177	0.105	14

Table S2.3: Results of the best fitting linear models of species' larval ingress phenology as a response of the environment. Models were selected by reverse-stepwise AIC comparisons. The overall model fit is shown alongside the effect sizes and significance levels of the environmental metrics included in each model. *P* values refer to significance of univariate relationship between environmental parameters and phenology. Species abbreviations are: A. ros = *Anguilla rostrata*, B. tyr = *Brevoortia tyrannus*, L. rho = *Lagodon rhomboides*, L. xan = *Leiostomus xanthurus*, M. und = *Micropogonias undulatus*, M. cep = *Mugil cephalus*, M. pun = *Myrophis punctatus*, P. alb = *Paralichthys albigutta*, P. den = *Paralichthys dentatus*, P. let = *Paralichthys lethostigma*.

	Model	R²	ΔAIC null	df	Terms*	Trend +/- S.E.	<i>p</i>
Beginning of ingress	A. ros ~ SST + OWSW + NAO	0.362	0.3	10	SST	-6.99 +/- 4.35	0.140
					OWSW	0.61 +/- 0.36	0.117
					NAO	-6.31 +/- 4.62	0.203
	B. tyr ~ SST + LW	0.328	5.9	22	SST	-10.39 +/- 6.26	0.111
					LW	18.94 +/- 6.53	0.0083
	L. rho ~ SST + NAO	0.384	8.6	23	SST	15.17 +/- 4.18	0.0014
					NAO	-9.33 +/- 4.38	0.0442
	L. xan ~ LW + NAO	0.202	2.1	24	LW	7.56 +/- 3.54	0.0429
					NAO	-5.72 +/- 4.16	0.181
	M. und ~ 1	0	0	21			
	M. cep ~ SST + AMO	0.196	0.1	16	SST	-9.59 +/- 6.98	0.189
					AMO	-68.12 +/- 39.04	0.100
	M. pun ~ LW + Tide	0.162	0.3	21	LW	8.23 +/- 6.01	0.185
					Tide	-1.31 +/- 0.79	0.111
Peak ingress	P. alb ~ AMO + NAO	0.421	6.9	17	AMO	-87.65 +/- 25.21	0.0029
					NAO	-7.62 +/- 5.16	0.158
	P. den ~ LW + NAO	0.577	7.2	10	LW	14.85 +/- 4.04	0.0043
					NAO	-7.84 +/- 4.23	0.0936
	P. let ~ SST + OWSW	0.328	2.8	14	SST	-4.89 +/- 2.25	0.0472
					OWSW	0.168 +/- 0.126	0.205
	A. ros ~ SST + OWSW + LW + Tide	0.873	18.8	8	SST	-9.68 +/- 2.11	0.0018
					OWSW	0.80 +/- 0.18	0.0024
					LW	10.65 +/- 2.75	0.0047
					Tide	1.35 +/- 0.53	0.0347
	B. tyr ~ SST + OWSW + LW + NAO + Tide	0.439	2.7	16	SST	-8.36 +/- 5.68	0.160
					OWSW	0.43 +/- 0.32	0.204
					LW	21.47 +/- 8.12	0.0177
					NAO	-16.46 +/- 7.41	0.0410
				Tide	-3.39 +/- 1.74	0.0686	
L. rho ~ LW	0.146	2.1	24	LW	11.22 +/- 5.53	0.0538	
L. xan ~ NAO	0.100	0.7	24	NAO	-5.44 +/- 3.34	0.116	
M. und ~ SST	0.341	7.2	20	SST	-13.81 +/- 4.29	0.0043	
M. cep ~ SST + OWSW + AMO	0.487	4.7	12	SST	-10.07 +/- 4.40	0.0410	
				OWSW	0.51 +/- 0.23	0.0456	
				AMO	-48.94 +/- 29.19	0.120	
M.pun ~ 1	0	1	23				

	Model	R²	ΔAIC null	df	Terms*	Trend +/- S.E.	p
Peak cont.	P. alb ~ SST + AMO	0.554	6.9	12	SST	-17.22 +/- 8.16	0.0565
	+ NAO				AMO	-100.50 +/- 34.70	0.0134
					NAO	-16.55 +/- 7.68	0.0522
	P. den ~ LW	0.494	4.1	7	LW	13.03 +/- 4.98	0.0346
	P. let ~ 1	0	1	15			
End of ingress	A. ros ~ SST	0.221	1.5	12	SST	-5.88 +/- 3.18	0.0895
	B. tyr ~ SST + AMO	0.265	3.1	20	SST	-8.90 +/- 3.80	0.0295
					AMO	-37.09 +/- 18.98	0.0648
	L. rho ~ OWSE + AMO	0.185	1.5	24	OWSE	0.17 +/- 0.083	0.0543
					AMO	36.69 +/- 24.98	0.155
	L. xan ~ SST + NAO	0.336	6.7	23	SST	-7.57 +/- 3.18	0.0260
					NAO	-5.21 +/- 3.61	0.162
	M. und ~ AMO + NAO	0.182	1.4	24	AMO	-35.71 +/- 24.03	0.150
					NAO	-11.39 +/- 5.29	0.0415
	M. cep ~ SST + LW + NAO + Tide	0.380	2.0	16	SST	-7.50 +/- 4.63	0.125
					LW	-13.50 +/- 7.55	0.0929
					NAO	11.23 +/- 7.10	0.133
					Tide	3.10 +/- 1.39	0.0411
	M. pun ~ AMO	0.0894	0.5	25	AMO	-31.2 +/- 19.9	0.130
	P. alb ~ SST	0.279	4.9	19	SST	-9.86 +/- 3.63	0.0138
	P. den ~ SST + OWSE + AMO + NAO	0.903	20.0	7	SST	-27.38 +/- 4.10	<0.001
					OWSE	0.26 +/- 0.04	<0.001
AMO					-49.85 +/- 11.06	0.0028	
NAO					10.88 +/- 3.15	0.0106	
P. let ~ SST + OWSE + AMO + Tide	0.688	16.4	16	SST	-7.30 +/- 1.80	<0.001	
				OWSE	0.08 +/- 0.03	0.0117	
				AMO	-10.89 +/- 8.57	0.222	
				Tide	1.32 +/- 0.42	0.0059	
A. ros ~ 1	0	0	12				
B. tyr ~ 1	0	0	21				
L. rho ~ SST + OWSE	0.352	7.3	23	SST	-18.46 +/- 5.73	0.0038	
				OWSE	0.23 +/- 0.09	0.0230	
L. xan ~ SST	0.181	3.2	24	SST	-10.14 +/- 4.40	0.0301	
M. und ~ 1	0	0	21				
M. cep ~ OWSE + NAO + Tide	0.700	13.3	12	OWSE	-0.34 +/- 0.13	0.0233	
				NAO	30.68 +/- 8.84	0.0046	
				Tide	2.24 +/- 0.57	0.0020	
M. pun ~ 1	0	0	23				
P. alb ~ AMO	0.268	3.0	14	AMO	77.34 +/- 34.19	0.0401	
P. den ~ 1	0	0	8				
P. let ~ OWSW + OWSE + Tide	0.469	4.1	12	OWSW	-0.27 +/- 0.18	0.165	
				OWSE	0.07 +/- 0.05	0.200	
				Tide	0.29 +/- 0.22	0.222	

*AMO units: days AMO⁻¹; LW = strength of southward winds local to the inlet, units: days (m s⁻¹)⁻¹; NAO units: day NAO⁻¹; OWSE = phenology of offshore winds to the southeast, units: days (wind day)⁻¹; OWSW = phenology of offshore winds to the southwest, units: days (wind day)⁻¹; SST units: days °C⁻¹; Tide units: days m⁻¹

Figure S2.1: Cumulative density of *Brevoortia tyrannus* caught over time during the 2009 Bridgenet season. The blue line shows a loess smoothed average of the points plotted (span = 0.75, degrees = 2). The grey shading shows standard error around the loess curve. The timing of the three phenology metrics (15%, 50%, and 85% of cumulative density) have been extrapolated to the x-axis.

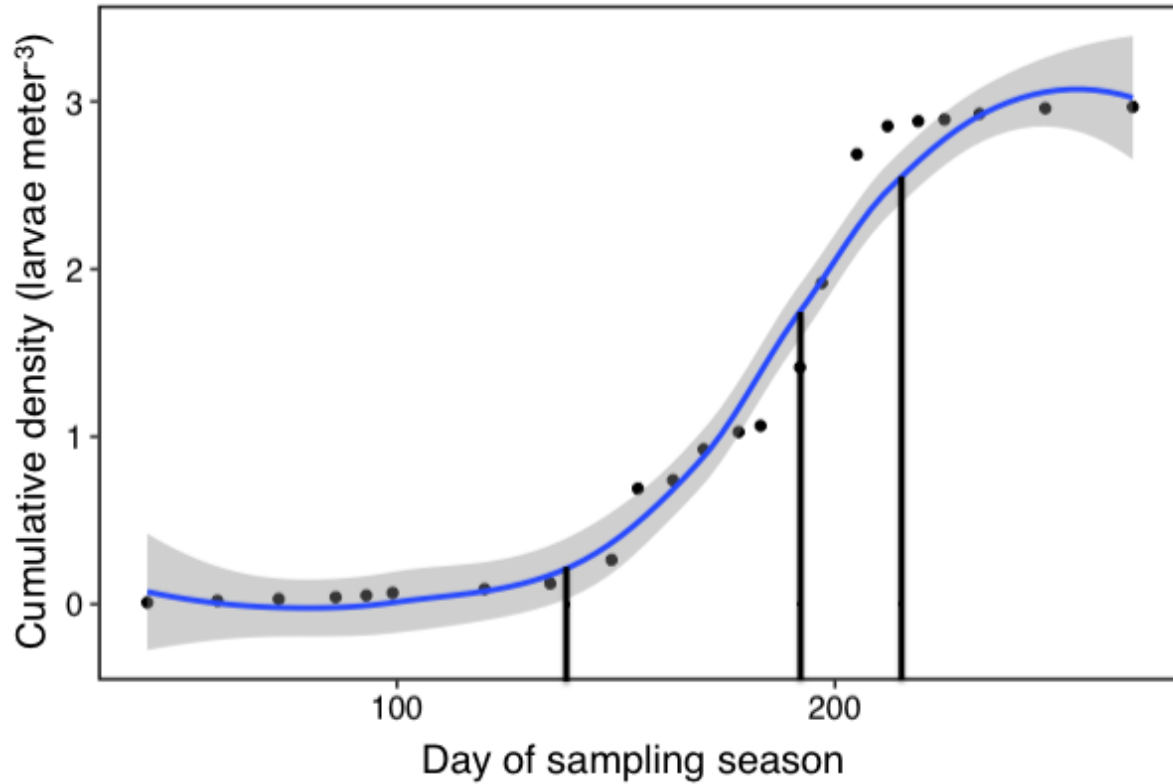


Figure S2.2: Correlation plots of sea surface temperature anomalies in satellite cells (above), and in buoys, weather stations, and spatially averaged satellite cells (below). Red and blue shading represent negative and positive correlations between sites, respectively. Point size represents the significance of each correlation, with larger points depicting more significant relationships. There were significant positive correlations between satellite cells and between buoys across the SAB. Weather station and buoy observations were from Diamond Shoals (DS - 41025), Frying Pan Shoals (FPS - 41013), Edisto, South Carolina (SC - 41004), Wrightsville Beach (WB - 41037), Gray's Reef, Georgia (GA - 41008), Beaufort Inlet (BF – BFTN7), and Cape Lookout (CL – CLKN7). Satellite grid cells are indicated below by their latitudinal and longitudinal coordinates.

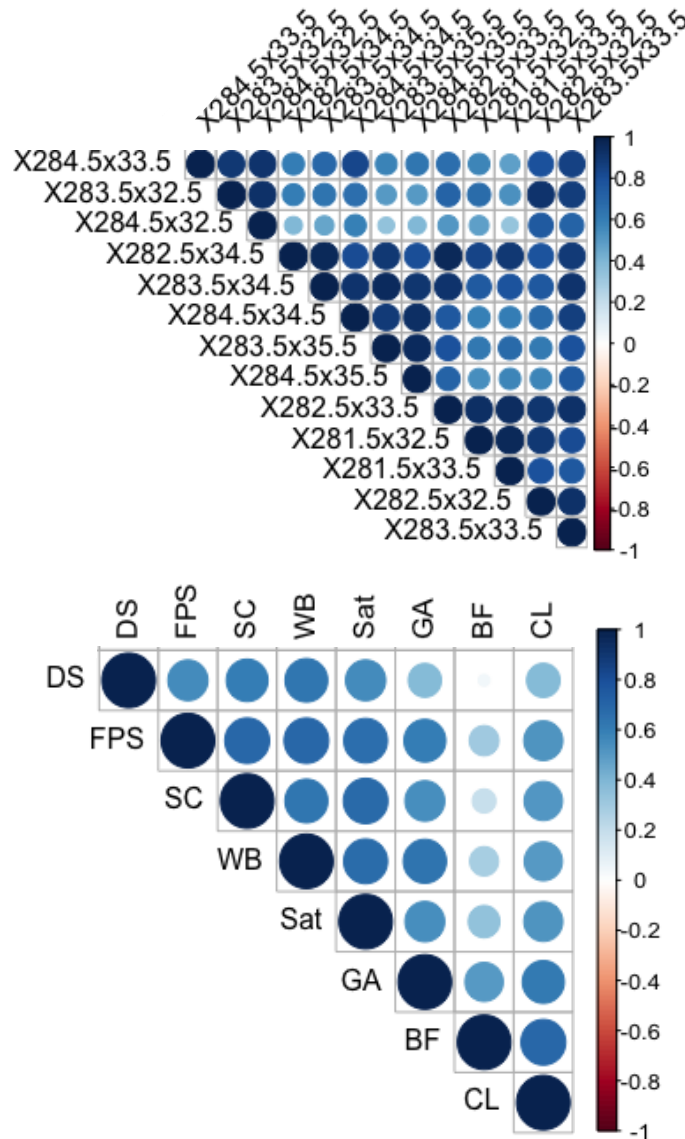


Figure S2.3: Correlation plots of daily wind vector velocity to the east (left) and north (right) observed by buoy and weather station observations (above), and Blended Sea Winds satellite grid cells (Sat) (below). Red and blue shading represent negative and positive correlations between sites, respectively. Point size represents the significance of each correlation, with larger points depicting more significant relationships. There were significant positive correlations between satellite cells and between buoys across the SAB. Weather station and buoy observations were from Diamond Shoals (DS - 41025), Frying Pan Shoals (FPS - 41013), Edisto, South Carolina (SC - 41004), Wrightsville Beach (WB - 41037), Gray's Reef, Georgia (GA - 41008), Beaufort Inlet (BF – BFTN7), Cape Lookout (CL – CLKN7), and Virginia Beach (VB – 44014).

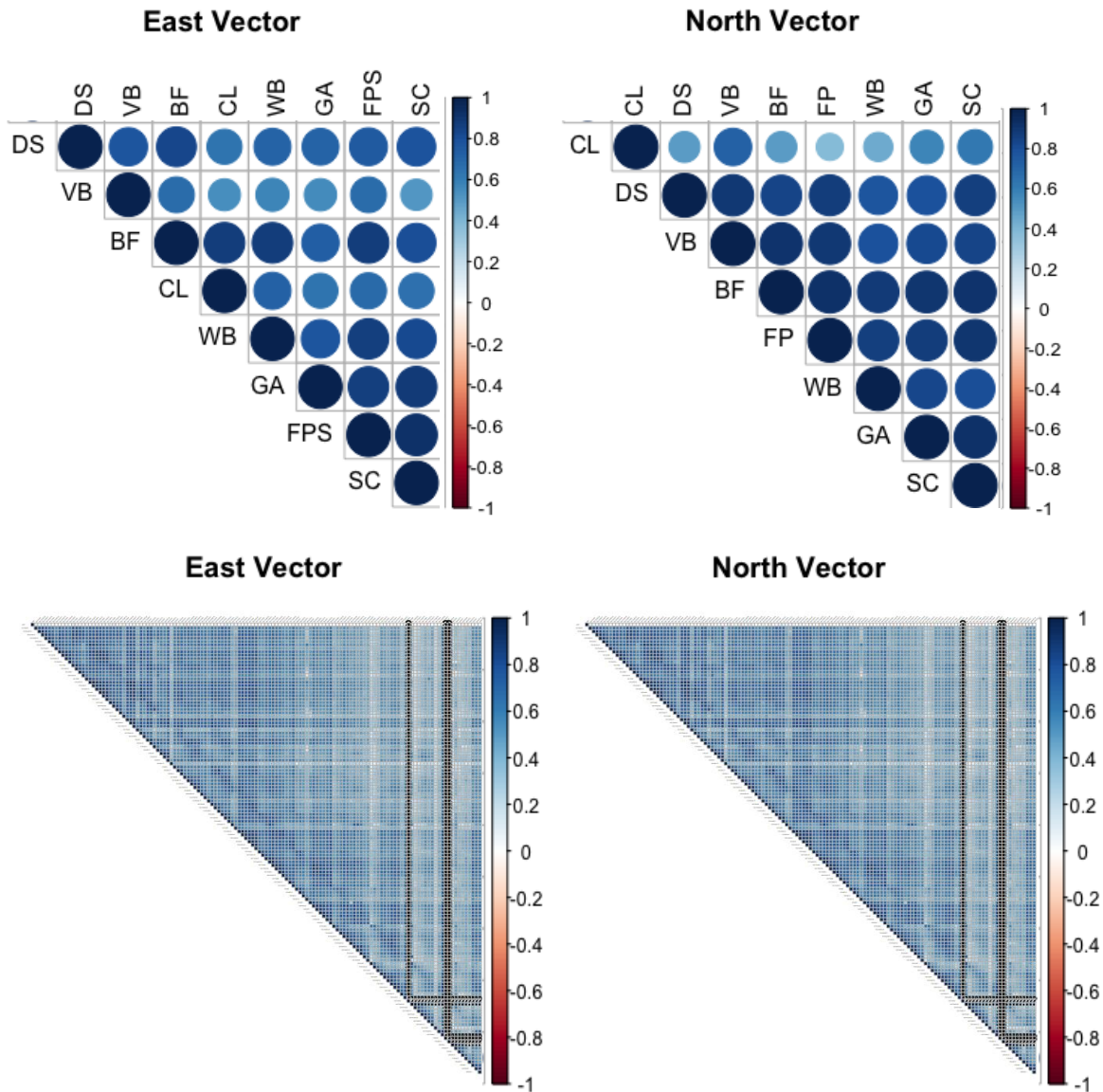


Figure S2.4: Wind climatology at weather stations and in satellite observations of the South Atlantic Bight (SAB). Vectors represent the average wind strength and direction for each month. During most months there is general consistency across the SAB in wind direction across the eight stations and satellite data examined below. Weather station and buoy observations were from Diamond Shoals (DS - 41025), Frying Pan Shoals (FPS - 41013), Edisto, South Carolina (SC - 41004), Wrightsville Beach (WB - 41037), Grays Reef, Georgia (GA - 41008), Beaufort Inlet (BF – BFTN7), Cape Lookout (CL – CLKN7), and Virginia Beach (VB – 44014). Satellite data (Sat) was obtained from the Blended Sea Winds database.

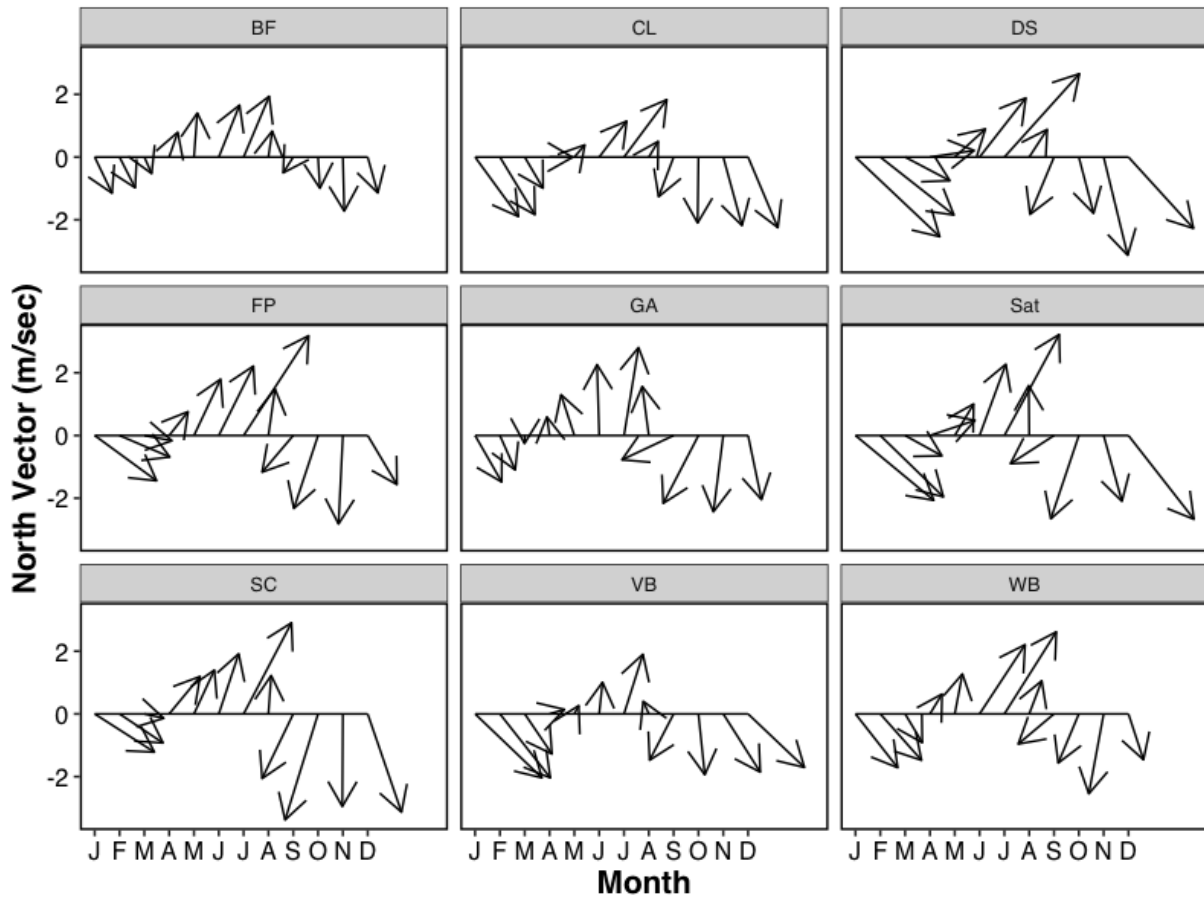


Figure S2.5: Cumulative wind stress to northwest observed in Onslow Bay during the fall/winter of 1990 and spring of 1991. The black dots are the observed winds stress. The blue line show a loess smoothed average of the points plotted (span = 0.75, degrees = 2). The grey shading shows standard error around the loess curve. The timing of the maximum wind stress to the northwest has been extrapolated to the x-axis. This point was used to determine the phenology of wind shift to the southwest.

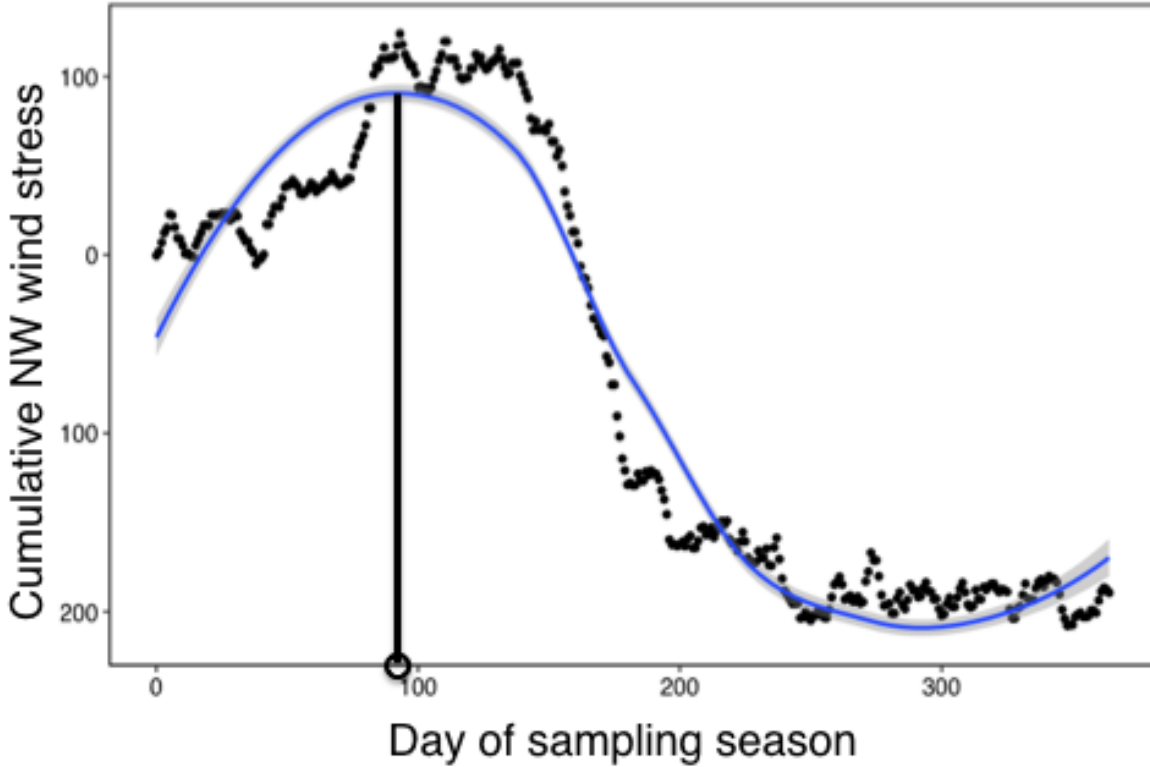
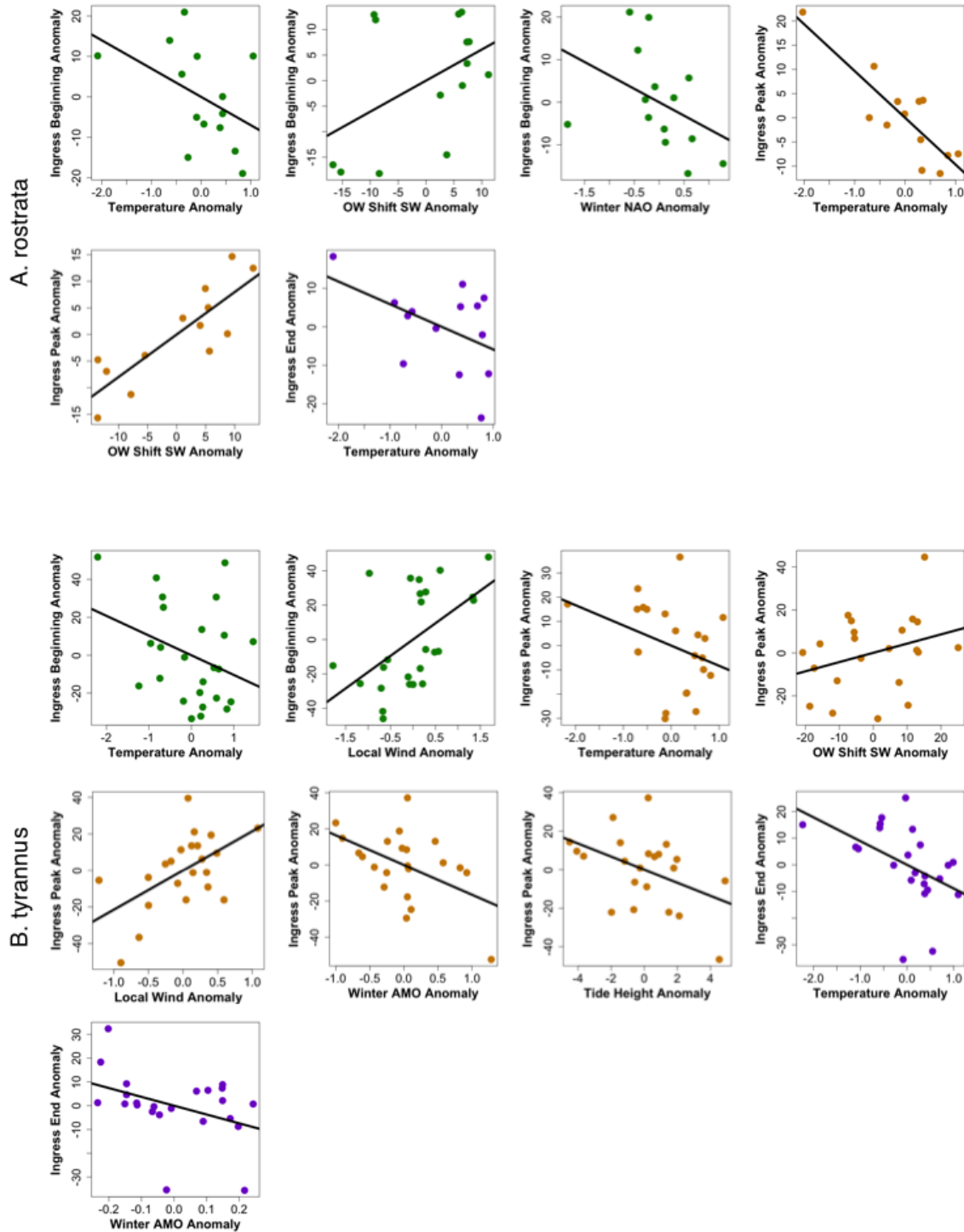
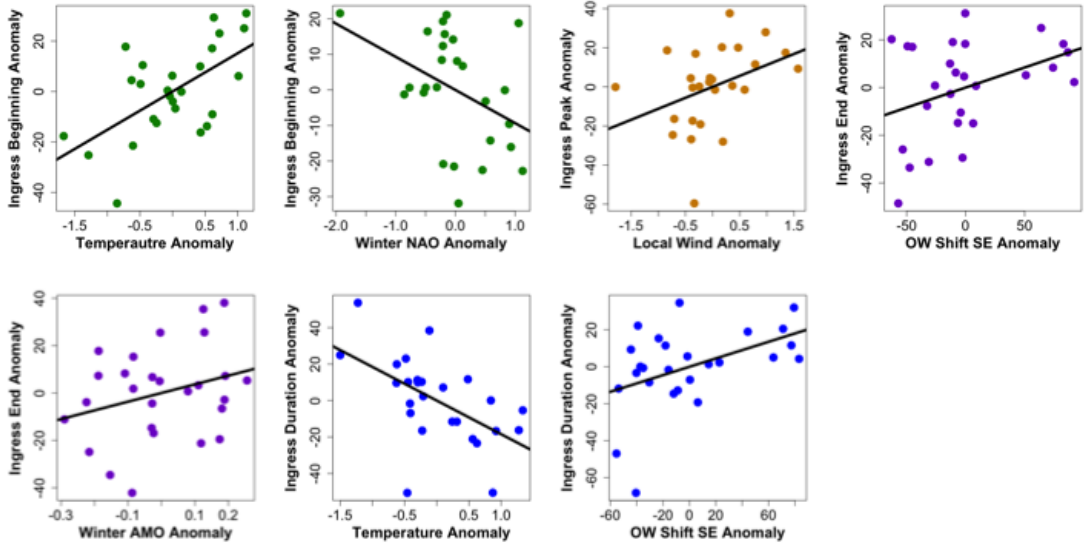


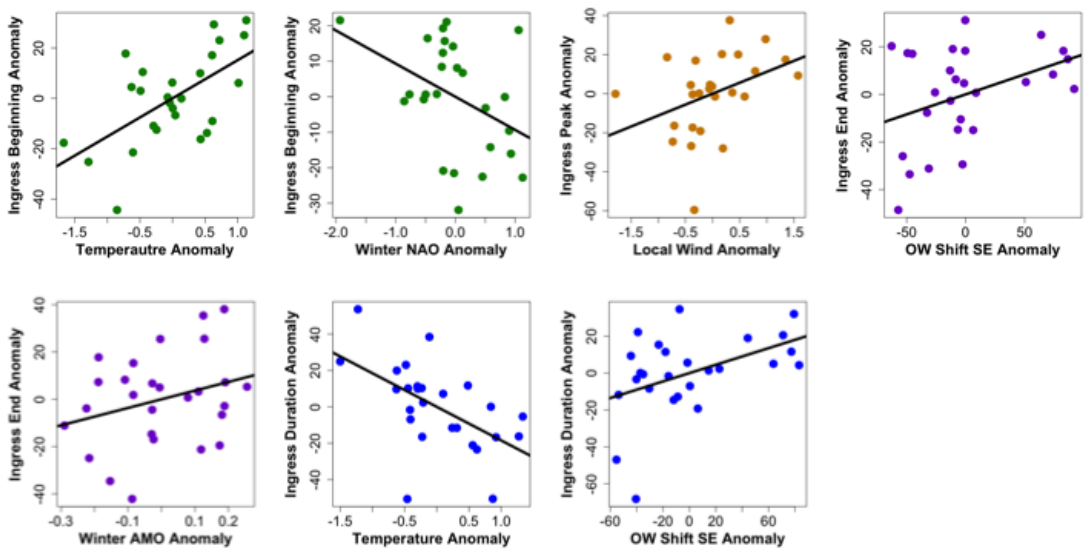
Figure S2.6: Added-variable plots of environmental metrics included in species' best models of ingress. Green, orange, purple, and blue points represent models of beginning, peak, end, and duration of ingress, respectively. Positive (negative) slopes indicate factors that delay (advance) ingress. Each point represents the specie's phenology in given year. See Table S2.3 for the specifications of each model.



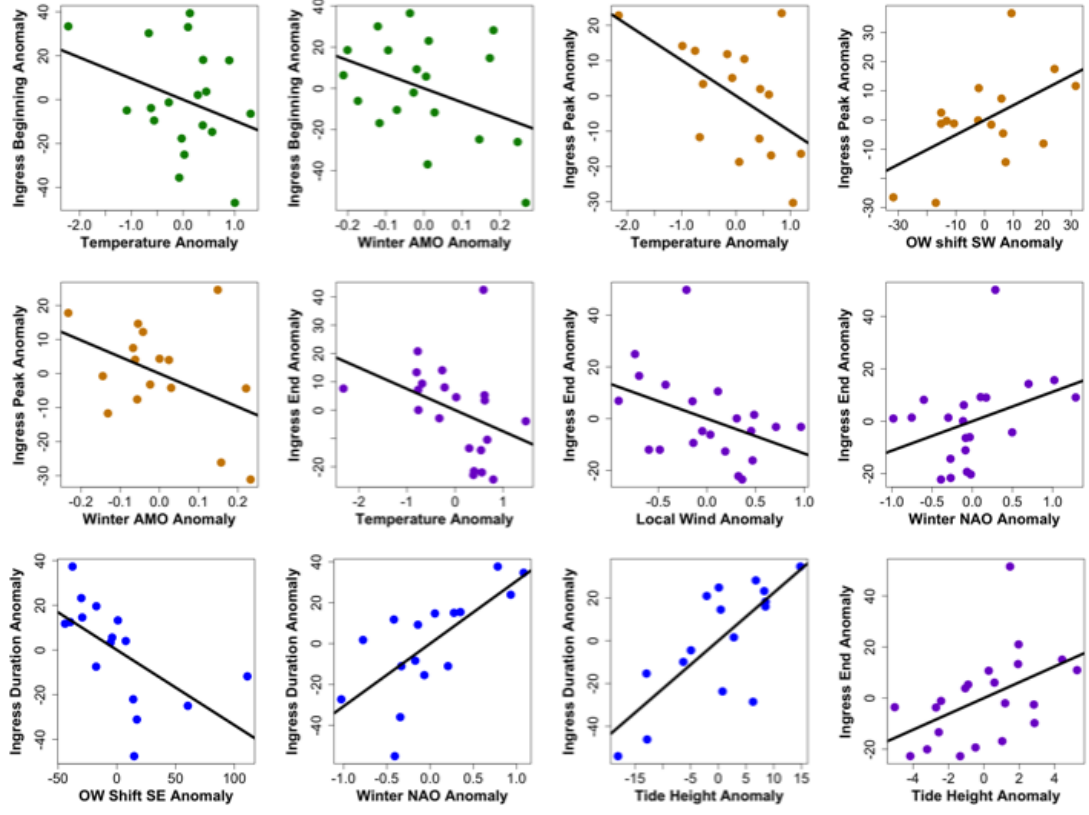
L. rhomboides



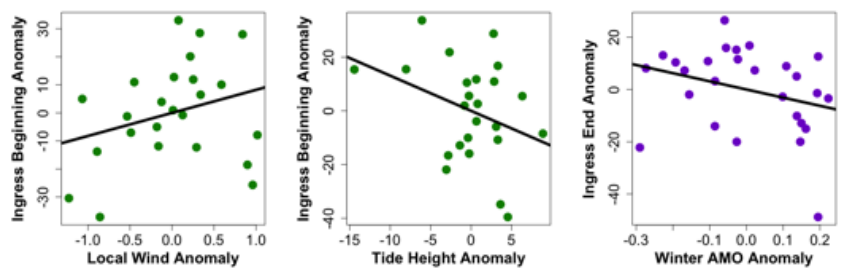
L. rhomboides



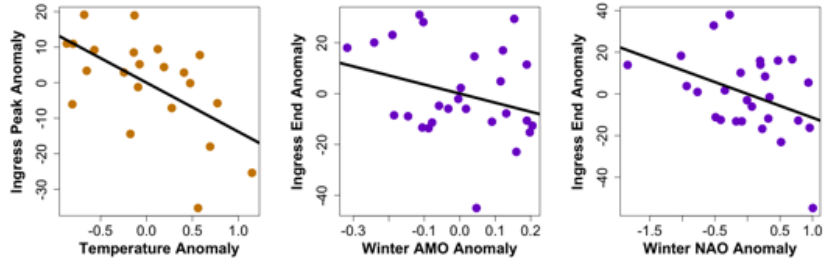
M. cephalus



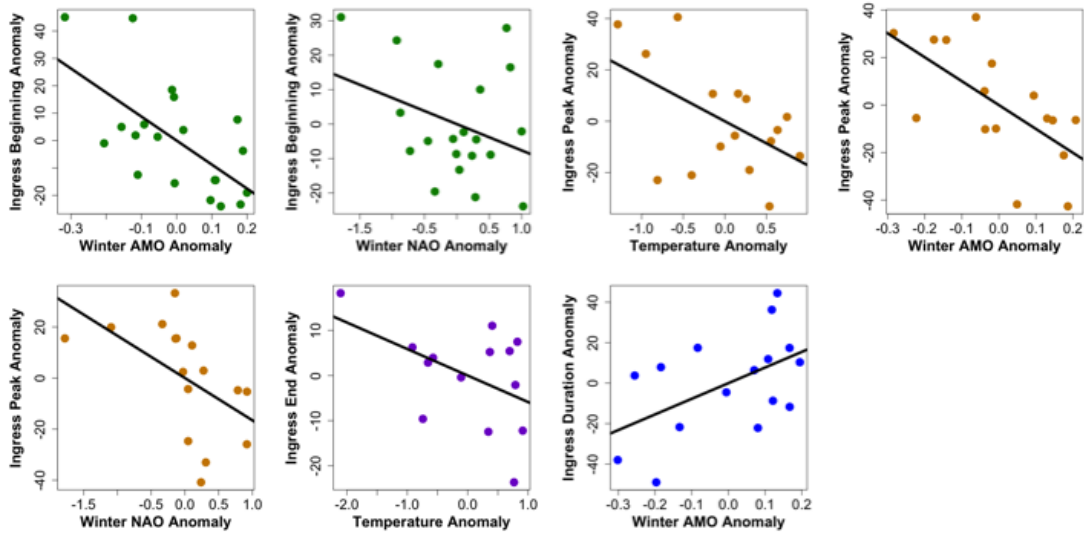
M. punctatus



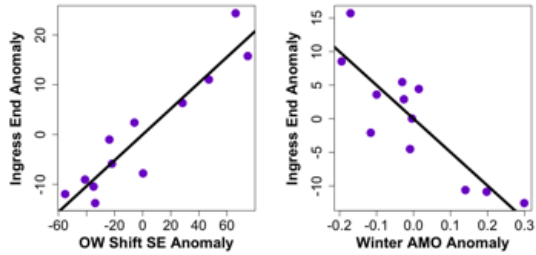
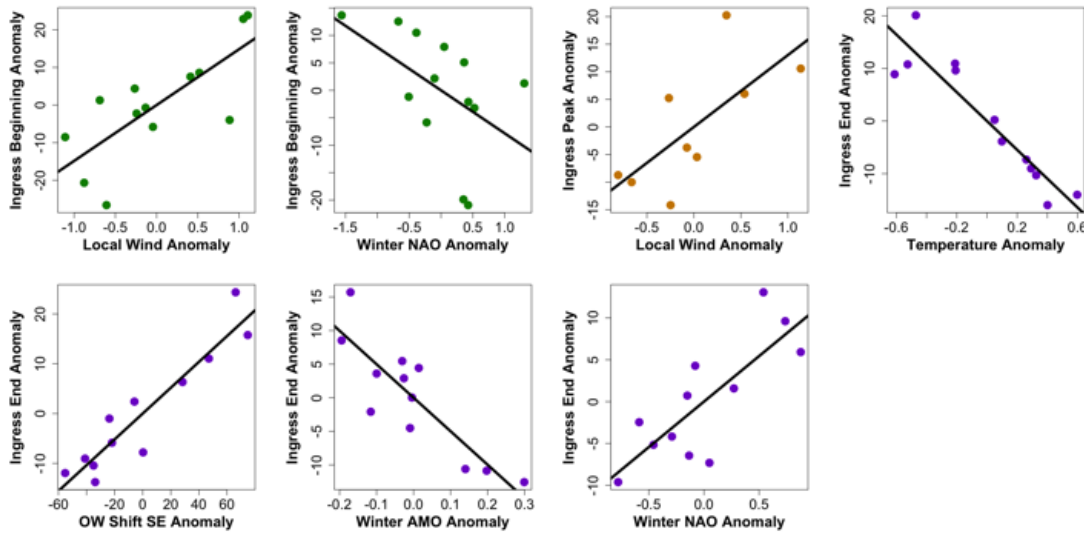
M. undulatus



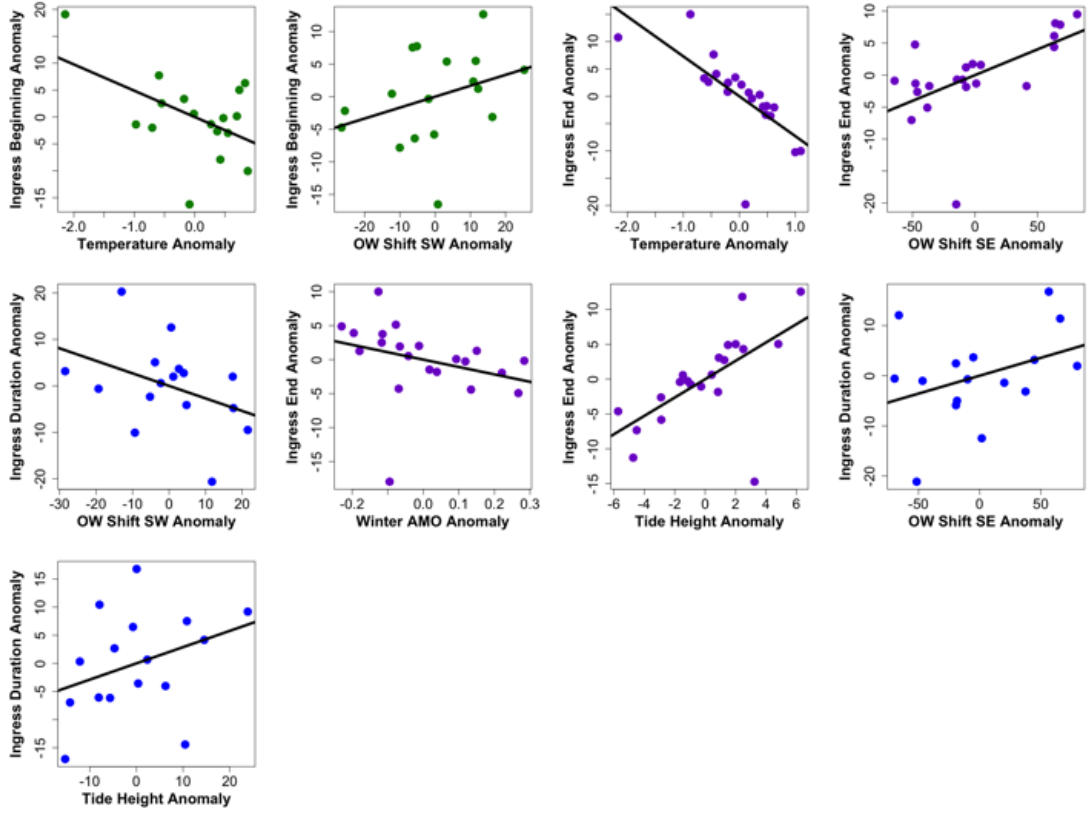
P. albigitta



P. denatus



P. lethostigma



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CHAPTER 3: MANAGEMENT IMPLICATIONS, FUTURE RESEARCH DIRECTIONS, AND CONCLUSIONS

Section 3.1: Management implications

This study found evidence that the timing of larval ingress through Beaufort Inlet, NC is related to environmental variables, such as sea surface temperature (SST), the Atlantic Multidecadal Oscillation, the North Atlantic Oscillation, wind phenology, and wind strength. The time at which these fish larvae enter their estuarine nursery habitat partially determines the conditions they experience as they develop, which can in turn impact species' recruitment (Cushing 1990). This study focused solely on how the environment affects larval ingress phenology, but variability in habitat conditions in the ocean and within the estuary can also impact larvae's survival. If future studies reveal certain ingress times and/or estuarine or pelagic habitat conditions to be more or less favorable to larval survival, this information could be incorporated into fisheries managers' interannual estimations of a species' recruitment. This information could also allow recruitment to be potentially forecasted in advance of the availability of other fisheries-independent sources of information on recruitment, giving managers a longer lead time to take action (Tommasi et al. 2017).

Knowledge of species ingress phenology may also be useful in the event of acute disturbances to the estuary, such as storms, pollution, and algal blooms. Knowledge of which species are likely affected during such events, which is in turn affected by their phenology, can inform the adaptive management of those species. Adaptive management could be in the form of altered recruitment estimates in the subsequent year's stock assessment, targeted efforts to mitigate the effects of the disturbance in species' known habitat, or research directed toward assessing the actual impact on species suspected to have been affected by a disturbance event.

Anthropogenic disturbances, such as dredging, can also be altered to minimize interference with suspected larval ingress periods, as well as the time period when juvenile fishes are resident within the estuary. This study and previous research suggests that northerly winds local to the inlet may hinder larval ingress (Luettich et al. 1999, Logan et al. 2000). Dredging and other disturbing activities in the inlet could be scheduled to coincide with periods that typically have moderate northerly winds or with ebbs in the tidal cycle, since larvae use strong incoming tides to enter the inlet (Churchill et al. 1999, Forward et al. 1999, Luettich et al. 1999).

Lastly, this study emphasizes the importance of long-term times series, such as the Beaufort Bridgenet program. These time series offer invaluable insight into ecological changes over time and in response to environmental variability. Federal and state management agencies and universities should continue to fund and implement these programs, as their importance will grow as we continue to realize the effects of climate change. Even small gaps in time series can have a disproportionately large effect on our ability to attribute ecological changes to climate change (Henson et al. 2010). Programs, such as Bridgenet, are especially important in the South Atlantic Bight (SAB), which is yet to experience the full effects of rising SST associated with climate change. As we begin to experience the 2°C warming projected by the Intergovernmental Panel on Climate Change (IPCC), this work and that of others suggests that the marine ecosystem will respond (Pinsky et al. 2013, IPCC 2014, Morley et al. 2016, Cohen et al. 2018). Long-term monitoring programs are key to further understanding and anticipating what these responses may be and to assessing these responses as they begin to happen.

Section 3.2: Future research direction

The findings of this study could be strengthened and contextualized by further research in a variety of areas. I examined how larval ingress phenology varied with respect to several environmental variables. The time of ingress is a function of several events though and the environment may affect each of them differently. This makes it hard to attribute my findings to any one life-history event in the fishes studied. I was able to use knowledge of certain species' life history to infer ways in which they may be influenced by the environment, but life history information was lacking for many of the species studied (Table 2.1). Further study of species' life histories would be useful for interpreting the results of this study. For example, a better resolution of species' spawning grounds would have provided more insight on the transport processes their larvae may be susceptible to and the oceanic conditions they may have experienced en route to the inlet.

Larval transport, especially near the shore, continues to be a black box in many species' life histories (Pineda et al. 2007, Cowen & Sponaugle 2009, Llopiz et al. 2014). The last concerted effort to study of larval transport in the SAB was the South Atlantic Bight Recruitment Experiment (SABRE), which took place in the 1990s (Ortner et al. 1999). Some of the SABRE studies proposed wind-driven currents have the potential to drive larvae shoreward (Luettich et al. 1999, Quinlan et al. 1999, Werner et al. 1999). My findings are consistent with this prior research. This study compared the timing of larval ingress to a proxy for wind-driven larval transport. A similar approach comparing ingress phenology with more sophisticated metrics of oceanographic processes could shed further light on larval transport. Modern advances in satellites' and profiling oceanic floats' ability to observe and model ocean circulation are

allowing us to quantify oceanographic phenomena in ways never before possible (Le Traon et al. 2015, Lumpkin et al. 2017).

Ocean eddies have also been shown to influence larval transport and survival. The larvae of coral reef fishes, for instance, grow faster and have lower mortality rates when entrained in an eddy (Lobel & Robinson 1986, Shulzitski et al. 2016). Eddies in the Charleston Gyre to the southwest of Onslow Bay cause upwelling and concentrate productivity, thus creating pelagic nursery habitat for fish larvae en route the coast (Govoni et al. 2010). Gulf Stream meanders, filaments, and eddies have long been hypothesized as a larval transport mechanism in the SAB, but few attempts have been made to test this concept (Govoni & Pietrafesa 1994, Govoni & Spach 1999). The recently-released AVISO+ (Archiving, Validation, and Interpretation of Satellite Oceanography) dataset of worldwide mesoscale eddy trajectories from 1993-2016 includes satellite observations of warm core eddies generated by the Gulf Stream. AVISO+ may be a useful tool for future exploration of how Gulf Stream intrusions influence ecology across the SAB (Mason et al. 2014, Faghmous et al. 2015).

Just as species' life history information can be used to infer how their environment may influence them, an understanding of the physiological mechanisms responsible for activities such as spawning can be used to infer how climate change may affect species. Previous work has addressed this in certain species, but fishes vary in their sensitivity to the environment (Pankhurst & Porter 2003, Pankhurst & Munday 2011). For example, increases in temperature advance the timing of Alaska Pollock spawning up to a certain threshold, but increases past this threshold have no additional effect (Rogers & Dougherty 2019). Similar thresholds have also been observed in temperature's relationship to growth rates, with growth initially occurring faster as waters warm, but eventually becoming inhibited past a certain level of warming

(Handeland et al. 2008, Neuheimer et al. 2011). Photoperiod's role in regulating spawning times will also become increasingly important as fish change their distributions in response to a warming ocean. Fish may be exposed to novel photoperiod regimes as they migrate to higher latitudes, making it all the more important for us to understand the roles temperature and photoperiod play in initiating and ending reproduction (Pankhurst & Porter 2003, Pankhurst & Munday 2011). Since both temperature and photoperiod vary as a function of latitude, these environmental covariates can often be cross-correlated in observational datasets, so this is an area where a greater mechanistic understanding of fish physiology and experiments would provide new insights beyond what can be obtained from environmental observations.

Changes in the timing of larvae's arrival to their nursery habitat can have ecological consequences for the species as a whole. It is hypothesized that many fishes spawn at a time or in response to conditions that historically correlate with a high likelihood of their larvae reaching their nursery habitat when prey are abundant (Cushing 1990). Historic connections between spawning times and favorable nursery conditions have the potential to be disrupted by climate change, since previous work suggests that organisms in different trophic levels often respond at different rates to changes in their environment (Beaugrand et al. 2003, Voigt et al. 2003, Edwards & Richardson 2004, Visser et al. 2012, Burkle et al. 2013). Research into the dynamics of larvae's and juvenile's zooplankton and benthic macroinvertebrate prey in the ocean and in estuaries beyond Beaufort Inlet would contextualize the results of this study and would provide a better understanding of how the recruitment of the species studied may be affected by climate change.

Lastly, the Beaufort Bridgenet time series could be analyzed for community composition changes over time and with the environment. Onslow Bay lies at the northern edge of the SAB

biogeographic zone and may mark the northern limit of some species' ability to migrate in response to climate change (Epifanio & Garvine 2001, Grieve et al. 2016). Interannual changes in the historic community composition of the inlet can be compared with environmental variables, similar to the way historic variation in phenology was examined in this study. This could provide insight on how the community may respond to future changes in these variables. It is also possible that climate change may cause a tropicalization of the community in the coming decades (Cheung et al. 2013, Morley et al. 2016). Researchers should continue to monitor the time series for both new species entering Onslow Bay and increased abundances of warm-water adapted species already present in the Bay.

Larval ingress dynamics through other inlets across North Carolina's Outer Banks should also be studied. Previous work has suggested that the fall and winter ichthyoplankton community may vary between inlets each year (Hettler & Barker 1993). A study of interannual changes in the communities of several inlets may provide further insight on how species move in response to changing water temperatures.

Section 3.3: Conclusions

I found evidence that the fall and winter ichthyoplankton community of Beaufort Inlet has advanced its time of ingress and that interannual variation in the time of ingress relates to several environmental variables. The ten species examined varied in their strength of response to the environment, but most shared common direction of effects. This was especially true of SST, since warmer SSTs were related to advances in ingress timing for eight of the ten species studied. The Atlantic Multidecadal Oscillation, the North Atlantic Oscillation, the timing in shifts of offshore winds, and the strength of winds local to the inlet were also associated with the

timing in ingress phenology of certain species. As the SAB experiences the effects of climate change, these relationships between species' ingress phenology and the environment may begin to have ecological consequences. The estuaries beyond Beaufort Inlet serve as a nursery for larvae as they metamorphose into juveniles. If climate change's effect on the phenology of larvae's prey is asynchronous with its effect on the larvae's ingress and/or spawning phenology, species' recruitment could suffer. To gain a better understanding of how populations may be impacted in the coming decades, researchers should continue to study how climate change may impact the early life history of fishes, as well as its effects on these fishes' nursery habitats.

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