Vol. 650: 269–287, 2020
https://doi.org/10.3354/meps13404

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 17

*Contribution to the Theme Section 'Latest advances in research on fish early life stages'*

# Climate-associated trends and variability in ichthyoplankton phenology from the longest continuous larval fish time series on the east coast of the United States

**W. Christopher Thaxton[1], J. Christopher Taylor[2], Rebecca G. Asch[1,*]**

[1]Department of Biology, East Carolina University, Greenville, North Carolina 27858, USA
[2]Marine Spatial Ecology Division, National Centers for Coastal Ocean Science, National Ocean Service, National Oceanic and Atmospheric Administration, Beaufort, North Carolina 28516, USA

ABSTRACT: As the effects of climate change become more pronounced, variation in the direction and magnitude of shifts in species occurrence in space and time may disrupt interspecific interactions in ecological communities. In this study, we examined how the fall and winter ichthyoplankton community in the Newport River Estuary located inshore of Pamlico Sound in the southeastern United States has responded to environmental variability over the last 27 yr. We relate the timing of estuarine ingress of 10 larval fish species to changes in sea surface temperature (SST), the Atlantic Multidecadal Oscillation, the North Atlantic Oscillation, wind strength and phenology, and tidal height. We also examined whether any species exhibited trends in ingress phenology over the last 3 decades. Species varied in the magnitude of their responses to all of the environmental variables studied, but most shared a common direction of change. SST and northerly wind strength had the largest impact on estuarine ingress phenology, with most species ingressing earlier during warm years and delaying ingress during years with strong northerly winds. As SST warms in the coming decades, the average date of ingress of some species (Atlantic croaker *Micropogonias undulatus*, summer flounder *Paralichthys dentatus*, pinfish *Lagodon rhomboides*) is projected to advance on the order of weeks to months, assuming temperatures do not exceed a threshold at which species can no longer respond through changes in phenology. These shifts in ingress could affect larval survival and growth since environmental conditions in the estuarine and pelagic nursery habitats of fishes also vary seasonally.

KEY WORDS: Phenology · Ichthyoplankton · Climate change · Climate variability · Southeastern US continental shelf · Larval transport · Estuarine ecology

## 1. INTRODUCTION

Many organisms rely on their environment to signal the seasonal timing of life history events, which is referred to as 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, Thackeray et al. 2016, Cohen et al. 2018). Temperature, water column stratification, and upwelling have been correlated with changes in marine fish reproductive phenology in the North Sea, California

---

*Corresponding author: aschr16@ecu.edu

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 have been hypothesized to be linked to recruitment success in several fish taxa, emphasizing the importance of fish reproductive phenology (Cushing 1990, Durant et al. 2007). Since sea surface temperature (SST) has risen globally at a mean rate of 0.13°C decade$^{-1}$ and this rate is expected to increase in coming decades (IPCC 2014), it is important to continue studying how changes may affect the phenology of fish reproduction and larval transport.

The ability to study the relationship between phenology and environmental conditions is limited by historical baseline knowledge (Visser & Both 2005). In the case of fish reproduction, long-term time series of ichthyoplankton abundance and occurrence best display how reproductive phenology has varied over time (Koslow & Wright 2016). The longest-running continuous time series of ichthyoplankton collections on the US east coast is located in Beaufort Inlet, North Carolina, near the seaward edge of the Newport River Estuary (Ortner et al. 1999). Since 1986, the NOAA Beaufort Inlet Ichthyoplankton Sampling Program, which is referred to as the 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 as larval fishes enter estuarine nursery habitat and insights into the environmental drivers influencing this interannual variability.

The southern-facing Beaufort Inlet is located in Onslow Bay, an embayment near the northern extreme of the southeastern US continental shelf (Epifanio & Garvine 2001; Fig. 1). During fall and winter, larvae spawned across Onslow Bay ingress into Beaufort Inlet while traveling to the nursery habitats of the Newport and Pamlico River estuaries (Fig. 1). Though the exact spawning areas of most species collected by Bridgenet are unknown, many of the region'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). SABRE examined temporal patterns in ichthyoplankton abundance, age, and size (Hettler & Chester 1990, Warlen & Burke 1990); comparisons of Beaufort's ichthyoplankton community to nearby inlets (Hettler & Barker 1993); daily variability in

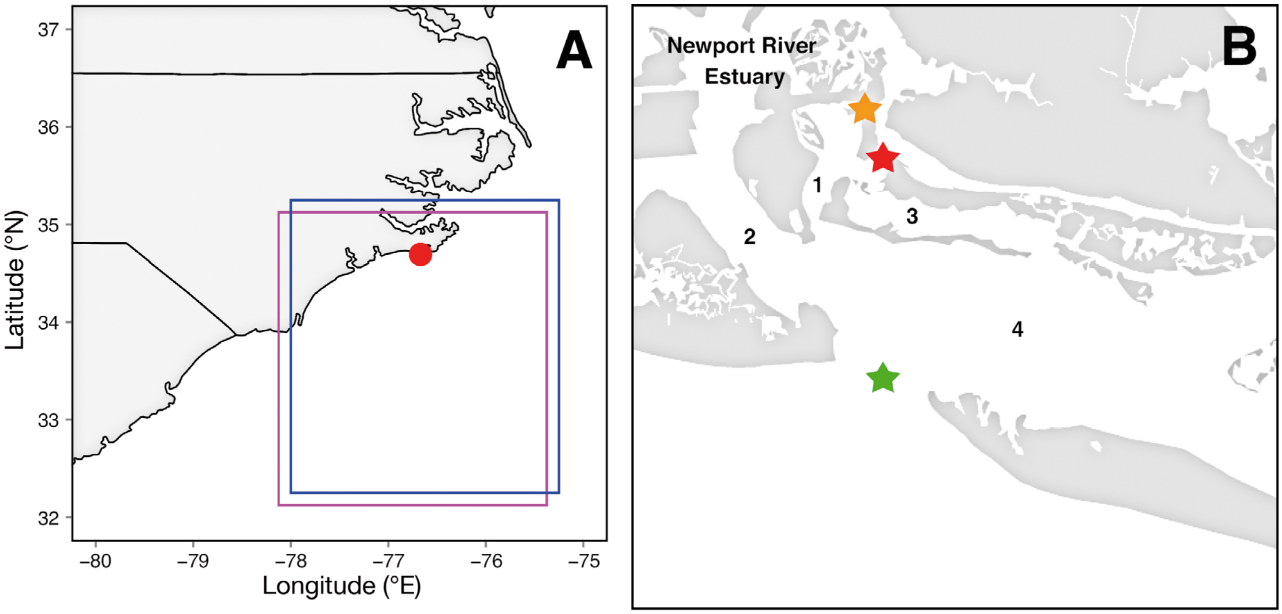

Fig. 1. Study site. (A) Purple and blue boxes indicate areas of Optimum Interpolation Sea Surface Temperature and Blended Sea Winds observations, respectively. The red circle indicates Beaufort Inlet, which is magnified in (B). The embayment to the south of Beaufort Inlet is Onslow Bay. (B) Grey areas represent land, while white regions are coastal and estuarine waters. Beaufort Inlet (green star) and the 4 major channels branching from the inlet (1: Bulkhead Channel; 2: Morehead City Channel; 3: Bird Shoal Channel; 4: Shackleford Channel) are pictured. The orange star 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

larval fish ingress (Hettler et al. 1997, Forward et al. 1999a, Joyeux 1999); and the implications of inlet and continental shelf flow dynamics on larval fish transport (Hettler & Hare 1998, Churchill et al. 1999a,b, Forward et al. 1999a, Hare et al. 1999, Quinlan et al. 1999, Rice et al. 1999, Werner et al. 1999). Variations in transport processes may contribute just as greatly as temperature to interannual variation in ingress phenology, but transport has not been thoroughly or quantitatively explored in previous research on environmental factors that influence variations in larval fish phenology (Edwards & Richardson 2004, Greve et al. 2005, Genner et al. 2010, Asch 2015, Chevillot et al. 2017), although Parrish et al. (1981) and Doyle et al. (2019) provide a conceptual analysis of how these processes may influence larval fish phenology. Changes in circulation can also lead to changes in local temperature, so these 2 factors influencing fish phenology could potentially interact with each other.

Conceptually, the process of estuarine ingress by larval fish spawned offshore can be divided into 3 stages: (1) transport from offshore to nearshore habitats, (2) alongshore transport until larvae reach the mouth of an estuary, and (3) transport through the estuary mouth towards habitat to be used by juvenile fishes upon settlement (Boehlert & Mundy 1988, Hettler & Hare 1998). At each stage, a different suite of physical variables can influence the phenology of larval ingress. During the first phase, transport can be influenced by wind-driven currents and eddies (Boehlert & Mundy 1988). Offshore temperatures can also affect this process by accelerating development (Houde 1989, Meekan et al. 2003, Laurel et al. 2008), thus controlling when larvae begin displaying behavioral responses that will influence transport. Nearshore wind-driven currents will exert a continued influence on transport during phase 2 as the larvae seek out the entrance to an estuary. Tidal fluxes can have a large influence on the third stage of ingress when larvae are transported from an estuarine inlet to settlement habitat (Boehlert & Mundy 1988). Here, we examine the full suite of processes that may influence the phenology of larval ingress in Beaufort, North Carolina.

We used 27 yr of the Bridgenet time series to investigate historical variability and trends in ichthyoplankton ingress phenology through Beaufort Inlet. The beginning, peak, end, and duration of larval ingress through the inlet were examined for 10 species both individually (species by species) and as a community. We then examined the relationship between variability in larval ingress phenology and environmental variables hypothesized to influence fish reproduction in Onslow Bay and larval transport into Beaufort Inlet. Relationships between ingress phenology and SST, winds across Onslow Bay, winds local to Beaufort Inlet, tidal strength, the Atlantic Multidecadal Oscillation (AMO), and the North Atlantic Oscillation (NAO) were examined. These factors were selected because they are highly variable from year to year, accounted for in long-term datasets, and susceptible to shifts as the climate changes (Saba et al. 2016, Yuan et al. 2017) and have been shown to influence fish phenology, distribution, abundance, or recruitment locally or in other regions (Churchill et al. 1999a, Taylor et al. 2010, Nye et al. 2014, Asch 2015, Morley et al. 2016, Roberts et al. 2019). Lastly, we assessed which of these variables were responsible for the long-term trends in ingress phenology that we detected.

## 2. MATERIALS AND METHODS

### 2.1. Bridgenet sampling design

NOAA has collected ichthyoplankton samples from Pivers Island Bridge since 1986 as part of the Bridgenet program (Fig. 1). These samples were taken from a 40 m wide channel located 3.5 km upstream of the inlet. Larvae were collected with a 2 $m^2$ rectangular plankton net with 1 mm stretch mesh equipped with an analog (pre-1998, 2016–present) or digital (1998–2016) flowmeter. While the mesh size used here is larger than in some other studies of larval fish dynamics (e.g. Asch 2015, Walsh et al. 2015), previous research at our study site indicates that selectivity of larval fishes was similar among nets with mesh sizes of 333, 505, and 1000 µm (Forward et al. 1999a). This net was attached to the Pivers Island Bridge where the average tidal current velocity at the time of sampling was 34.0 ± 11.5 cm $s^{-1}$ (mean ± SD). All samples were collected just below the water's surface during nighttime flood tides, approximately 2.5 h before the predicted high tide. Since most larval fishes in this area engage in selective tidal stream transport (Forward et al. 1999a), near-surface samples during flood tides are likely to be representative of most species in this assemblage. Three (1986–1988) or 4 (1988–present) replicate tows were conducted during each sampling event, which occurred weekly from October/November to April/May. Samples were preserved in 95% ethanol and enumerated to species either at the NOAA Beaufort Laboratory (pre-2001) or the Sea Fisheries Institute's Plankton Sorting and Identification Center in Gdynia, Poland (2001–present). We examined samples collected between fall 1986 and spring 2013. Note that henceforth sampling season, season, and year refer to the year sampling ended (i.e. the season 1987 was from November 1986 to April 1987).

While the Bridgenet site is located 3.5 km shoreward of Beaufort Inlet, previous research showed that larval fish concentrations at this site are correlated with concentrations sampled immediately outside the inlet (Hettler & Hare 1998). Based on typical current velocities near the inlet (Churchill et al. 1999a,b), larval fishes would be transported between the inlet and the sampling site within 1 to 2 flood tide cycles. Also, the 4 channels that transport larvae from the Beaufort Inlet to estuarine habitat have similar species composition of fishes but show variations in the overall abundance of larvae (Forward et al. 1999a). As a result, this site is considered a good proxy for measuring relative larval ingress into Beaufort Inlet.

### 2.2. Phenology metrics

The cumulative catch of each species was plotted throughout each week of a sampling season. A loess smoothed average function (span = 0.75, degrees = 2) was fitted to these plots. This function was used to calculate the date when 15, 50, and 85 % of individuals were captured in a given season. These dates were referred to as the beginning, peak, and end of each species' ingress season, respectively. These metrics are preferred to the actual first and last occurrence of a given species, since first and last occurrence can vary greatly with sampling effort (Edwards & Richardson 2004, Greve et al. 2005, Batten & Mackas 2009, Mackas et al. 2012). Phenology metrics based on loess smoothed data were used rather than each metric's raw date of occurrence to account for the effect of Bridgenet's weekly sampling frequency, which could affect 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 entire period of the selected species' ingress, but there were exceptions. The beginning and end metrics were excluded if they occurred within 2 wk of the start or end date of a sampling season, indicating that the Bridgenet season might not have captured the entirety of the ingress period. If either the beginning or end metric was removed in a given season, then that season's peak and duration metrics were also removed. Entire seasons were excluded when species were captured on <13 wk of the sampling season, since such seasons did not typically show a distinct seasonal pattern of ingress. Peak ingress metrics were removed for years that displayed bimodal ingress. A quantitative, but heuristic, definition of bimodality based on Asch (2013, 2015) was used. See Table S1 in the Supplement at www.int-res.com/articles/suppl/m650p269_supp.pdf for metrics removed for each species.

Species were selected for inclusion in this study based on whether (1) they were consistently and accurately identified to species level; (2) the Bridgenet sampling season captured their entire ingress season for >10 yr based on the above criteria; and (3) they were abundant enough in samples to demonstrate a clear beginning, peak, and end of ingress. Of the ~150 taxa collected by Bridgenet, 10 species met these criteria: American eel *Anguilla rostrata*, Atlantic menhaden *Brevoortia tyrannus*, pinfish *Lagodon rhomboides*, spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, striped mullet *Mugil cephalus*, speckled worm eel *Myrophis punctatus*, Gulf flounder *Paralichthys albigutta*, summer flounder *P. dentatus*, and southern flounder *P. lethostigma* (Table S2).

### 2.3. Environmental variables

#### 2.3.1. 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; www.ncdc.noaa.gov/oisst/data-access) database (Fig. 1). SST anomalies during the month of each species' mean beginning of ingress and the month prior were used in statistical models of ingress phenology. SST for species-specific spawning grounds was not used, because the spawning location of many of these fishes is not fully known (Able & Fahay 2010). However, the monthly SST anomalies from OISST were highly correlated with anomalies from 7 weather stations and buoys across the southeastern USA and were moderately correlated with air temperature anomalies at Cape Lookout, North Carolina (Thaxton 2019). This analysis and that of Joyce (2002) both suggested that SST changed in a uniform manner across the region, implying that the SST data used should capture temperature variability across spawning grounds.

#### 2.3.2. Offshore wind

Wind vectors were obtained from NOAA's Blended Sea Winds database (https://www.ncdc.noaa.gov/data-access/marineocean-data/blended-global) and were averaged across Onslow Bay (32.25°–35.35° N, 75.25°–78.0° W; Fig. 1). Research-quality data from Sea Winds was only available for the years 1987 to 2011, so data from the Cape Lookout weather station (National Buoy Data Center [NBDC] station CLKN7) were used during 1986 and 2011 to 2013. Monthly average north and east wind vectors from Sea Winds, NBDC weather stations (BFTN7 and CLKN7), and 5 NBDC buoys (41025, 41037, 41013, 41004, and 41008) across the southeastern USA were highly correlated (Thaxton 2019). This suggested that the seasonal and interannual wind patterns were relatively uniform across the region and that winds from Cape Lookout were a reasonable proxy for the missing years from Sea Winds.

Along the southeastern USA, winds blow predominantly to the north in the spring and summer, then blow towards the south during the fall and winter (Fig. S1). Wind-driven currents have been hypothesized to be the main transport mechanism for larval advection. Due to Ekman transport, winds to the southwest drive surface and mid-depth water to the northwest, which could funnel ichthyoplankton into southern-facing inlets along the coast of our study region (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 Beaufort Inlet. Similarly, the time at which winds shift to blowing to the southeast may be related to the end of ingress, since this wind direction results in currents moving offshore from the inlet.

To determine the timing of these shifts, we plotted each season's cumulative offshore wind stress to the northwest from July 1 to June 30 of each year and fitted a loess function to this relationship (span = 0.75, degrees = 2; Fig. S2). The date at which the cumulative northwest wind stress began to decrease (the maximum of the loess function) corresponded to winds moving counterclockwise past the southwest direction, which was associated with Ekman transport toward the estuary. The southwest wind phenology was hypothesized to relate to the beginning, peak, and duration of ichthyoplankton ingress. A similar analysis was repeated examining cumulative southeast wind stress, which is associated with Ekman transport away from the mouth of the estuary. The southeast wind phenology was hypothesized to relate to the end and duration of ichthyoplankton ingress.

#### 2.3.3. Nearshore northerly wind strength

Nearshore winds local to Beaufort Inlet may influence inter-weekly tidal stream strength, thus affecting the timing of when larvae entered Beaufort Inlet. Nearshore wind vectors were obtained from the NBDC CLKN7 weather station at Cape Lookout. Winds near Beaufort, North Carolina, typically blow to the south during the Bridgenet sampling season. Modeling has shown that these northerly (southward) winds may hinder particle ingress through the inlet (Luettich et al. 1999, Logan et al. 2000). To determine its effect on ingress phenology, we averaged daily northerly wind stress for the month of and month prior to each species' mean date of beginning, peak, and end of ingress (Table S2a) and used these wind strengths in statistical models of the respective phenology metrics.

#### 2.3.4. Tidal height

Like wind, sea level may indirectly drive ichthyoplankton ingress patterns through its effect on tidal stream strength (Churchill et al. 1999b). Whereas nearshore wind on a given night may affect tidal stream strength in the short term, variations in sea level may influence cumulative tidal stream strength on a seasonal to interannual basis. Tide level was obtained from the buoy NBDC BFTN7 at the Duke Marine Lab. We calculated cumulative maximum daily tidal height for the 2 mo prior to each species' mean date of beginning, peak, and end of ingress (Table S2a). Tidal height metrics were used in models of the respective ingress phenology metrics. Cumulative tidal height from October to May was used to model ingress duration.

#### 2.3.5. AMO and NAO

The AMO index was obtained from the National Center for Atmospheric Research (Trenberth & 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). These modes of climate variability affect water temperatures and wind stress across the region, with positive phases corresponding to warmer temperatures (Hurrell et al. 2003, Visbeck et al. 2003, Knight et al. 2006). The NAO is variable on monthly to decadal scales (Hurrell et al. 2003) and associated with temperature fluctuations on the order of 0.3 to 0.7°C around the region (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). Both the NAO and AMO were correlated with variations in the abundance and composition of the larval fish community in Roanoke River, North Carolina (McCulloch 2017), and could influence fish phenology throughout the southeastern USA. The value of including these basin-scale indices is that they integrate temperature and wind stress effects across a larger area, which can be important in cases where the exact spawning location and trajectory of larval dispersal are unknown. In other ecosystems, basin-scale climate indices have been shown at times to explain more variance in larval fish concentration and diversity than local environmental variables (Auth et al. 2011). Winter (December–February) averages of the monthly unsmoothed, detrended Hadley AMO and monthly NAO indices were used in statistical models of all ingress metrics.

While river flow can influence the reproductive phenology of anadromous fishes (Anderson & Beer 2009, Peer & Miller 2014), we did not include this indicator in our analysis because tidal circulation and winds play a larger role affecting larval fish ingress in our study system than freshwater input, especially in the eastern and central sectors of the Newport River estuary where our study site is located (Churchill et al. 1999b).

### 2.4. Phenology changes over time

Temporal changes in the 4 phenological metrics were assessed for individual species and the community as a whole. Linear regression between species phenology and year was used to calculate trends in phenology and the associated uncertainty in trends. Due to large differences in the mean date of ingress for each of the species, community analyses of phenological trends were performed using anomalies in the time series of ingress phenology for each species. The 4 phenological metrics of each species were analyzed for temporal autocorrelations at lags of 1 to 5 yr. Approximately 5% of these 200 autocorrelation tests were significant at a significance threshold of $p < 0.05$, which is the amount expected to be significant based solely on spurious results associated with multiple testing. There was no pattern across the species, phenology metrics, or time lags in which significance of autocorrelation tests was more likely to occur. Therefore, autocorrelation was not considered further in subsequent analyses.

### 2.5. Environmental influences on interannual variations in phenology

We used both a regression-based approach and principal component analysis (PCA) to examine the influence of oceanic variables on ichthyoplankton phenology. This dual approach was applied because oceanic variables often exhibit collinearity with each other, which can be accounted for through the PCA since each principal component (PC) is independent of other PCs (Quinn & Keough 2002).

Multiple regression was used to test for relationships between ingress phenology and SST, offshore wind shifts to the southwest and southeast, nearshore northerly wind strength, tidal height, AMO, and NAO. Separate regressions were calculated for each of the 4 phenology metrics of the 10 species of interest, for a total of 40 species-level analyses. Community relationships were initially analyzed with mixed effects modeling in which species were included as a random effect and oceanic variables as fixed effects. In an initial analysis, interspecific difference in phenology explained significantly more variance in each of the models than environmental effects. This was due primarily to large differences in the mean date of ingress for each species. To better highlight the environmental effects, the final community analyses were performed using anomalies in the time series of ingress phenology for each species.

Environmental variables that resulted in the most parsimonious model of each species' and the community's phenology were chosen by a reverse-stepwise process in which the Akaike's information criterion (AIC) was minimized. Model fit was assessed by p value, AIC, and $r^2$ comparisons (Nakagawa & Schielzeth 2013). Effect size, SE, and univariate significance were calculated for each environmental variable included in models. 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.

In complementary analyses, PCA and PC regression were used to assess correlations between environmental variables, reduce the dimensionality of the environmental data matrix, and test for relationships between ingress phenology and combinations of environmental variables. To standardize across 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 used a different range of months for wind and tidal variables (November–February for beginning of ingress; January–April for peak ingress; February–May for end of ingress; October–May for duration of ingress). These ranges were chosen because they coincide as closely as possible with the timing of phenological events for all 10 species. The SD and percent of variance explained by each PC were calculated along with the correlations between PCs and the 7 original environmental variables. The first 2 PCs were included as terms in multiple regressions of ingress phenology. Separate multiple linear regressions were calculated for the 4 phenological metrics of the 10 species of interest for a total of 40 species-level analyses. Community relationships were analyzed similarly but with anomalies in the ingress phenology for each species. Model fit was assessed in the same way as described above.

### 2.6. Environmental influences on phenology trends

We analyzed which environmental variables influenced multidecadal trends in the beginning of species' ingress. We focused solely on the start of ingress for this analysis because fewer multidecadal trends were seen among other phenology metrics (Fig. 2). Linear regressions were used to estimate the magnitude and direction of the temporal trend in start of ingress phenology predicted by the best model for each species. This process was repeated after dropping individual environmental variables from the model for each species. The observed phenology trend, selected model trend, and predicted trends from models with some variables removed were compared to determine which environmental variables exerted the greatest directional influence on trends in phenology.

All analyses were conducted in R v3.3.3 (R Development Core Team 2013).

## 3. RESULTS

### 3.1. Historic variation and trends in larval fish ingress phenology

Based on the results of the community analysis of phenology trends, the ichthyoplankton community of Beaufort Inlet advanced the beginning of its arrival to estuarine habitat on average by 3 wk over the past 27 yr, with the peak of larval ingress occurring 2 wk earlier (Table 1). However, there is no evidence that the end of larval fish ingress has shifted, which has resulted in an increase in ingress duration by ~1 wk decade$^{-1}$. Although species varied in the magnitude and significance of their seasonal shifts in ingress, most showed similarities in the direction of shifts (Fig. 2, Table S3). The beginning of ingress became earlier among 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.* However, there was no common trend in the direction of shifts in the end of species' ingress. Some species shifts in ingress were particularly drastic (Table S3). *Mugil cephalus* (−1.5 d yr$^{-1}$; p 0.051), *Myrophis punctatus* (−1.4 d yr$^{-1}$; p = 0.003), *M. undulatus* (−0.9 d yr$^{-1}$; p = 0.054), and *Paralichthys albigutta* (−1.3 d yr$^{-1}$; p = 0.016) all had significant advances in their arrival to the inlet. The peak ingress of *Brevoortia tyrannus* (1.2 d yr$^{-1}$; p = 0.030) has also significantly advanced, and the ingress duration has lengthened in *M. cephalus* (2.8 d yr$^{-1}$; p = 0.002) and *P. albigutta* (1.7 d yr$^{-1}$; p = 0.020). No significant changes were seen among any species for the end of ingress.

### 3.2. Environmental influences on interannual variations in community phenology

Relationships between phenology and environmental variables were examined at the community level using PCA, PC regression, and multiple linear regression. Both PC regression and linear regression revealed significant relationships between ichthyoplankton ingress and the environment.

The first 2 PCs calculated for the environmental datasets associated with each of the 4 phenology metrics were very similar. In all 4 PCAs, PC1 captured 32.1 to 33.0% of the environmental variance, and PC2 captured 25.8 to 31.1% (Table S4, Fig. 3). PC1 was negatively associated with SST and the AMO and positively associated with the

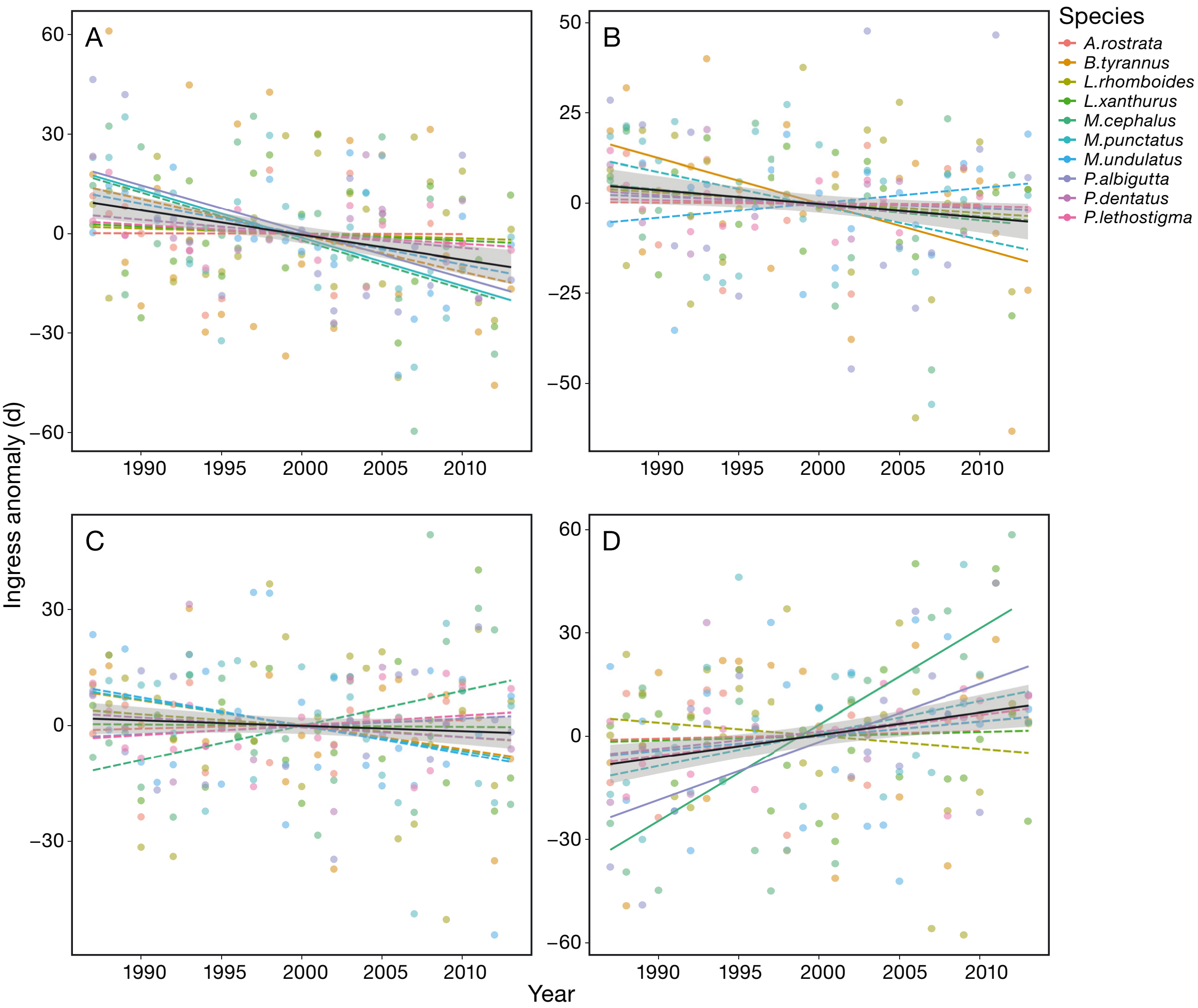

Fig. 2. Temporal change in ingress phenology. Species are shown by colored lines and the community by a solid black line. Grey shading shows ±1 SE around the community's temporal trend. For species, dashed and solid lines indicate insignificant and significant trends, respectively. (A–D) Beginning, peak, end, and duration of larval ingress phenology, respectively. Full species names are *Anguilla rostrata*, *Brevoortia tyrannus*, *Lagodon rhomboides*, *Leiostomus xanthurus*, *Mugil cephalus*, *Myrophis punctatus*, *Micropogonias undulatus*, *Paralichthys albigutta*, *Paralichthys dentatus*, and *Paralichthys lethostigma*

Table 1. Linear mixed models of community changes in larval fish ingress phenology over time. $R^2$: variance explained by the model; $\Delta AIC_{null}$: difference between each full and null model; p: significance of the year term in each model

| Model | $R^2$ | $\Delta AIC_{null}$ | df | Intercept (d) | Trend ± SE (d $yr^{-1}$) | p |
|---|---|---|---|---|---|---|
| Start anomaly ~ Year + (1\|Species) | 0.0894 | 17.5 | 205 | 1482.2 | −0.74 ± 0.16 | <0.0001 |
| Peak anomaly ~ Year + (1\|Species) | 0.0291 | 3.6 | 188 | 759.8 | −0.38 ± 0.16 | 0.019 |
| End anomaly ~ Year + (1\|Species) | 0.0050 | −0.9 | 217 | 282.1 | −0.14 ± 0.13 | 0.296 |
| Duration anomaly ~ Year + (1\|Species) | 0.0563 | 9.0 | 188 | −1301.7 | 0.65 ± 0.19 | 0.001 |

NAO. PC2 was positively associated with the timing of when offshore wind shifted to the southeast, northerly wind strength near Beaufort Inlet, and cumulative tide height (Table S4, Fig. 3). PCs 1 and 2 explained a significant amount of variability in beginning of ingress phenology and the duration of ingress for the ichthyoplankton community. PC1 was associated with an advance in beginning

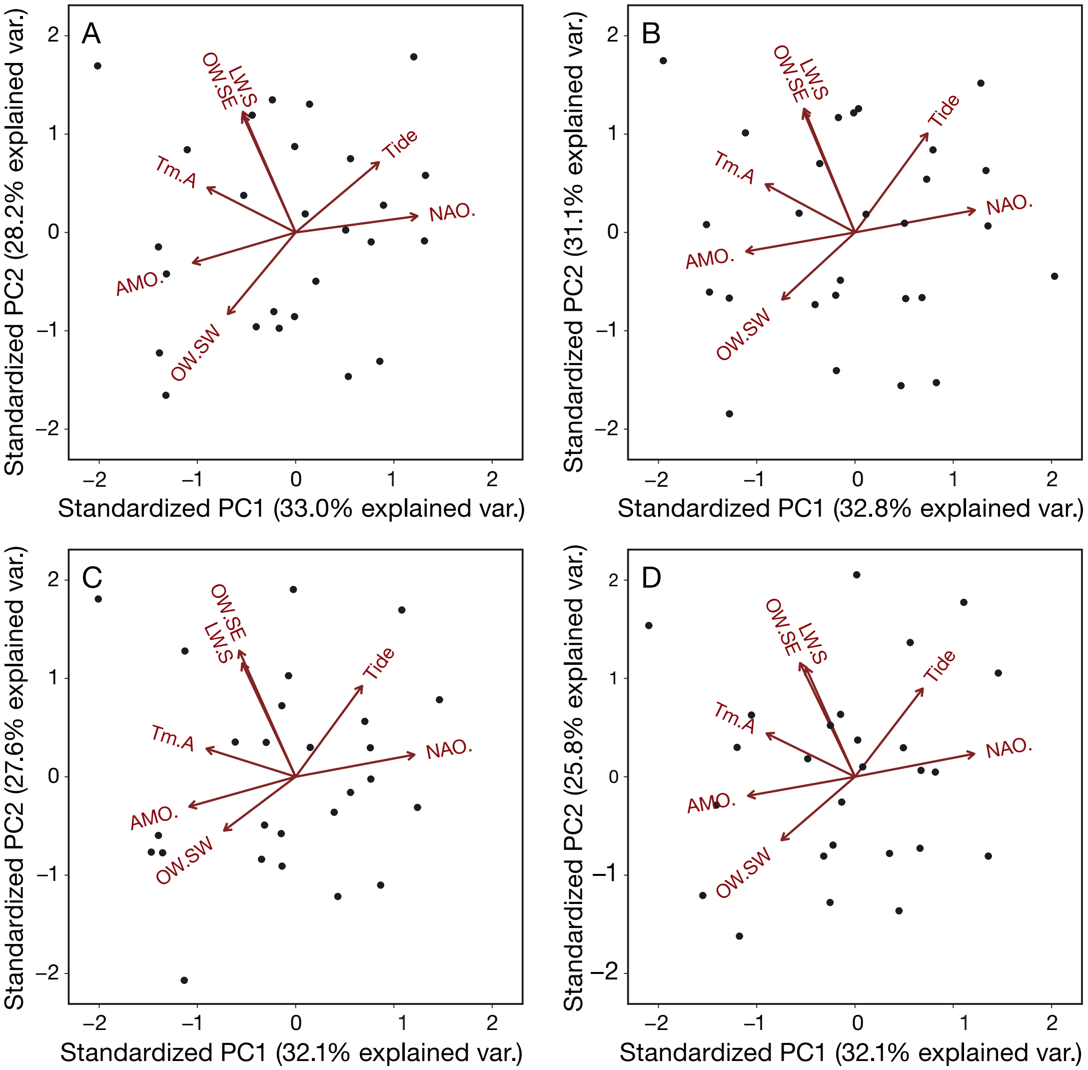

Fig. 3. Biplots of principal components (PCs) 1 and 2 of environmental variables associated with each phenology metric. Vector sizes and directions show the weight of each environmental variable in the 2 PCs, with longer vectors indicating greater influence of a particular environmental variable on a PC. PC1 was typically associated with sea surface temperature anomalies (Tm.A) and the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) indices. PC2 was typically associated with the timing of wind shifts to the southeast (OW.SE), southward wind strength near Beaufort Inlet (LW.S), and cumulative tide height. The angle between vectors relates to the correlation between environmental variables. Angles approaching 0° indicate strong positive correlations, angles approaching 180° indicate strong negative correlations, and angles approaching 90° indicate no correlation. (A–D) Beginning, peak, end, and duration of larval ingress phenology, respectively. OW.SW: offshore wind shift to the southwest

of ingress phenology and increases in the duration of ingress (Table 2). PC2 was associated with a delay in beginning of ingress phenology and a shorter duration of ingress (Table 2). No PC explained a significant amount of variability in peak or end of ingress phenology.

Multiple regression using environmental variables provided further insight into how each variable was related to phenology. Environmental factors included in the best community model for each phenology metric are plotted in Fig. 4. Interannual variation in the initial arrival of the fall/winter ichthyoplankton community to Beaufort Inlet was best explained by southward wind strength and the winter AMO and NAO indices (Table 2). Stronger southward winds were related to a delay in ingress by 6.1 ± 1.8 d $(\text{m s}^{-1})^{-1}$ (mean ± SE) of the change in mean wind strength during the ingress season. Positive values of the AMO and NAO were correlated with earlier ichthyoplankton ingress at rates of −17.6 ± 8.9 d $\text{AMO}^{-1}$ and −4.7 ± 1.9 d $\text{NAO}^{-1}$.

Table 2. Linear mixed models and principal component (PC) regressions of environmental effects on community changes in larval fish ingress phenology. p: significance of the specified model; $R^2$: variance explained by the model; $\Delta AIC_{null}$: difference between each metric's specified and null model. Effect size and SE are given for terms included in each metric's specified model. LW: strength of southward winds local to the inlet (d (m $s^{-1}$)$^{-1}$); AMO: Atlantic Multidecadal Oscillation (d $AMO^{-1}$); NAO: North Atlantic Oscillation (d $NAO^{-1}$); SST: sea surface temperature (d °$C^{-1}$); Tide: tide height (d $m^{-1}$); OWSE: phenology of offshore winds to the southeast (d per wind day)

| Model | p | $R^2$ | $\Delta AIC_{null}$ | df | Term | Trend ± SE |
|---|---|---|---|---|---|---|
| Start anomaly ~ LW + AMO + NAO | <0.0001 | 0.103 | 16.5 | 203 | LW | 6.14 ± 1.75 |
| | | | | | AMO | −17.55 ± 8.91 |
| | | | | | NAO | −4.74 ± 1.89 |
| Start anomaly ~ PC1 + PC2 | <0.005 | 0.0494 | 6.6 | 204 | PC1 | −2.22 ± 0.90 |
| | | | | | PC2 | 1.87 ± 0.95 |
| Peak anomaly ~ SST + LW+ AMO + NAO + Tide | <0.0001 | 0.138 | 18.2 | 184 | SST | −5.90 ± 1.73 |
| | | | | | LW | 3.16 ± 1.40 |
| | | | | | AMO | −27.47 ± 8.66 |
| | | | | | NAO | −3.60 ± 1.92 |
| | | | | | Tide | 0.47 ± 0.34 |
| Peak anomaly ~ PC1 + PC2 | 0.363 | 0.0106 | −2.0 | 187 | PC1 | −0.51 ± 0.88 |
| | | | | | PC2 | 1.15 ± 0.92 |
| End anomaly ~ SST + OWSE + AMO + NAO | <0.0001 | 0.11 | 17.5 | 214 | SST | −6.11 ± 1.51 |
| | | | | | OWSE | 0.06 ± 0.02 |
| | | | | | AMO | −11.18 ± 7.03 |
| | | | | | NAO | −6.11 ± 1.51 |
| End anomaly ~ PC1 + PC2 | 0.200 | 0.0145 | −0.8 | 216 | PC1 | 0.71 ± 0.71 |
| | | | | | PC2 | 1.15 ± 0.76 |
| Duration anomaly ~ SST + NAO + Tide | <0.01 | 0.0621 | 6.2 | 186 | SST | −5.25 ± 2.14 |
| | | | | | NAO | 4.05 ± 2.50 |
| | | | | | Tide | 0.39 ± 0.15 |
| Duration anomaly ~ PC1 + PC2 | 0.011 | 0.0459 | 5.0 | 187 | PC1 | 3.06 ± 1.06 |
| | | | | | PC2 | −0.72 ± 1.11 |

SST, southward wind strength, AMO, NAO, and tidal height best explained community variability in peak ingress phenology (Table 2). Greater tidal heights were correlated with delays in peak ingress by 0.5 ± 0.3 d $m^{-1}$ of cumulative high tide height. Stronger southward winds were related to delayed peak ingress by 3.2 ± 1.4 d (m $s^{-1}$)$^{-1}$ of the change in wind strength. Increases in SST and the AMO and NAO were correlated with earlier peak ingress phenology, with effect sizes of −5.9 ± 1.7 d °$C^{-1}$, −27.5 ± 8.7 d $AMO^{-1}$, and −3.6 ± 1.9 d $NAO^{-1}$, respectively.

Community variability in end of ingress phenology was best explained by SST, offshore wind phenology to the southeast, and the AMO and NAO indices (Table 2). Offshore winds to the southeast were correlated with delays in ingress end by 0.06 ± 0.02 d per wind day. Warmer SST and positive values of the AMO and NAO were associated with advances in phenology for the end of ingress metric by 6.1 ± 1.5 d °$C^{-1}$, 11.2 ± 7.0 d $AMO^{-1}$, and 3.1 ± 1.6 d $NAO^{-1}$, respectively.

Lastly, the duration of ichthyoplankton community ingress was best explained by SST, NAO, and tidal height (Table 2). Warmer SST was related to shortened duration by 5.3 ± 2.1 d °$C^{-1}$. Increases in NAO and tidal height were correlated with increased ingress duration by 4.1 ± 2.5 d $NAO^{-1}$ and 0.4 ± 0.2 d $m^{-1}$ of tide height.

### 3.3. Environmental influences on interannual variations in species ingress phenology

The environmental factors included in each species-level model are shown in a box and whisker plot (Fig. 5) and partial regression plots (Fig. S3). Statistics for each species-level model can be found in Table S5. In some cases, the selected model with the lowest AIC differed between the null model by less than 2, making it difficult to determine if the environmental model was truly an improvement over the null model (Burnham & Anderson 2002). Examples of this can be seen in Table S5.

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

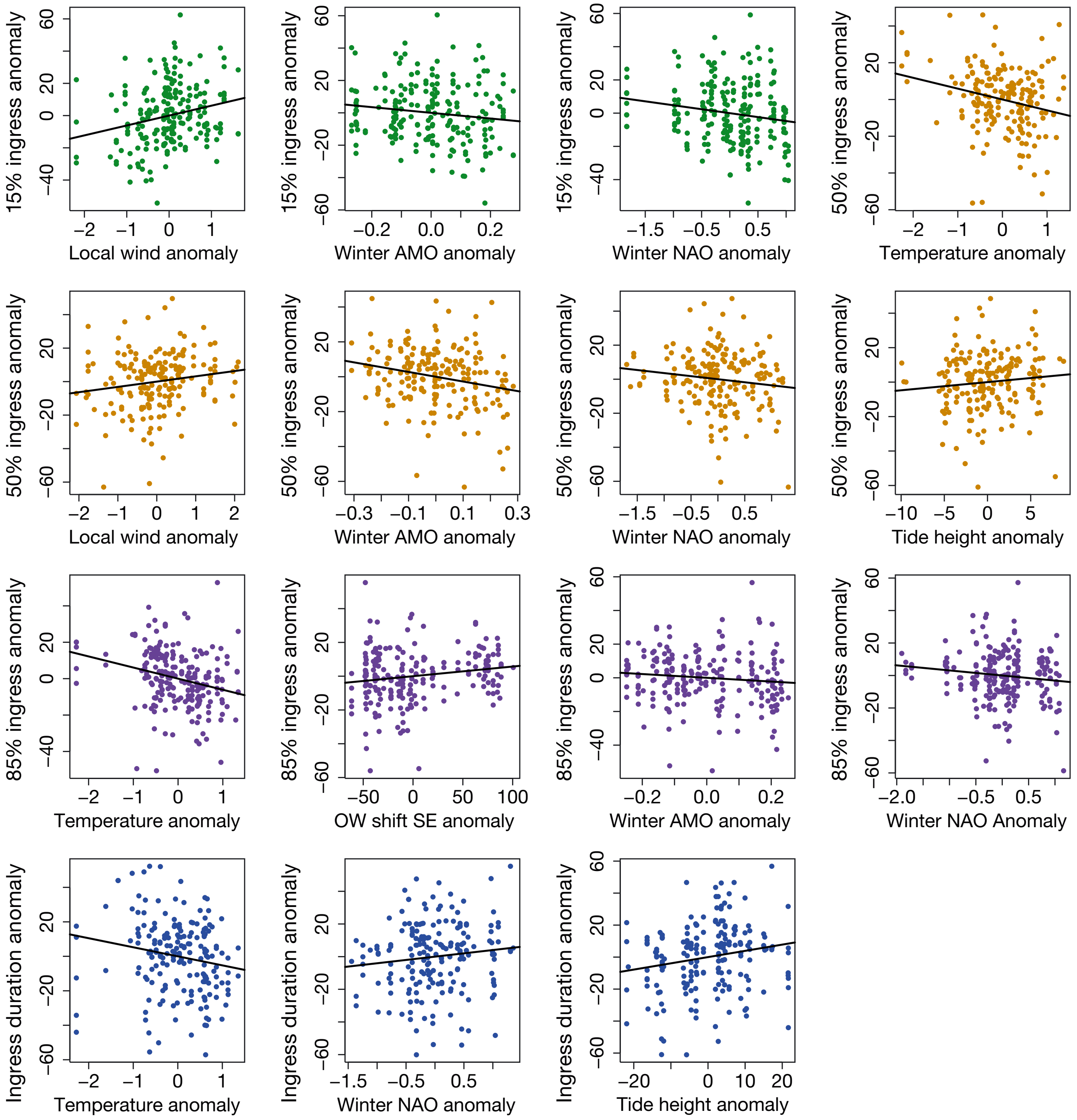

Fig. 4. Added-variable plots of environmental factors included in best models of ingress phenology for the ichthyoplankton community. Green, orange, purple, and blue points represent models of beginning, peak, end, and duration of ingress, respectively. Positive (negative) slopes indicate factors that delay (advance) ingress. Each point represents species phenology in given year. See Table 2 for model specifications. OW: offshore wind; AMO: Atlantic Multidecadal Oscillation; NAO: North Atlantic Oscillation

wind strength, AMO, NAO, and tidal height had consistent effect directions across species (Fig. 5). Delayed shifts in offshore winds to the southwest and stronger nearshore southward winds resulted in significant delays in the start of season ingress among 2 and 4 species, respectively. Positive AMO, NAO, and higher tidal height were related to earlier ingress among 2, 5, and 1 of the species, respectively (Fig. 5). These effect directions were consistent with those included in the community-level model for nearshore winds, NAO, and tidal height. SST was generally associated with advances in ingress affecting 4 species. The exception was *L. rhomboides*, which ingressed later in warm years.

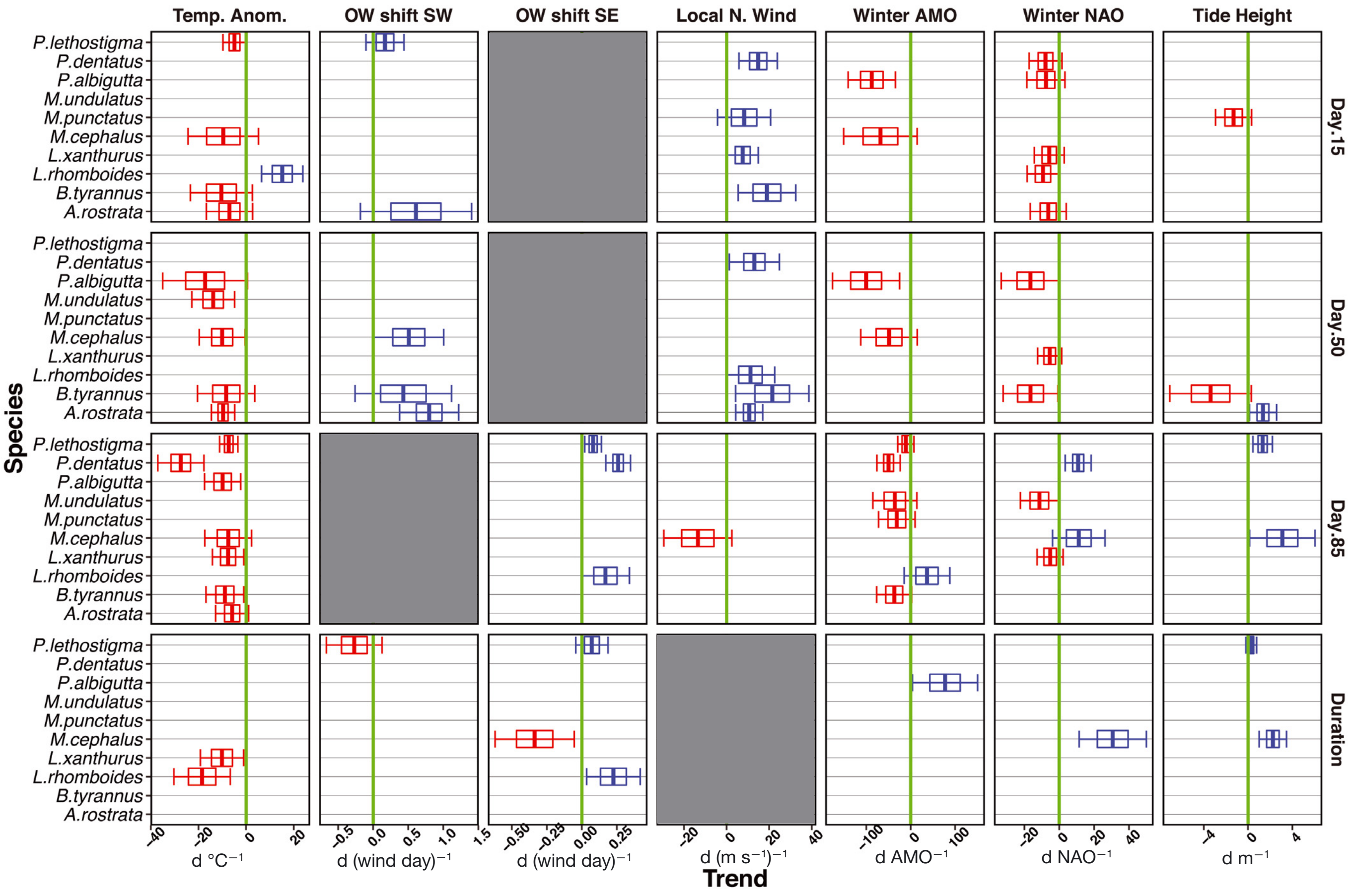

Fig. 5. Boxplots of effects of environmental factors on species' phenology metrics. Centerlines, boxes, and whiskers show the trend, SE, and 95 % CI, respectively. Trends are color coded by effect direction: red = advancing ingress; blue = delayed ingress. Green lines show an effect size of zero. Grey boxes indicate that an environmental factor was not considered in models of a phenology metric. Boxplots are only included for metrics that were used in species' best model of environmental influences on phenology. Acronyms described in Table 2; full species names as in Fig. 2

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, nearshore southward wind strength, AMO, and NAO had consistent effect directions across species. Delayed offshore wind to the southwest and stronger nearshore southward winds were related to delayed ingress in 3 and 4 species, respectively. Warmer SST and positive values of the AMO and NAO were associated with earlier ingress among 5, 3, and 2 species, respectively (Fig. 5). These species-level effect directions of SST, AMO, and NAO were consistent with those of the community model. The effect of tidal height on peak ingress varied between the 2 species for which it was included in models; higher tidal height correlated with earlier ingress for *B. tyrannus* and later ingress for *A. rostrata*.

All species' end of ingress was better explained by some combination of environmental factors than a null model. SST, offshore wind phenology to the southeast, nearshore wind strength, and tidal height had consistent effect directions across species. Delays in offshore winds and higher tidal height delayed the end of ingress in 3 and 2 species, respectively (Fig. 5). Warmer SST and stronger southward winds advanced the end of ingress in 7 and 1 species, respectively. These effect directions were consistent with community model results for offshore wind phenology, tidal height, and SST. Species-level relationships between the AMO index and end of ingress were also mostly consistent with those seen at the community level (4 species ingressed earlier as AMO increased), with the exception of *L. rhomboides.* The NAO, however, had varying effects on the species for which it was statistically significant; *M. undulatus* and *Leiostomus xanthurus* had an earlier end of ingress during the positive NAO phase, whereas *M. cephalus* and *P. dentatus* had a delayed end of ingress during years with a positive NAO.

Half of the species' ingress durations were better explained by a combination of environmental factors than a null model (Table S5). Warmer SST (*L. rhomboides* and *L. xanthurus*) and delayed offshore wind phenology to the southwest (*P. lethostigma*) were 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 related to shortened ingress duration in *M. cephalus* and longer duration in *L. rhomboides* and *P. lethostigma*.

### 3.4. Environmental influences on phenology trends

To determine which variables were the predominant drivers of trends in fish phenology, we removed each environmental variable one by one from multiple regression models to assess whether phenological trends in the model would persist without a given variable. For species that exhibited significant long-term trends, this analysis was performed solely on the start of ingress metric since the greatest number of trends was detected for that metric. Long-term trends towards earlier phenology in modeled ingress start dates were no longer evident when the AMO was removed from the models of *M. cephalus* (full model: 0.77 ± 0.29 d $yr^{-1}$, $p = 0.016$; full model minus AMO: 0.07 ± 0.16 d $yr^{-1}$, $p = 0.649$) and *P. albigutta* (full model: −1.21 ± 0.29 d $yr^{-1}$, $p < 0.001$; full model minus AMO: 0.10 ± 0.06 d $yr^{-1}$, $p = 0.084$), indicating the AMO was the predominant covariate associated with the shift towards earlier ingress (Fig. S4). For *M. punctatus*, trends towards earlier ingress were influenced by the strength of nearshore winds and tidal height. A temporal trend towards earlier phenology was evident when both of these metrics were modeled separately, and a stronger and more significant trend was present when the 2 were modeled together (full model: −0.74 ± 0.15 d $yr^{-1}$, $p < 0.001$; full model minus nearshore wind: −0.30 ± 0.14 d $yr^{-1}$, $p = 0.048$; full model minus tidal height: −0.33 ± 0.10 d $yr^{-1}$, $p = 0.003$).

## 4. DISCUSSION

Over the past 3 decades, the ichthyoplankton community has changed its phenology to enter Beaufort Inlet earlier in the year. Though significance varied between species, we found the beginning of ingress has advanced for all fishes examined. The direction of these temporal shifts in phenology is consistent with SST's effect on ingress phenology, even though SST has not warmed in the region during recent decades (Shearman & Lentz 2010, Morley et al. 2016). Our analysis indicates instead that changes in the AMO, nearshore wind strength, and tidal height may be responsible for the trend towards earlier ingress into the estuary among species. Seasonal 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 closely linked to environmental changes, whereas variation in peak and end of ingress phenology may be mediated by biotic factors, such as predation on ichthyoplankton or prey availability.

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. We excluded species' beginning and end of ingress for years in which they occurred within 2 wk of the respective start or end date of sampling. These exclusions may dampen some of the detected trends in species' phenology. For example, trends towards earlier ingress identified herein may be underestimated in cases in which recent years were removed due to ingress starting before the seasonal Bridgenet survey began. This was potentially the case for *Mugil cephalus*, *Myrophis punctatus*, *Paralichthys dentatus*, and *P. lethostigma* (Table S1).

Although we did not find evidence of an SST-driven temporal shift in the timing of larval ingress, our results suggest that SST may be a significant driver of interannual variability in ingress phenology. With the exception of *Lagodon rhomboides*, warmer offshore SST was consistently related to earlier phenology. This indicates that the timing of ingress may be set early in the process of transport into estuaries during the initial stage when fish are transported from offshore to nearshore habitats. 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 observed relationship between SST and ingress phenology is consistent with similar studies of fish reproduction and early life history. Fishes 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, USA, plankton blooms in the North Sea, and egg laying in seabirds (Poloczanska et al. 2016, Mills et al. 2017). While the direction of trends observed here is consistent with previous research, the strengths of some of these trends are greater than those in other ecosystems. A meta-analysis by Poloczanska et al. (2013) found, on average, a 4.4 d decade$^{-1}$ advance in the phenology of marine species. By comparison, we observed advances in ingress phenology on the order of 9 to 14 d decade$^{-1}$ in 5 species studied.

As temperatures cool in the fall and winter, 6 of the 10 species examined moved offshore to spawn (Table S2b). 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 et al. 2004). This may also occur in the southeastern USA, and there is evidence that the spawning migrations of the 3 paralichthyids studied herein may relate to temperature (Stokes 1977, Able & Fahay 2010, Wang et al. 2018; Table S2c). The ingress of *P. dentatus*, and to a slightly lesser extent *P. albigutta* and *P. lethostigma*, had the strongest relationships with environmental variables of all species studied. Warmer temperatures and positive AMO or NAO indices were related to advances in either the beginning, middle, or end of ingress for all 3 species. If these groundfishes vary their offshore migration route based on temperature in a way similar to groundfishes in other areas (Myers 1998, Sims et al. 2004), they may 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.

Warmer SST may also lead to quicker reproductive maturation for some species (Pankhurst & Munday 2011). In the presence of adequate resources, larvae grow faster in warmer waters (Houde 1989, Meekan et al. 2003, Laurel et al. 2008). Faster growth may result in faster transport in larvae that can actively swim due to increases in swimming speed with faster development. It is hypothesized that the transport of *Anguilla rostrata* larvae is augmented by active swimming (Wuenschel & Able 2008). 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 (Smith 1968, Power & McCleave 1983). We found *A. rostrata* larvae arrive at Beaufort Inlet sooner in warm years. In warmer waters with adequate food, these larvae may grow faster, transform into leptocephali sooner, and ultimately 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 offshore temperature. These temperature effects could also potentially influence our ability to observe larval fishes in the Bridgenet time series through a few mechanisms: accelerated development and increased swimming ability could lead to greater net avoidance; earlier ingress due to changes in temperature could increase the likelihood that the onset of ingress might be missed by seasonal sampling; and temperature-related changes in mortality could affect the patterns detected.

We mostly found consistency between the effect directions of SST, the AMO, and the NAO, which is expected since SST is used in the calculation of the AMO (albeit at a broader scale than Onslow Bay) and the NAO is calculated based on variations in air pressure that are indicative of large-scale temperature patterns in the North Atlantic (Hurrell et al. 2003). The wide spatial area captured by these basin-scale indices may be more representative of the temperatures, wind patterns, ocean circulation, and mixed layer depth that fishes experience as they migrate over time. Temperature changes associated with the AMO and NAO can affect fish phenology via its impact on spawning habitat location, spawning timing, or stage duration, whereas changes in ocean circulation associated with the AMO and NAO could impact ingress phenology via larval transport.

The influence of temperature and photoperiod on fish phenology has been well studied (Pankhurst & Munday 2011) compared to the effects of winds, currents, tides, and other hydrographic processes. In our study area, both near- and offshore winds exhibited the hypothesized effects on larval phenology. Stronger southward winds near Beaufort Inlet delayed the beginning and peak timing of ingress in cases when they were included in environmental ingress models. Since Beaufort Inlet opens to the south, this is likely due to these winds weakening northward tidal streams that larvae use to enter the inlet. Delayed offshore wind phenology correlated with delayed ingress phenology. We focused on the timing of offshore wind 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, winds to the west and northwest partially explain recruitment variability in *P. lethostigma* in North Carolina estuaries (Taylor et al. 2010).

Of the 7 environmental metrics examined, tidal height had the least frequently observed influence on 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 did not translate to appreciable interannual differences in ingress phenology. The PCA found that variability in tide height was associated with offshore wind phenology and the strength of southward winds near Beaufort Inlet. While this connection between tidal height and wind strength has not been well studied in the western Atlantic, this is consistent with research from the western Pacific, where variations in regional sea level are associated with fluctuations in trade wind strength (Timmermann et al. 2010, Merrifield & Maltrud 2011). The few observed relationships in our study between tides and ingress phenology could be artifacts of covariance between winds and tides near Beaufort Inlet.

Aspects of the environment besides those examined can also impact fish early life history. Gulf Stream eddies, meanders, and filaments have been hypothesized to influence larval transport (Govoni & Pietrafesa 1994, Govoni & Spach 1999). Tropical storms and winter storms also play a role in the transport of larval fishes and have been related to settlement of blue crab *Callinectes sapidus* and larval drift of *Brevoortia tyrannus* into North Carolina estuaries (Checkley et al. 1988, Eggleston et al. 2010).

As larvae approach Beaufort Inlet, localized processes can affect larval ingress on a shorter time scale. River discharge has been related to spawning seasonality in some fishes and to the recruitment and distribution of *P. lethostigma* in North Carolina (Trépanier et al. 1996, Taylor et al. 2010, Todd et al. 2012). Strong river flow may also impede ingress by weakening the strength of the incoming tidal stream, similar to the effect of northerly wind stress. River discharge also impacts the salinity of the water in and around the inlet (Churchill et al. 1999b). These changes in salinity may affect the ability of larvae to detect the tidal streams that transport them through the inlet (Forward et al. 1999b). The shape and size of the inlets of North Carolina also change over time due to natural sedimentation, erosion, and anthropogenic dredging (Cleary & FitzGerald 2003). Though changes in inlet hydrography are unlikely to affect ingress timing, they could affect the distribution of fish within the inlet from year to year.

Alternatively, changes in fish population abundance, age structure, and size structure could also be a driver of shifts in fish phenology (Stige et al. 2016, McQueen & Marshall 2017, Rogers & Dougherty 2019). Spawning behaviors vary across ages and sizes of fishes, with older fishes spawning earlier among certain species, such as Atlantic cod *Gadus morhua* and walleye pollock *G. chalcogrammus* (McQueen & Marshall 2017, Rogers & Dougherty 2019). Similarly, changes in age class, or size structure, which may influence phenology, could have occurred in North Carolina since several of the species in our analysis have undergone long-term changes in abundance (e.g. *A. rostrata* and *B. tyrannus*) over the last 30 yr (Simpson et al. 2016, Rudershausen et al. 2019).

One uncertainty associated with our study is a lack of data on variations in the location and timing of offshore spawning, which could affect ingress phenology. While there is no ichthyoplankton time series covering the offshore habitats of Onslow Bay, the NOAA Northeast Fisheries Science Center does have an ichthyoplankton monitoring program, whose southern extent is Cape Hatteras (Walsh et al. 2015). There is overlap between 4 of the species monitored by that program and by our research. For 2 of these species (*Leiostomus xanthurus* and *P. dentatus*), Walsh et al. (2015) did not detect any changes in offshore larval distribution or phenology over the last ~40 yr, suggesting little to no changes in the location and timing of spawning. For *Micropogonias undulatus*, no changes in offshore larval phenology were detected, but Walsh et al. (2015) noted that this species has shifted its distribution northward and inshore. Lastly, for *B. tyrannus*, a shift toward later larval occurrence was detected by Walsh et al. (2015). This differs from our results examining the ingress phenology of *B. tyrannus*. This difference could be because these 2 studies considered different years, had different frequencies of seasonal sample collection, used different metrics to assess phenological changes, and conducted ichthyoplankton surveys using different types of nets. Also, larvae found offshore may have been exposed to different conditions than those caught near Beaufort Inlet.

## 5. CONCLUSIONS

Sustained warming 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 into how species may respond when warming does occur. Extrapolation of the trends observed here with the potential for a 2°C mean surface temperature change on the southeastern US continental shelf under a medium emissions climate change scenario (IPCC 2014) would result in substantial changes to mean ingress phenology of some species we studied. This would result in a 30 d delay in the beginning of *Lagodon rhomboides* ingress, a 27 d advance in the peak ingress of *Micropogonias undulatus*, and a 55 d advance in the end of *Paralichthys dentatus* ingress. These projections assume linear responses of phenology to temperature, although there may be thresholds beyond which 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 prey and predators respond to climate change. Previous research has shown that phenological responses to climate change vary across trophic levels (Beaugrand et al. 2003, Voigt et al. 2003, Edwards & Richardson 2004, Thackeray et al. 2010, Visser et al. 2012, Burkle et al. 2013, Asch et al. 2019), so shifts in larval ingress phenology may not match shifts in the phenology of their prey.

This study expands upon previous work on climate change and fish phenology by examining factors beyond SST. We 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. We 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 further examine how transport by currents relates to the movement of larvae on the southeastern US continental shelf and other ecosystems.

In conclusion, we found intuitive relationships between fish phenology and environmental variables that were consistent across taxa and could be interpreted in terms of life history traits. The 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 into the future of certain fishes as they change their range with changing ocean conditions and would also elucidate whether environmental influences on phenology are consistent across a species' range. Lastly, factors besides the environment, such as effects of population size and age structure, may influence phenology and are worthy of future study.

*Acknowledgements*. W.C.T. was supported by a Knauss Marine Policy Fellowship, a North Carolina Wildlife Federation scholarship, and the East Carolina University Department of Biology. R.G.A. was supported by a Sloan Foundation Research Fellowship. The manuscript benefited from constructive comments provided by R. A. Rulifson, E. Reyes, and 2 anonymous reviewers. Completion of this research would not have been possible but for the efforts of many NOAA scientists and volunteers who have maintained the Beaufort Bridgenet time series and database since its initiation in 1986. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the Department of Commerce.

## LITERATURE CITED

Able KW, Fahay MP (2010) Ecology of estuarine fishes: Temperate waters of the Western North Atlantic. Johns Hopkins University Press, Baltimore, MD

Able KW, Allen DM, Bath-Martin G, Hare JA and others (2011) Life history and habitat use of the speckled worm eel, *Myrophis punctatus*, along the east coast of the United States. Environ Biol Fishes 92:237–259

Allen DM, Barker DL (1990) Interannual variations in larval fish recruitment to estuarine epibenthic habitats. Mar Ecol Prog Ser 63:113–125

Anderson JJ, Beer WN (2009) Oceanic, riverine, and genetic influences on spring Chinook salmon migration timing. Ecol Appl 19:1989–2003

Asch RG (2013) Interannual-to-decadal changes in phytoplankton phenology, fish spawning habitat, and larval fish phenology. PhD dissertation, University of California, San Diego, CA

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci USA 112:E4065–E4074

Asch RG, Stock CA, Sarmiento JL (2019) Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob Change Biol 25: 2544–2559

Auth TD, Brodeur RD, Soulen HL, Ciannelli L, Peterson WT (2011) The response of fish larvae to decadal changes in environmental forcing factors off the Oregon coast. Fish Oceanogr 20:314–328

Batten SD, Mackas DL (2009) Shortened duration of the annual *Neocalanus plumchrus* biomass peak in the Northeast Pacific. Mar Ecol Prog Ser 393:189–198

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Boehlert GW, Mundy BC (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am Fish Soc Symp 3:51–67

Burkle LA, Marlin JC, Knight TM (2013) Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339:1611–1615

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY

Checkley DM Jr, Raman S, Maillet GL, Mason KM (1988) Winter storm effects on the spawning and larval drift of a pelagic fish. Nature 335:346–348

Chevillot X, Drouineau H, Lambert P, Carassou L, Sautour B, Lobry J (2017) Toward a phenological mismatch in estuarine pelagic food web? PLOS ONE 12:e0173752

Churchill JH, Forward RB, Luettich RA, Hench JL, Hettler WF, Crowder LB, Blanton JO (1999a) Circulation and larval fish transport within a tidally dominated estuary. Fish Oceanogr 8:173–189

Churchill JH, Hench JL, Luettich RA, Blanton JO, Werner FE (1999b) Flood tide circulation near Beaufort Inlet, North Carolina: implications for larval recruitment. Estuaries 22:1057–1070

Cleary WJ, FitzGerald DM (2003) Tidal inlet response to natural sedimentation processes and dredging-induced tidal prism changes: Mason Inlet, North Carolina. J Coast Res 19:1018–1025

Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. Nat Clim Chang 8:224–228

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293

Doyle MJ, Strom SL, Coyle KO, Hermann AJ and others (2019) Early life history phenology among Gulf of Alaska fish species: strategies, synchronies, and sensitivities. Deep Sea Res II 165:41–73

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884

Eggleston DB, Reyns NB, Etherington LL, Plaia GR, Xie L (2010) Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement. Fish Oceanogr 19:89–106

Epifanio CE, Garvine RW (2001) Larval transport on the Atlantic continental shelf of North America: a review. Estuar Coast Shelf Sci 52:51–77

Forward RB Jr, Reinsel KA, Peters DS, Tankersley RA and others (1999a) Transport of fish larvae through a tidal inlet. Fish Oceanogr 8:153–172

Forward RB Jr, de Vries MC, Tankersley RA, Rittschof D and others (1999b) Behaviour and sensory physiology of Atlantic menhaden larvae, *Brevoortia tyrannus*, during horizontal transport. Fish Oceanogr 8:37–56

Genner MJ, Sims DW, Southeward AJ, Budd GC and others (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Glob Change Biol 16:517–527

Govoni JJ, Pietrafesa LJ (1994) Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. Fish Oceanogr 3:120–132

Govoni JJ, Spach HL (1999) Exchange and flux of larval fishes across the western Gulf Stream front south of Cape Hatteras, USA, in winter. Fish Oceanogr 8:77–92

Greve W, Prinage S, Zidowitz H, Nast J, Reiners F (2005) On the phenology of North Sea ichthyoplankton. ICES J Mar Sci 62:1216–1223

Hare JA, Quinlan JA, Werner FE, Blanton BO and others (1999) Larval transport during winter in the SABRE study area: results of a coupled vertical larval behaviour — three-dimensional circulation model. Fish Oceanogr 8:57–76

Hettler WF Jr, Barker DL (1993) Distribution and abundance of larval fishes at two North Carolina inlets. Estuar Coast Shelf Sci 37:161–179

Hettler WF Jr, Chester AJ (1990) Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. Mar Ecol Prog Ser 68:157–168

Hettler WF Jr, Hare JA (1998) Abundance and size of larval fishes outside the entrance to Beaufort Inlet, North Carolina. Estuaries 21:476–499

Hettler WF Jr, Peters DS, Colby DR, Laban EH (1997) Daily variability in abundance of larval fishes inside Beaufort Inlet. Fish Bull 95:477–493

Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull 87:471–495

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) An overview of the North Atlantic Oscillation. Geophys Monogr 134:1–35

IPCC (Intergovernmental Panel on Climate Change) (2014) Climate change 2014: synthesis report. In: Core Writing Team, Pachauri RK, Meyer LA (eds) Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Joyce TM (2002) One hundred plus years of wintertime climate variability in the eastern United States. J Clim 15: 1076–1086

Joyeux JC (1999) The abundance of fish larvae in estuaries: within-tide variability at inlet and immigration. Estuaries 22:889–904

Knight JR, Folland CK, Scaife AA (2006) Climate impacts of the Atlantic Multidecadal Oscillation. Geophys Res Lett 33:1–4

Knudsen MF, Seidenkrantz MS, Jacobsen BH, Kuijpers A (2011) Tracking the Atlantic Multidecadal Oscillation through the last 8,000 years. Nat Commun 2:178

Koslow JA, Wright M (2016) Ichthyoplankton sampling design to monitor marine fish populations and communities. Mar Policy 68:55–64

Laurel BJ, Hurst TP, Copeman LA, Davis MW (2008) The role of temperature on the growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*). J Plankton Res 30:1051–1060

Logan DG, Morrison JM, Pietrafesa LJ, Hopkins TS, Churchill J (2000) Physical oceanographic processes affecting inflow/outflow through Beaufort Inlet, North Carolina. J Coast Res 16:1111–1125

Luettich RA Jr, Hench JL, Fulcher CW, Werner FE, Blanton BO, Churchill JH (1999) Barotropic tidal and wind-driven larval transport in the vicinity of a barrier island inlet. Fish Oceanogr 8:190–209

Mackas DL, Greve W, Edwards M, Chiba S and others (2012) Changing zooplankton seasonality in a changing ocean: comparing time series of zooplankton phenology. Prog Oceanogr 97–100:31–62

McCulloch T (2017) Effects of temperature, flow, and climate factors on inter-annual variation of larval fish assemblages in a coastal watershed. MS thesis, East Carolina University, Greenville, NC

McQueen K, Marshall CT (2017) Shifts in spawning phenology of cod linked to rising sea temperatures. ICES J Mar Sci 74:1561–1573

Meekan MG, Carleton JH, McKinnon AD, Flynn K, Furnas M (2003) What determines the growth of tropical reef fish larvae in the plankton: food or temperature? Mar Ecol Prog Ser 256:193–204

Merrifield MA, Maltrud ME (2011) Regional sea level trends due to a Pacific trade wind intensification. Geophys Res Lett 38:L21605

Mills KE, Pershing AJ, Hernández CM (2017) Forecasting the seasonal timing of Maine's lobster fishery. Front Mar Sci 4:1–10

Morley JW, Batt RD, Pinsky ML (2016) Marine assemblages respond rapidly to winter climate variability. Glob Chang Biol 23:2590–2601

Myers RA (1998) When do environment–recruitment correlations work? Rev Fish Biol Fish 8:285–305

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Neuheimer AB, Thresher RE, Lyle JM, Semmens JM (2011) Tolerance limit for fish growth exceeded by warming waters. Nat Clim Chang 1:110–113

Nye JA, Baker MR, Bell R, Kenny A and others (2014) Ecosystem effects of the Atlantic Multidecadal Oscillation. J Mar Syst 133:103–116

Ortner PB, Crowder LB, Hoos DE (1999) The South Atlantic Bight recruitment experiment: introduction and overview. Fish Oceanogr 8:1–6

Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. Mar Freshw Res 62:1015–1026

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. Biol Oceanogr 1:175–203

Peer AC, Miller TJ (2014) Climate change, migration, phenology, and fisheries management interact with unanticipated consequences. N Am J Fish Manage 34:94–110

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925

Poloczanska ES, Burrows MT, Brown CJ, Molinos JG, Halpern BS, Hoegh-Guldberg O (2016) Responses of marine organisms to climate change across oceans. Front Mar Sci 3:1–21

Power J, McCleave JD (1983) Simulation of the North Atlantic ocean drift of *Anguilla* leptocephali. US Fish Bull 81:483–500

Quinlan JA, Blanton BO, Miller TJ, Werner FE (1999) From spawning grounds to the estuary: using linked individual-based and hydrodynamic models to interpret patterns and processes in the oceanic phase of Atlantic menhaden *Brevoortia tyrannus* life history. Fish Oceanogr 8:224–246

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rice JA, Quinlan JA, Nixon SW, Hettler WF, Warlen SM, Stegmann PM (1999) Spawning and transport dynamics of Atlantic menhaden: inferences from characteristics of immigrating larvae and predictions of a hydrodynamic model. Fish Oceanogr 8:93–110

Roberts SM, Boustany AM, Halpin PN, Rykaczewski RR (2019) Cyclical climate oscillation alters species statistical relationships with local habitat. Mar Ecol Prog Ser 614:159–171

Rogers LA, Dougherty AB (2019) Effects of climate and demography on reproductive phenology of a harvested marine fish population. Glob Change Biol 25:708–720

Rudershausen PJ, Lee LM, Lombardo SM, Merrell JH, Buckel JA (2019) Survival and habitat of yellow-phase American eels in North Carolina tidal creeks. Trans Am Fish Soc 148:978–990

Saba VS, Griffies SM, Anderson WG, Winton M and others (2016) Enhanced warming of the Northwest Atlantic Ocean under climate change. J Geophys Res Oceans 121: 118–132

Shearman RK, Lentz SJ (2010) Long-term sea surface temperature variability along the US East Coast. J Phys Oceanogr 40:1004–1017

Simpson CA, Wilberg MJ, Bi H, Schueller AM, Nesslage GM, Walsh HJ (2016) Trends in relative abundance and early life survival of Atlantic menhaden during 1977–2013 from long-term ichthyoplankton programs. Trans Am Fish Soc 145:1139–1151

Sims DW, Mouth VJW, Genner MJ, Southward AJ, Hawkins SJ (2004) Low-temperature-driven early spawning migration of a temperate marine fish. J Anim Ecol 73:333–341

Smith DG (1968) The occurrence of larvae of the American eel, *Anguilla rostrata*, in the Straits of Florida and nearby areas. Bull Mar Sci 18:280–293

Sparks TH, Jeffree EP, Jeffree CE (2000) An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. Int J Biometeorol 44:82–87

Stige LC, Yaragina NA, Langangen Ø, Bogstad B, Stenseth NC, Ottersen G (2017) Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. Proc Natl Acad Sci USA 114:1347–1352

Stokes GM (1977) Life history studies of southern flounder (*Paralichthys lethostigma*) and gulf flounder (*P. albigutta*) in the Aransas Bay area of Texas. Tech Ser No. 25, Texas Parks and Wildlife Department, Austin, TX

Taylor JC, Miller JM, Pietrafesa LJ, Dickey DA, Ross SW (2010) Winter winds and river discharge determine juvenile southern flounder (*Paralichthys lethostigma*) recruitment and distribution in North Carolina estuaries. J Sea Res 64:15–25

Thackeray SJ, Sparks TH, Frederiksen M, Burthes S and others (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16:3304–3313

Thackeray SJ, Henrys PA, Hemming D, Bell JR and others (2016) Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245

Thaxton WC (2019) The effects of climate variability on the timing of ichthyoplankton ingress through Beaufort Inlet, NC, USA. MS thesis, East Carolina University, Greenville, NC

Timmermann A, McGregor S, Jin FF (2010) Wind effects on past and future regional sea level trends in the southern Indo-Pacific. J Clim 23:4429–4437

Todd CD, Friedland KD, MacLean JC, Whyte BD, Russell IC, Lonergan ME, Morrissey MB (2012) Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. ICES J Mar Sci 69: 1686–1698

Trenberth KE, Shea DJ (2006) Atlantic hurricanes and natural variability in 2005. Geophys Res Lett 33:L12704

Trépanier S, Rodriguez MA, Magnan P (1996) Spawning migration in landlocked Atlantic salmon: time series modeling of river discharge and water temperature effects. J Fish Biol 48:925–936

Visbeck M, Chassignet EP, Curry RG, Delworth TL, Dickson RR, Krahmann G (2003) The ocean's response to North Atlantic Oscillation variability. Geophys Monogr Ser 134: 113–145

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proc Biol Sci 272:2561–2569

Visser ME, te Marvelde L, Lof MEL (2012) Adaptive phenological mismatches of birds and their food in a warming world. J Ornithol 153:S75–S84

Voigt W, Perner J, Davis AJ, Eggers T and others (2003) Trophic levels are differentially sensitive to climate. Ecology 84:2444–2453

Walsh HJ, Richardson DE, Marancik KE, Hare JE (2015) Long-term changes in the distributions of larval and adult fish in the northeast US shelf ecosystem. PLOS ONE 10:e0137382

Wang VH, White JW, Arnott SA, Scharf FS (2018) Population connectivity of southern flounder in the US South Atlantic revealed by otolith chemical analysis. Mar Ecol Prog Ser 596:165–179

Warlen SM, Burke JS (1990) Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461

Werner FE, Blanton BO, Quinlan JA, Luettich RA (1999) Physical oceanography of the North Carolina continental shelf during the fall and winter seasons: implications for the transport of larval menhaden. Fish Oceanogr 8:7–21

Wuenschel MJ, Able KW (2008) Swimming ability of eels (*Anguilla rostrata*, *Conger oceanicus*) at estuarine ingress: contrasting patterns of cross-shelf transport? Mar Biol 154: 775–786

Yuan Y, Castelao RM, He R (2017) Variability in along-shelf and cross-shelf circulation in the South Atlantic Bight. Cont Shelf Res 134:52–62

*Editorial responsibility: Ignacio A. Catalán (Guest Editor), Esporles, Spain*

*Submitted: December 6, 2019; Accepted: June 26, 2020*
*Proofs received from author(s): September 10, 2020*