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Phenology of penaeid shrimp nursery habitat use: trends and environmental drivers over four decades

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ABSTRACT: White shrimp *Penaeus setiferus* and brown shrimp *P. aztecus* are key predators of benthic infauna and important prey resources for higher trophic levels in coastal waters of the southeastern USA. Both species rely on estuaries as nursery habitat and are subject to the dynamic environmental conditions typical of these ecosystems. Understanding the phenology of juvenile penaeid shrimp estuarine habitat use, detecting changes in phenology over time, and linking interannual variability in phenological metrics to environmental conditions will provide an improved understanding of the degree to which global change is impacting the life history of these key members of estuarine communities. We analyzed nearly 4 decades of catch data (1984–2022) from a tidal creek in South Carolina, USA, comparing the timing, synchrony, and duration of juvenile shrimp habitat utilization across years to identify shifts in phenology. We then investigated linkages between environmental and climatological conditions and shrimp phenology to understand potential drivers of interannual variation in these metrics. Brown shrimp phenology showed no directional change over time; however, salinity and winter water temperature were strong predictors of variability in all 3 phenological metrics. Conversely, white shrimp nursery habitat use has become less synchronized and occurs over a longer interval, but no single environmental variable strongly predicts all 3 metrics. Differences in life history strategy and environmental tolerances likely contribute to the variation in phenological responses observed for these species. Our findings demonstrate that climate-change-related shifts in phenology will be species- and life-history-specific.

KEY WORDS: *Penaeus setiferus* · *Penaeus aztecus* · Nekton · Tidal creeks · Duration · Synchrony · Timing · Climate

1. INTRODUCTION

Estuarine habitats serve as nurseries for numerous species of fishes, cephalopods, and crustaceans (collectively, nekton) around the world (McDevitt-Irwin et al. 2016, Lefcheck et al. 2019). The functional role of estuaries as nursery habitat is linked to the availability of refugia from predators and the abundant food resources needed to facilitate rapid growth, both of which lead to increased survival during early life stages (Beck et al. 2001, Dahlgren et al. 2006). The value of estuarine nurseries is dynamic over time and across spatial scales, resulting in differences in the functional role of estuarine habitats (Sheaves et al. 2013, Nagelkerken et al. 2015). Some habitats within estuarine seascapes, such as seagrass and emergent marsh vegetation, exhibit distinct intra-annual variations in physical structure. Likewise, the food re-

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*Corresponding author: batchel@email.sc.edu sources targeted by juvenile nekton, such as phytoplankton, zooplankton, and benthic infauna, tend to exhibit seasonal variations in abundance as a function of environmental conditions present in the estuary (Beseres Pollack et al. 2011, Carstensen et al. 2015, Connelly et al. 2020). The seasonality of environmental conditions in estuaries, including water temperature, primary production, and salinity, among other parameters, can exhibit high interannual variability and is expected to change significantly with anthropogenic climate change (Doney et al. 2012, Rybczyk et al. 2012, Colombano et al. 2021). In the southeastern USA more specifically, water temperatures are generally increasing, driven largely by significant increases in winter water temperatures. Likewise, salinity in this region is highly variable and site-specific (Mallick & Dunn 2024). These changes in environmental conditions may in turn lead to alterations in the patterns of seasonal use and function of nursery habitats for a number of fish and invertebrate species.

The seasonality or periodicity of biological phenomena is known as phenology (Thel et al. 2022). Since the inception of this term in the late 1840s (Demarée & Rutishauser 2011), the phenology of major life history events including reproduction, migration, and metamorphosis has been studied for a diverse range of taxa including plants (Cleland et al. 2007), mammals (Kerby & Post 2013), fishes (Asch 2015), and crustaceans (Richards 2012). From these investigations, we have gained tremendous insight into the connections between phenology and reproductive cues (Burbank et al. 2022), species interactions (Renner & Zohner 2018), and life history strategies (García et al. 2019), among other ecological processes. However, the metrics used to describe phenology are numerous and differ between studies, reducing the ability to compare among taxa and across ecosystems (Thel et al. 2022). Two useful metrics to describe the phenology of a life history event are its 'timing,' which describes when in a year an event occurs, and synchrony, which describes the distribution of an event's occurrence throughout a year (i.e. the variation; Thel et al. 2022). Related to synchrony, a life history event has a measurable duration, which describes the period of time over which a majority of individuals undergo the focal event. The timing, synchrony, and duration of life history events such as spawning are commonly queued by environmental stimuli, and, as such, changes in environmental conditions are likely to alter the phenology of these events (Brown et al. 2016). Changes in phenology may be taxon-specific, occur at varying rates, and lead to a wide range of consequences (see Prather et al. 2023 for review), necessitating investigations of phenology across taxa and ecosystems.

Studies identifying the environmental drivers of phenology have increased in recent decades (e.g. Edwards & Richardson 2004, Ji et al. 2010, Anderson et al. 2013, Staudinger et al. 2019, Schneider et al. 2024). Generally, these have revealed extensive yet variable phenological consequences of global climate warming and associated changes to environmental conditions (see Thackeray et al. 2016, Renner & Zohner 2018, Prather et al. 2023 for review). When changes to phenology result in a shift or disruption in the timing of a major life history event, it may lead to asynchrony between interdependent ecological processes (Thackeray et al. 2016). For example, seabird reproductive phenology is advancing more slowly than that of their marine nekton prey in response to warming sea surface temperatures, leading to insufficient resources during the laying season of many seabirds globally (Keogan et al. 2018). This asynchrony between consumers and their prey resource, known as the match—mismatch hypothesis (Cushing 1973), has been used to explain variation in recruitment by aquatic and terrestrial species around the globe (Renner & Zohner 2018). In aquatic ecosystems, abiotic environmental conditions including water temperature can dictate the large-scale availability of vital prey resources and influence consumer growth rates; therefore, populations of consumers can respond to environmental conditions on regional and basin-wide scales (Koeller et al. 2009). A shift in the phenology of prey availability could lead to a trophic mismatch and a corresponding decline in the abundance of consumers (Edwards & Richardson 2004, Asch et al. 2019). In estuaries, juvenile fishes and crustaceans act as both low-level consumers and valuable prey resources, thereby serving as a key link between primary producers and higher trophic levels. Thus, changes in the phenology of estuarine nursery habitat use by nekton may lead to perturbations of broader estuarine and coastal food webs.

The spatiotemporal dynamics of nursery habitat use are likely to be affected by changes in environmental conditions beyond trophic mismatch alone. Functionally similar species may exhibit temporal partitioning of their nursery period, which can reduce the potential for competition over shared resources and allow species to take advantage of optimal environmental conditions (Rooker et al. 1998, Deary et al. 2017, Sbragaglia et al. 2019). This temporal partitioning of space can lead to a community structure that varies seasonally as the resource needs of community members change through ontogeny (Sheaves et al. 2013). In the absence of natural habitat structural diversity and connectivity, behavioral and ontogenetic shifts in habitat use may decrease, leading to a loss of the typical spatiotemporal partitioning of habitats (Munsch et al. 2016). Additionally, if altered conditions lead to more temporal overlap in nursery habitat use, increases in competition for space and prey may negatively affect the recruitment of key estuarine-dependent species.

Brown shrimp *Penaeus aztecus* and white shrimp *P. setiferus* (collectively penaeid shrimp) are abundant components of estuarine communities throughout their geographic range (Massachusetts, USA, to Campeche, Mexico, for *P. aztecus* and New York, USA, to Campeche, Mexico, for *P. setiferus*; Williams 1984, Kneib & Wagner 1994, Rozas & Minello 1998), including South Carolina, USA (DeLancey et al. 2008, Upchurch & Wenner 2008, Kimball et al. 2023). After hatching in nearshore waters, early post-larval shrimp are delivered into estuaries via tidal transport, where they settle into benthic habitats (Wenner et al. 1998, 2005). Successful recruitment of penaeid shrimp has been linked to tidal patterns, water temperature, and salinity experienced during ingress and settlement (Zein-Eldin 1963, Wenner et al. 1998). Similarly, water temperature and salinity have been linked to the abundance and growth of juvenile penaeid shrimp during their nursery phase across their geographic range, revealing generally positive relationships with increasing water temperature and variable response to salinity (Zein-Eldin & Renaud 1986, Rozas & Minello 2011, Glover et al. 2023). Conversely, cold winter water temperatures (below 11°C) in estuaries have been shown to have a particularly negative impact on juvenile white shrimp abundance in the following season, largely by killing overwintering adults (DeLancey et al. 2008). Due to these connections between abiotic conditions and shrimp population dynamics, environmental and climate data can be used to effectively predict the abundance and distribution of penaeid shrimp during their estuarine phase (Schlenker et al. 2023). While the relationships between juvenile shrimp abundance and key environmental and climatic variables have been previously identified, exploration of the phenology of nursery habitat use, a key stage in the development of penaeid shrimp, is lacking.

To understand factors influencing the phenology of penaeid shrimp estuarine nursery habitat use, we used a suite of long-term environmental and biological data sets to examine multiple phenological metrics over 4 decades. These data sets included a 38 yr collection series of juvenile shrimp abundance and size, daily water quality monitoring and meteorological data, and a large-scale climatic index: the Multivariate El Niño Southern Oscillation Index (MEI). We calculated the annual timing, synchrony, and duration of nursery habitat use for both brown and white shrimp and then investigated the relationships between each phenological metric and environmental variables. The specific objectives of this study were to (1) determine if the phenology of estuarine nursery habitat use by penaeid shrimp has changed over the period 1984–2022 and (2) link observed interannual variability in phenology to environmental conditions prior to and during the penaeid shrimp nursery period. We reveal significant relationships between environmental conditions and shrimp nursery habitat use phenology, indicating that changes in environmental conditions in estuaries may alter the phenology of this key period in shrimp life history.

2. MATERIALS AND METHODS

2.1. Biological data

Biological data on brown and white shrimp abundance and size were collected in the Oyster Landing Creek basin, located within the North Inlet estuary in Georgetown SC, USA (33° 21′ 5.43″ N, 79° 11′ 28.07″ W). The North Inlet estuary is a well-mixed, polyhaline, bar-built estuary, with semi-diurnal tides and a mean tidal range of 1.4 m (Allen et al. 2014). Oyster Landing Creek is the main intertidal creek bisecting the 5.1 ha marsh basin. It is located on the northwest side of the estuary near the forest border, about 3 km from the mouth of North Inlet, and is subject to periodic influence from rainwater runoff from the adjacent forested watershed. Nekton collections occurred biweekly in a ~250 m stretch of Oyster Landing Creek and followed 2 primary protocols over the study period (n = 874 biweekly sampling events total, 24–26 annually). From 1984–2003 and 2012–2022, nekton collections occurred in an intertidal creek pool using a bag seine (15.2 m long × 1.2 high, 6 mm mesh) pulled through a creek pool once during daylight hours at slack low tide when creek pools were typically isolated from other parts of the creek (Kimball et al. 2023). From 2003–2011, nekton collections were made using a high-tide marsh enclosure (6 mm mesh block net at the mouth of the low-lying extension of the intertidal creek) that passively collected nekton as the tide ebbed and was retrieved at low tide (Allen et al. 2017). Between August 1994 and

October 2022, high-tide and low-tide nekton collections overlapped on 67 dates, and when catch differences between the low-tide and high-tide collections were analyzed, both brown and white shrimp were in the top 10 ranked species in both collections (brown: 10th at high tide, 4th at low; white: 2nd at high and low tides; Allen et al. 2017). However, white shrimp had higher abundance and lengths were greater in the high tide collections and brown shrimp had higher abundance in the low tide collections but did not exhibit differences in size (Allen et al. 2017). The abundance of both species caught at high tide was significantly correlated with the abundance of that species caught at low tide (Allen et al. 2017), indicating that any differences in abundance caused by methodological changes would present as changes in absolute abundance and not relative abundance within a year; thus, the phenological metrics calculated here should not be affected. All individuals caught in the nekton collections were identified to species and counted. In addition, the lengths of 30–100 individuals of each species were haphazardly chosen and measured. For shrimp, we measured rostrum–carapace length (RCL; tip of rostrum to posterior of carapace, in mm; Ditty 2011) at the time of collection, then later converted RCL to total length (TL) using species-specific conversion relationships derived from ~1000 individuals of various lengths caught during the later years of these monitoring efforts (Table S1 in the Supplement at www.int-res.com/articles/suppl/m751p079_supp.pdf). We calculated phenological metrics based on these estimates of shrimp abundance and length.

2.2. Environmental data

We gathered abiotic data from *in situ* monitoring sources, local meteorological observations, and large-scale climate indices. *In situ* water conditions (temperature and salinity) within the Oyster Landing Creek basin were measured daily at 10:00 h over the duration of the study period, first via measurements made by hand, and beginning in 1995, with autonomous data sondes as part of the North Inlet-Winyah Bay National Estuarine Research Reserve System-Wide Monitoring Program. Daily observations of salinity were used to calculate the mean salinity in Oyster Landing Creek during the primary nursery period of each species (April–July for brown shrimp and June–October for white shrimp). Daily water temperature observations were used to calculate the mean nursery water temperature during the same nursery periods described above (Fig. S1). In addition, we calculated 4 winter water temperature metrics, including consecutive days below 8°C, consecutive days below 11°C, total days below 8°C, and total days below 11°C. Here, winter includes the months of January, February, and March, as this is the period of the year when water temperatures are lowest in the North Inlet estuary. Winter temperatures below 8° and 11°C were tested for their relationship to phenology because both thresholds have been linked to decreased survival of overwintering white shrimp and corresponding decreases in juvenile abundance (DeLancey et al. 2008, Fowler et al. 2018). Mean annual precipitation was calculated from daily total precipitation observations sourced from the Global Historical Climatology Network's Brookgreen Garden station (Station ID USC00381093; 33° 31′ 17.04″ N, 79° 5′ 50.99″ W), located approximately 19 km northeast of Oyster Landing Creek basin (Fig. S2). Annual mean MEI was calculated from bi-monthly MEI values retrieved from NOAA's National Center for Atmospheric Research (https://psl.noaa.gov/data/correlation/meiv2.data). The El Niño phase of this oscillation (MEI > 0.5) is typically associated with cold, wet winters in the southeastern USA and can affect the prevalence of disease in penaeid shrimp in South Carolina (Kendrick et al. 2021).

2.3. Phenological data analysis

All analyses were performed separately for the 2 species, following identical procedures. We used circular statistics to calculate the timing and synchrony of brown and white shrimp habitat use within a given year. Circular statistics are used to analyze variables that are distributed around a circle; for example, direction of movement (Dunn et al. 2018) and birth dates (Paré et al. 1996). This approach is well adapted for analysis of phenology, as the metrics are not dependent on an origin set by the researcher (Thel et al. 2022). In practice, this means that dates with close temporal proximity (e.g. January 1 and December 31) that would be treated as opposite ends of a linear distribution are weighted similarly using a circular approach. The date of every sampling event was converted first to ordinal day (0–365), then to degrees (0–360), and finally to radians. A separate vector was created for each year in which the sampling date (as radians) was repeated for every individual captured during that sampling event. To estimate timing, the mean vector orientation was calculated for each year using the 'mean.circular' function in the 'CircStats' package in R (Lund & Agostinelli 2018). Importantly, this corresponds to the mean date of abundance in the estuary, not the date of highest abundance. To estimate synchrony, the mean vector length was calculated for each year using the 'est.rho' function in the 'CircStats' package. This measure of dispersion ranges from 0–1, wherein a value of 0 indicates abundance is equally distributed across all sampling periods (very low synchrony) and 1 indicates that abundance is concentrated to a single sampling event (absolute synchrony). In a comprehensive meta-analysis of phenology metrics (including 11 metrics describing timing and 25 describing synchrony), mean vector orientation and mean vector length were determined to be the most accurate for measuring timing and synchrony, respectively (Thel et al. 2022). To calculate the duration of estuarine habitat use and determine if changes in timing and synchrony were the result of changes in the timing of juvenile ingress, the ordinal day on which 25 and 75% of shrimp were collected was first estimated for each year. These values were chosen instead of the date of first and last occurrence as these can vary greatly from year to year (Thaxton et al. 2020). Due to the biweekly sampling schedule, it was possible that the true date of 25 and 75% ingress occurred between sampling events. To account for this possibility, a cumulative distribution function (CDF) of abundance was calculated for each year and a generalized additive model (GAM) of CDF by ordinal day was created. The GAM for each year was then used to predict a CDF across simulated 365 d. This allowed the 25 and 75% ingress points to be estimated even for years in which these time points occurred between sampling events. The duration of residency (in days) was then calculated as the date of 75% ingress minus the date of 25% ingress. Duration is distinct from synchrony in that it is a measure of the number of days that the majority of shrimp occur in collections as opposed to how juvenile shrimp abundance is distributed over the nursery period (synchrony). Finally, to determine if the size of juvenile shrimp is changing in relation to phenological shifts, the mean TL of individuals caught during the month that included the mean vector orientation (for each species individually) was calculated for each year. Simple linear regressions were used to test for directional change in timing, synchrony, duration, and size (TL) over the time series (1984–2022). From 2012–2018, shrimp caught in the collections were not enumerated, but their presence or absence was noted and lengths were measured as described above. This resulted in missing abundance data required for calculating the phenological measures for these 7 yr but did not affect our ability to characterize shifts in size over the full study period.

After we calculated annual phenology metrics (timing, synchrony, and duration) for each species, we fit 6 sets of GAMs to investigate the relationships between environmental variables and each metric for both species. First, a full model containing all 10 abiotic variables was created (mean winter temperature, number of days with water temperature below 8°C, number of days with water temperature below 11°C, consecutive days with water temperature below 8°C, consecutive days with water temperature below 11°C, mean nursery water temperature, mean nursery salinity, mean MEI, mean daily precipitation, and total annual precipitation). All models used a Gaussian distribution and minimized generalised cross-validation to fit splines. The number of basis functions was manually restricted to 4 but all models estimated degrees of freedom <4 for all variables (see Table 1). Model selection followed a backward stepwise variable elimination (BSVE) procedure wherein the variable with the largest probability value was eliminated, and Akaike's information criterion corrected for small sample sizes (AICc) and percent deviance explained (%DE) were recorded. The selected final model for each phenology–species combination exhibited the minimal AICc value, and ΔAICc was always >2 between the final and the next-best-fitting model. This procedure, common in ecological studies, results in the most parsimonious final model that has the highest explanatory power possible with the given variables (Burnham & Anderson 2002, Wood & Augustin 2002, Furey & Rooker 2013). The relationship between predictor variables in a GAM can be examined using concurvity (the GAM analog to collinearity), which can reveal non-linear relationships between smoothed predictors. Values for concurvity range from 0–1, and while there is no established threshold, concurvity of >0.5 is often considered problematic (Yi et al. 2016, Dos Santos Schmidt et al. 2020, Compaire et al. 2024). Here, after a final model was selected using the procedure above, the resulting model was tested for concurvity. If 'worst-case' concurvity of >0.5 was detected between 2 variables in a model, selection continued until concurvity was no longer an issue. This model selection was verified using the dredge method, which returned all potential models ranked by AICc. In all cases, the top model chosen by BSVE was within the top-ranked model set generated by the dredge. The relative importance of each variable retained in a final GAM was determined using the leave-one-out method. A variable was removed from the model and the change in %DE (ΔDE) was recorded. Variables that resulted in a larger ΔDE have a higher relative explanatory power in the final model and are therefore more important for explaining a response variable.

To illustrate how a key environmental variable can be used to predict the timing, synchrony, and duration of penaeid shrimp nursery habitat use, we used the final selected GAMs to predict each phenology metric for both species across a simulated set of consecutive days below 11°C, ranging from the minimum number observed in our data (3) to the maximum (53), with all other variables held at their mean value. Each phenology metric was then predicted using the final model for that variable.

All statistical analyses described above were performed in R (v.4.3.1) (R Core Team 2021) using packages 'mgcv' (Wood 2023), 'MuMin' (Bartoń 2023), and 'CircStats' (Lund & Agostinelli 2018). For all statistical tests, significance was determined with $\alpha = 0.05$.

3. RESULTS

Since 1984, a total of 134 175 brown shrimp and 408 147 white shrimp were captured in the Oyster Landing Creek nekton collections (excluding years 2012–2018 when shrimp abundance was not quantified). Juvenile brown shrimp were typically first collected in seines in April, exhibited peak relative abundances (catch-per-unit-effort [CPUE]) in May and June, and were collected in lower numbers through October (Fig. 1A). White shrimp were most often first collected in June, peaked in relative abundance in August and September, and were collected in lower numbers through November (Fig. 1A). June and July were the main months of nursery period overlap in Oyster Landing Creek (Fig. 1A). Relative abundance of both juvenile white and brown shrimp showed high interannual variability (Fig. 1B). Annual brown shrimp CPUE ranged from 8.60 (2010) to 829.96 (2022), while annual white shrimp CPUE ranged from 4.24 (1984) to 1443.54 (1987). Though white shrimp relative abundance was consistently higher than brown shrimp abundance, both species followed similar inter-annual patterns, often increasing or decreasing in the same years (Fig. 1B).

Brown shrimp timing (mean day of habitat use) ranged from 17 May (1995) to 27 August (2004), synchrony ranged from 0.46 (2004) to 0.99 (1992), and duration ranged from 23 d (1991) to 129 d (2004) (Fig. 2A,C,E). White shrimp timing, synchrony, and duration ranged from 7 July (2020) to 29 September (1993), 0.63 (2022) to 0.95 (1996), and 27 d (2005) to 103 d (2022), respectively (Fig. 2B,D,F). The timing, 25% ingress, and 75% ingress of nursery habitat use did not change significantly over time for brown shrimp (linear regressions, $p = 0.91$, $R^2_{adj} = -0.03$; $p = 0.12$, $R^2_{adj} = 0.05$; $p = 0.47$, $R^2_{adj} = -0.02$, respectively) or white shrimp ($p = 0.36$, $R^2_{adj} = -0.004$; $p = 0.13$, $R^2_{adj} = 0.04$; $p = 0.73$, $R^2_{adj} = -0.03$, respectively; Fig. 2A,B). Brown shrimp synchrony and duration similarly showed no significant change since 1984 ($p = 0.17$, $R^2_{adj} = 0.03$; $p = 0.20$, $R^2_{adj} = 0.02$, respectively; Fig. 2C,E). However, the synchrony of white shrimp nursery habitat use has decreased significantly since 1984 ($p = 0.03$, $R^2_{adj} = 0.13$; Fig. 2D),

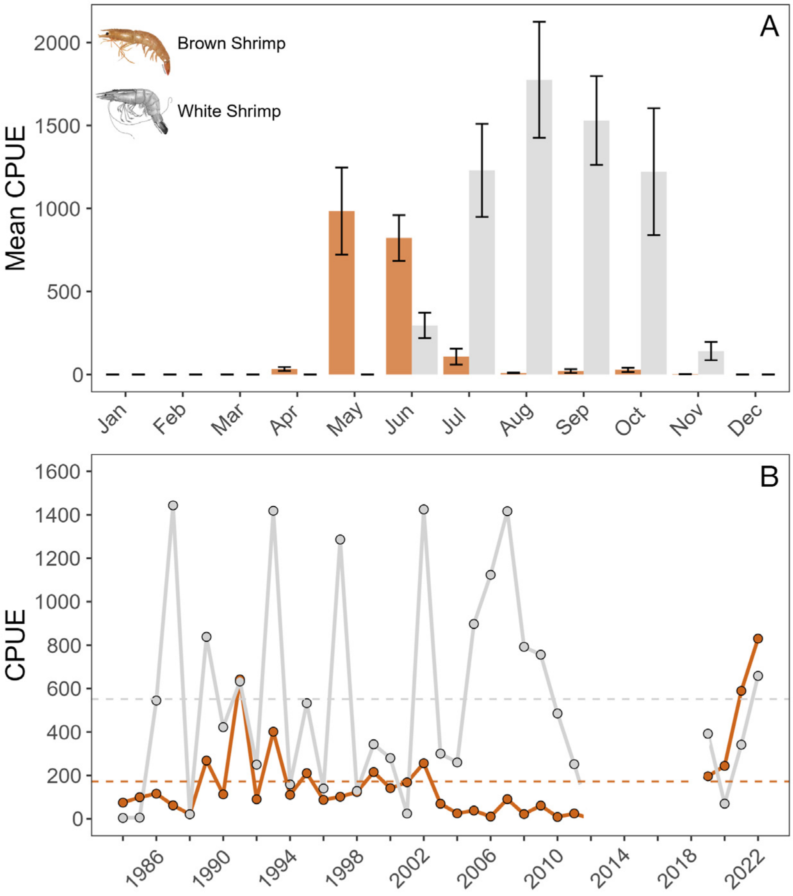

Fig. 1. Brown (brown lines and circles) and white (gray lines and circles) shrimp (A) monthly mean catch per unit effort (CPUE) and (B) annual CPUE from Oyster Landing Creek nekton collections, 1984–2012 and 2017–2022. Error bars: ±1 SE. Dashed lines represent mean annual CPUE from 1984 to 2022

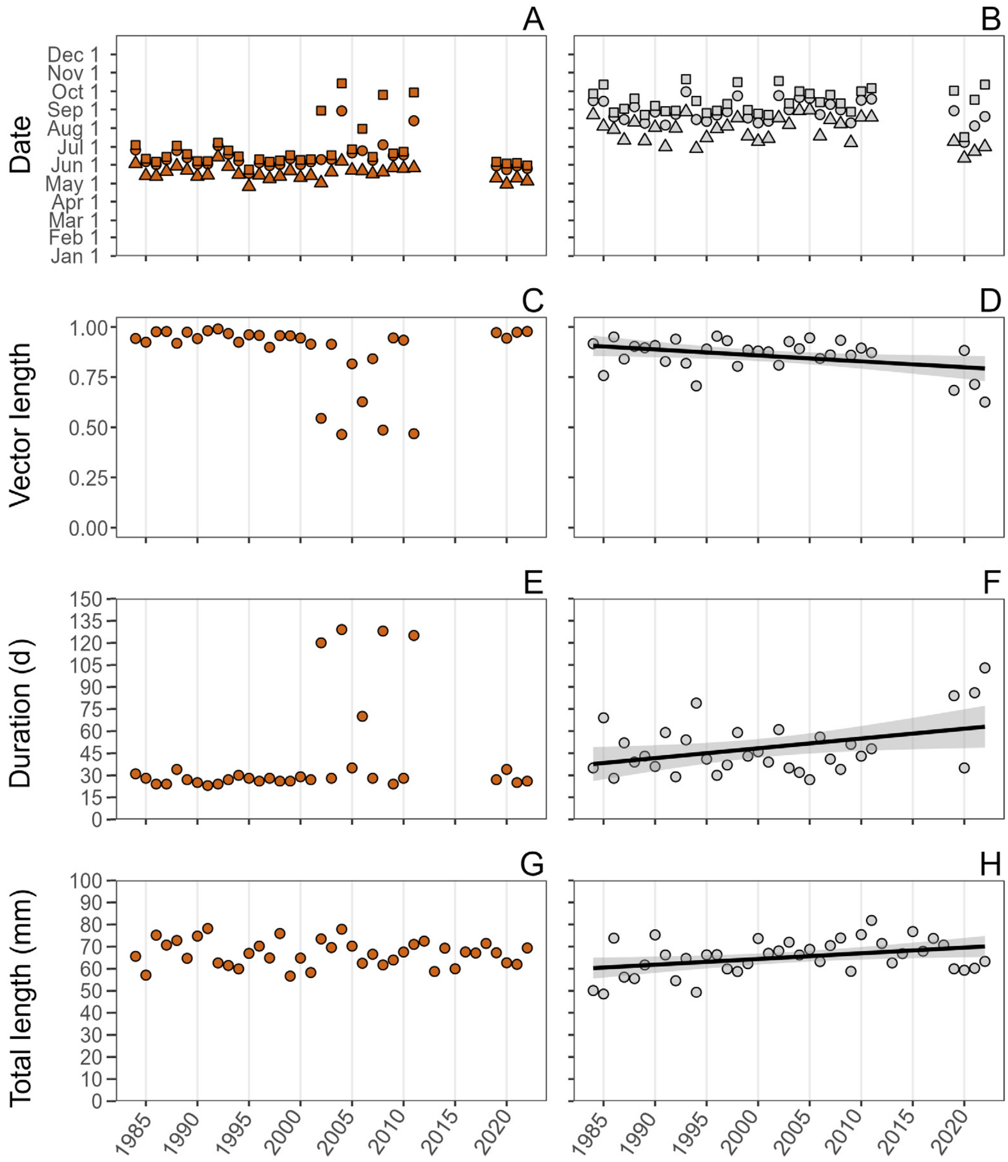

Fig. 2. Mean vector orientation (timing) (○), 25% ingress (Δ), and 75% ingress (□) for (A) brown shrimp and (B) white shrimp annually from 1984 to 2022. (C,D) Mean vector length (synchrony), (E,F) duration (75–25% ingress), and (G,H) total length by vector orientation for brown shrimp (left panels; brown circles) and white shrimp (right panels; gray circles). Presence of regression line indicates a significant relationship ($p < 0.05$)

while the duration of white shrimp nursery habitat use has increased ($p = 0.03$, $R^2_{adj} = 0.12$; Fig. 2F). The mean size of brown shrimp in June (identified as their mean month of habitat use) ranged from 56.7–78.2 mm TL and has not significantly changed since 1984 ($p = 0.55$, $R^2_{adj} = -0.02$; Fig. 2G), but mean white shrimp size in August (48.5–81.8 mm TL) has significantly increased at a rate of 0.26 mm yr^{-1} ($p = 0.02$, $R^2_{adj} = 0.12$; Fig. 2H).

Final GAMs investigating relationships between environmental variables and the timing, synchrony, and duration of brown shrimp nursery habitat use had high explanatory power (DE = 75, 74.2, and 72.9%, respectively; Table 1). Models describing each of the 3 phenology metrics for brown shrimp retained both mean nursery salinity and consecutive days below 11°C (Fig. 3A). Moreover, mean nursery salinity had strong relative explanatory power (ΔDE) for all 3 phenology metrics (ΔDE = 21.5, 46.1, and 43.4%, respectively; Table 1). Mean nursery salinity exhibited a positive relationship with brown shrimp timing across the range of salinity observations (~24 to ~35 psu; Fig. 4A). Mean nursery salinity exhibited a non-linear relationship with brown shrimp synchrony; specifically, we observed a negative relationship with brown shrimp synchrony at salinities below 28 psu, a

Table 1. Output from generalized additive models of each response variable (mean vector orientation, mean vector length, and duration) and their relationship with environmental variables retained in each final model for brown shrimp and white shrimp. Model performance (deviance explained [DE], Akaike's information criterion corrected for small samples sizes [AICc], R^2_{adj}, and minimized generalized cross-validation [GCV] score) are provided for each model. Estimated degrees of freedom (EDF), p-values, and ΔDE are given for all variables retained in a given model and listed in order of relative variable importance as determined by ΔDE. MEI: Multivariate El Niño Southern Oscillation Index. Significant variables ($p < 0.05$) are shown in **bold**

Model	Predictor variable	EDF	p	ΔDE (%)
Brown shrimp				
Vector orientation (timing)				
DE: 75.0%	Consecutive days <11°C	1.87	**<0.001**	43.4
AICc: 258.4	Mean nursery salinity (psu)	2.34	**<0.01**	21.5
R^2_{adj}: 0.706				
GCV: 161.16				
Vector length (synchrony)				
DE: 74.2%	Mean nursery salinity (psu)	2.86	**<0.001**	46.1
AICc: −52.4	Consecutive days <11°C	1.74	**0.043**	7.7
R^2_{adj}: 0.697				
GCV: 0.009				
Duration (75–25% ingress)				
DE: 72.9%	Mean nursery salinity (psu)	2.87	**<0.001**	43.4
AICc: 290.3	Consecutive days <11°C	1.85	**0.047**	8.4
R^2_{adj}: 0.680				
GCV: 434.95				
White shrimp				
Vector orientation (timing)				
DE: 48.3%	Consecutive days <11°C	1.00	**<0.01**	15.1
AICc: 278.8	Mean daily precipitation (cm)	2.35	0.096	14.3
R^2_{adj}: 0.399	Mean nursery water temp (°C)	1.00	0.067	5.4
GCV: 312.85				
Vector length (synchrony)				
DE: 41.5%	Mean MEI	2.81	0.094	18.5
AICc: −69.1	Mean daily precipitation (cm)	1.00	**0.036**	10.8
R^2_{adj}: 0.308	Mean nursery salinity (psu)	1.00	**0.031**	10.0
GCV: 0.006				
Duration (75–25% ingress)				
DE: 42.5%	Mean MEI	2.93	**<0.01**	37.3
AICc: 276.0	Consecutive days <11°C	1.49	0.165	9.6
R^2_{adj}: 0.33				
GCV: 280.55				

slight positive relationship at intermediate salinities, peaking around 31 psu, and a strong negative relationship at salinities >32 psu (Fig. 4C). The relationship between mean nursery salinity and brown shrimp duration was the inverse of that of synchrony: positive at lowest and highest salinities and decreasing at intermediate salinities (Fig. 4E). Consecutive days below 11°C was the first or second strongest predictor in models for timing (ΔDE = 43.4%), synchrony (ΔDE = 7.7%), and duration (ΔDE = 8.4%) of brown shrimp nursery habitat use (Table 1). Consecutive days below 11°C exhibited a positive relationship with timing (Fig. 4B), a negative relationship with synchrony (Fig. 4D), and a corresponding positive relationship with duration (Fig. 4F).

Final GAMs investigating relationships between environmental variables and the timing, synchrony, and duration of white shrimp nursery habitat use had lower overall explanatory power than models for brown shrimp, but total deviance explained was still high (DE = 48.3, 41.5, and 42.5%, respectively; Table 1). However, no single environmental variable was retained in all 3 final GAMs for white shrimp phenology (Table 1, Fig. 3B). The timing of nursery habitat use by white shrimp showed a positive linear relationship with consecutive days below 11°C (Fig. 5A). Consecutive days below 11°C was also the strongest predictor of timing (ΔDE = 15.1%) and the only variable retained in this model that showed a statistically significant relationship ($p < 0.01$)

(Table 1). Mean daily precipitation exhibited a linear negative relationship with white shrimp synchrony across the entire range of precipitation observations (Fig. 5B). Similarly, mean nursery salinity exhibited a linear negative relationship with synchrony across the observed range (~26 to ~36 psu; Fig. 5C). While mean MEI was also retained in the final model for white shrimp synchrony, it did not exhibit a significant relationship ($p = 0.094$; Table 1), although it did exhibit a significant relationship with the duration of white shrimp nursery habitat use ($p < 0.01$, $\Delta DE = 37.7\%$; Table 1). This relationship was negative when MEI was between −1.5 and −0.5, positive between −0.5 and 0.5, and negative when MEI > 0.5 (Fig. 5D). Consecutive days below 11°C was retained in the final model but did not show a significant relationship with duration ($p = 0.165$; Table 1).

When predicted across a simulated range of consecutive days below 11°C (3–53 d), the timing of nursery habitat use for both white shrimp and brown shrimp occurred earlier as the number of days with cold conditions decreased. The slope of this relationship for brown shrimp became less steep as the number of consecutive days below 11°C decreased, while this relationship was approximately linear for white shrimp (Fig. 6A,B). Predicted brown shrimp synchrony was lowest around 50 consecutive days below 11°C, increasing until 25 consecutive days where it remained high (close to 1) as the number of consecutive days below 11°C continued to approach 0 (Fig. 6C). The duration of brown shrimp nursery habitat use showed a complementary pattern to that of synchrony, where duration remained low (~20–40 d) until the number of consecutive days below 11°C exceeded 25 (Fig. 6D). Consecutive days below 11°C was not retained in the final model for white shrimp synchrony, and while it was retained in the final model for white shrimp duration, this environmental variable did not show a significant relationship ($p = 0.165$) (Fig. 6E).

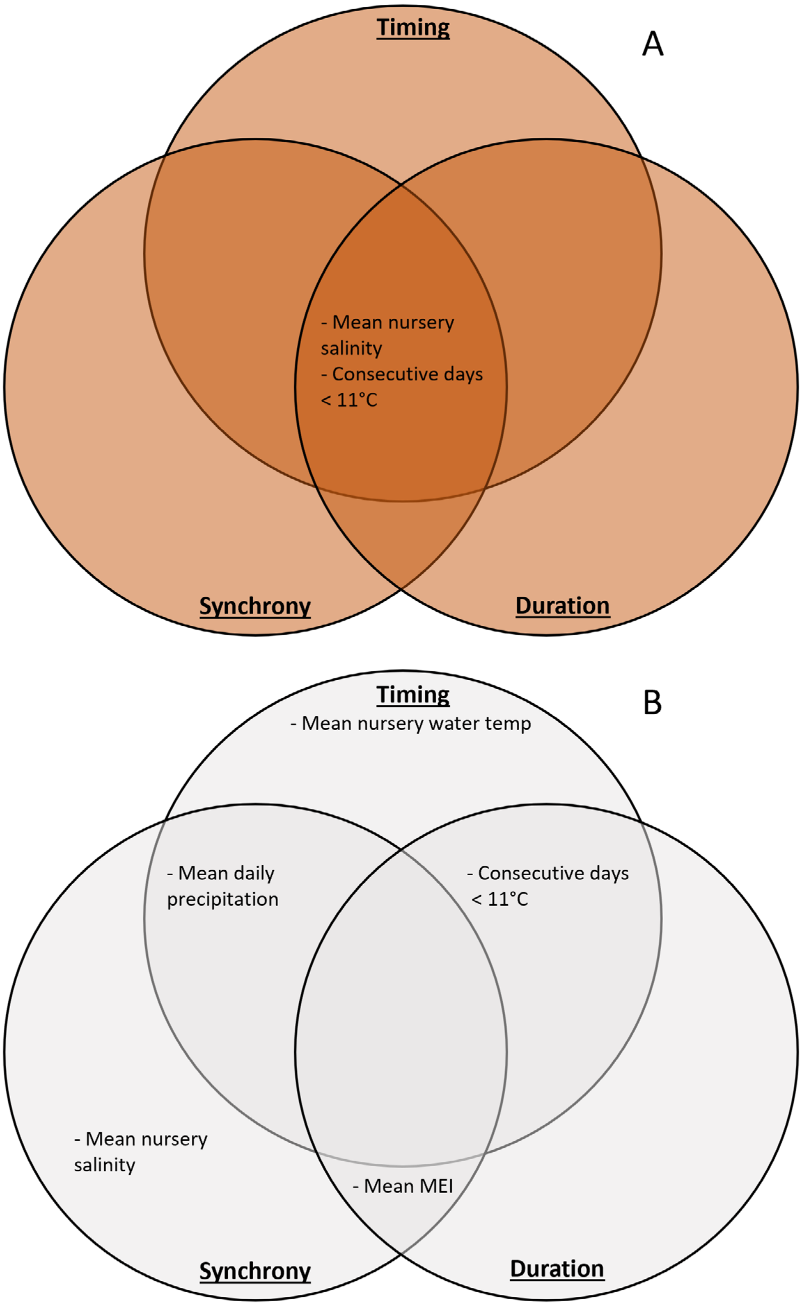

Fig. 3. Venn diagram showing variables retained in the final generalized additive models for phenology of (A) brown shrimp and (B) white shrimp. Circles represent separate models. Variables retained in each are listed within

4. DISCUSSION

Based on a nearly 4 decade time series, we reveal changes in multiple aspects of the phenology of penaeid shrimp estuarine nursery habitat use, a critical life stage for these ecologically and economically important species. In addition, we demonstrate links between interannual variability in phenology and

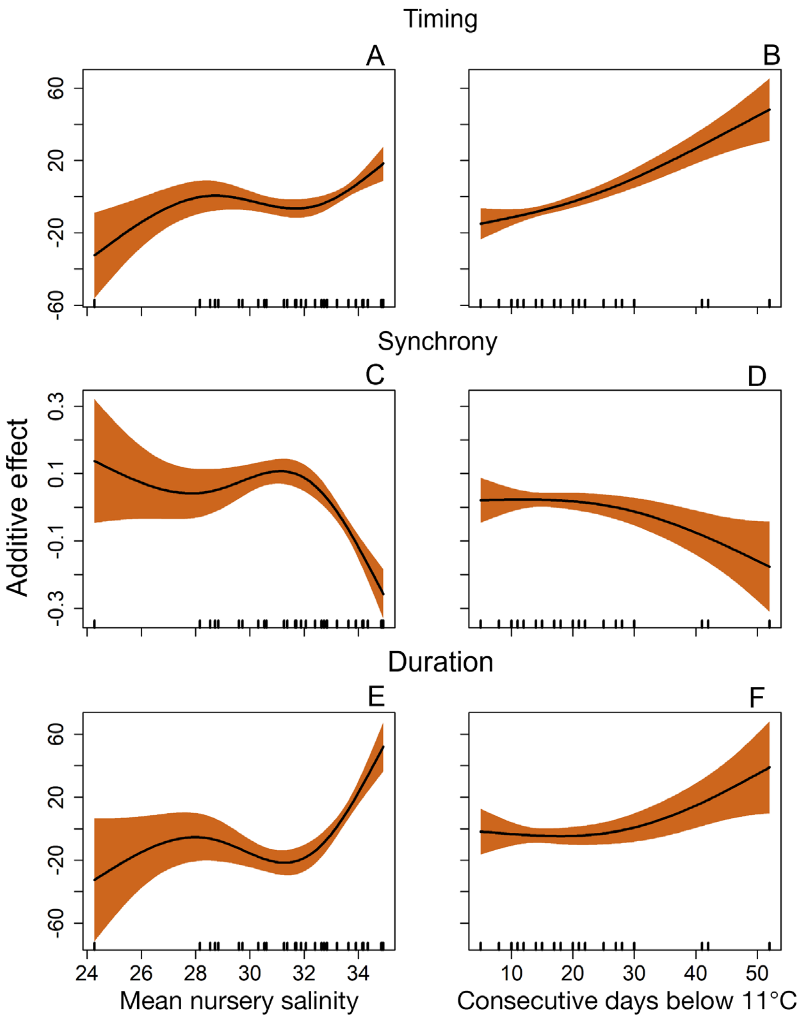

Fig. 4. Generalized additive model (GAM) response plots showing the relationship between a significant environmental variable (shown on the *x*-axis) and the (A,B) mean vector orientation (timing), (C,D) mean vector length (synchrony), and (E,F) duration (75–25% ingress) for brown shrimp. Solid line: model fit; shading: 95% confidence interval around fit. Internal ticks on the *x*-axis indicate an observation at that level of a variable. Positive response indicates later timing, increased synchrony, and increased duration, respectively

key environmental conditions that are expected to change substantially in the next several decades. The different responses between brown shrimp and white shrimp nursery habitat phenology over our nearly 40 yr study period are most likely due to differences in the life history and environmental preferences of each species. Brown shrimp did not show a directional change in timing, synchrony, or duration over the period 1984–2022, while white shrimp nursery habitat use has become less synchronized and occurs over a longer interval (increased duration of residency for the middle 50% each year). Conversely, the timing of white shrimp nursery habitat use and ingress into these habitats has not changed in the North Inlet estuary since 1984. This closely mirrors the pattern of phenology shifts in northern shrimp *Pandalus borealis* in the Gulf of Maine, the spawning period of which has expanded to start earlier and end later without a corresponding shift in timing (Richards 2012). While the timing metric we utilize is distinct from peak abundance (e.g. period of highest catch), the timing calculated here for brown and white shrimp matches the period of peak abundance estimated in estuaries in other parts of the southeastern USA, including South Carolina (Wenner & Beatty 1993, Fowler et al. 2018, Kimball et al. 2023), and Georgia (Webb & Kneib 2002). In estuaries in the northern Gulf of Mexico, brown shrimp CPUE in fisheries-independent surveys also peaked in May, while white shrimp CPUE peaked later in the year, in October (Olsen et al. 2022). This later peak in abundance may be an artefact of the different habitats sampled in Texas (shallow bay habitat as opposed to tidal creeks) or a product of a delay in nursery habitat use farther south in the geographic range of white shrimp. While white shrimp timing of tidal creek habitat use has not changed, our results indicate that the decrease in synchrony and increase in duration are accompanied by an increase in the average length of juvenile white shrimp during their mean period of abundance (August). Slightly earlier ingress (particularly evident during the final 4 yr of our study) may allow juvenile white shrimp more time to grow and, when paired with increasing summer water temperatures in the North Inlet estuary (Kimball et al. 2020), could be resulting in a significantly larger mean size by August without a corresponding significant change in the date of mean abundance.

The significant trends in each white shrimp model are likely influenced by the 4 most recent points. Continued analysis of this time series will be necessary to determine if this trend holds as the number of observations beyond the period of missing data increases. Importantly, the change in methodology (e.g. high-tide sampling instead of low-tide) during the middle years of the survey did not appear to contribute to the increasing trend in size of white shrimp from 1984–2022 because both very small and very large mean sizes

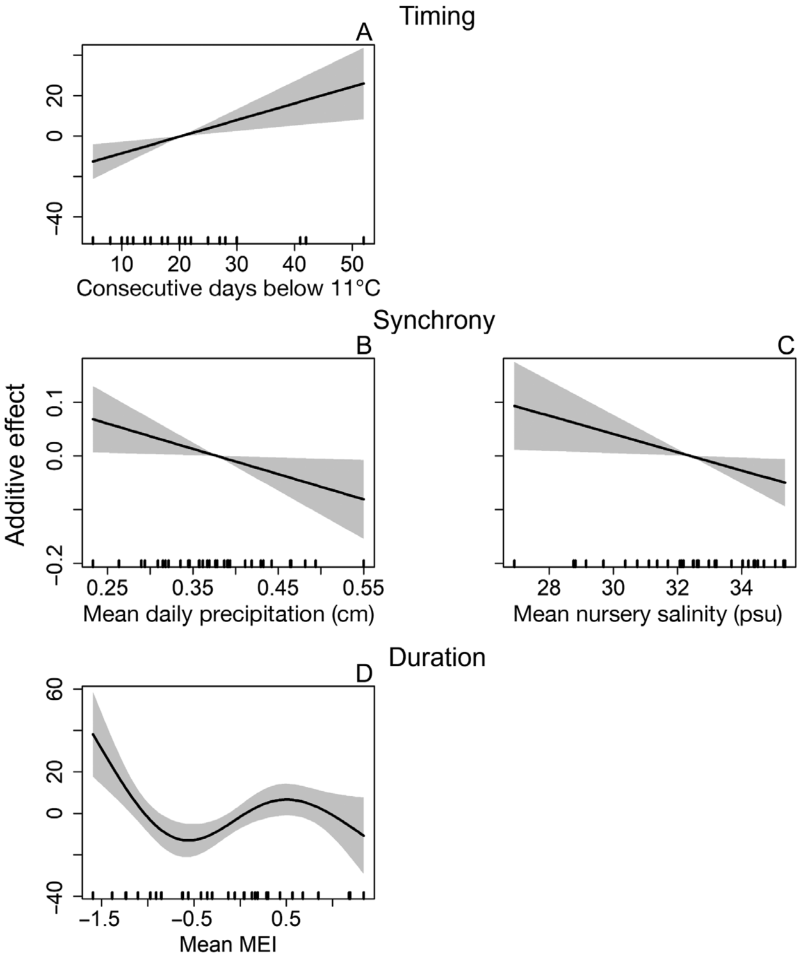

Fig. 5. GAM response plots showing the relationship between a significant environmental variable retained in the final model (shown on the *x*-axis) and the (A) mean vector orientation (timing), (B,C) mean vector length (synchrony), and (D) duration (75–25% ingress) for white shrimp. MEI: Multivariate El Niño Southern Oscillation Index. Solid line: model fit; shading: 95% confidence interval around fit. Internal ticks on the *x*-axis indicate an observation at that level of a variable. Positive response indicates later timing, increased synchrony, and increased duration, respectively

were captured early in the time series, all during low-tide sampling. Similarly, the smallest mean size year in the latter half of the time series was captured during high-tide sampling. This all suggests that mean shrimp size in August is increasing and both gear types were effective in documenting this change. The temporal expansion of habitat use and increase in size caused by a shift in phenology demonstrates the impact that exposure to new environmental conditions such as increased water temperatures may have on estuarine species with complex life histories, a trait shared by many other ecologically and economically important estuarine organisms.

In addition to differing life history strategies, phenological responses for brown and white shrimp are also impacted by species-specific tolerances to environmental conditions. Brown shrimp enter and leave estuarine nursery habitats earlier in the year than white shrimp, recruiting to tidal creeks in spring (May–June) as water temperatures rise and moving to deeper, open-water estuarine habitats around the same time that white shrimp become most abundant in tidal creeks (August–September). The white shrimp nursery habitat phase starts later in the year and is constrained by the drop in water temperatures that occurs in the fall, at which time white shrimp seek thermal refuge and move to deeper estuarine waters (outside of our sampling area) or into the coastal ocean where they overwinter. Warming water temperatures that cue the egress of brown shrimp and the ingress of white shrimp are occurring earlier as a result of climate change, slightly constraining the brown shrimp nursery period while expanding that of white shrimp. A recent study examining a time series of similar length likewise documented the earlier onset of blue crab spawning in Chesapeake Bay due to warming spring temperatures but did not observe any realized change in the duration of spawning over the 30 yr study period (Schneider et al. 2024). Rather, interannual variability in spring temperatures determined the initiation of spawning (warmer springs led to earlier spawning), while duration was simply a function of the onset of spawning rather than fall temperatures (Schneider et al. 2024). Environmental cues (especially water temperature) for life history events and habitat use are critical signals in the marine environment and often interact with other conditions, including dissolved oxygen and salinity, to trigger biological and ecological processes (Richards 2012, Staudinger et al. 2019, Crear et al. 2020, Langan et al. 2021). Here, the significant relationships between multiple environmental variables, as revealed by their retention in our statistical models for both species (Fig. 3A,B), indicate that several abiotic conditions are combining to influence the phenology of penaeid shrimp nursery habitat use and should be considered together to effectively understand the impacts of climate change on penaeid shrimp and their nursery habitats more broadly.

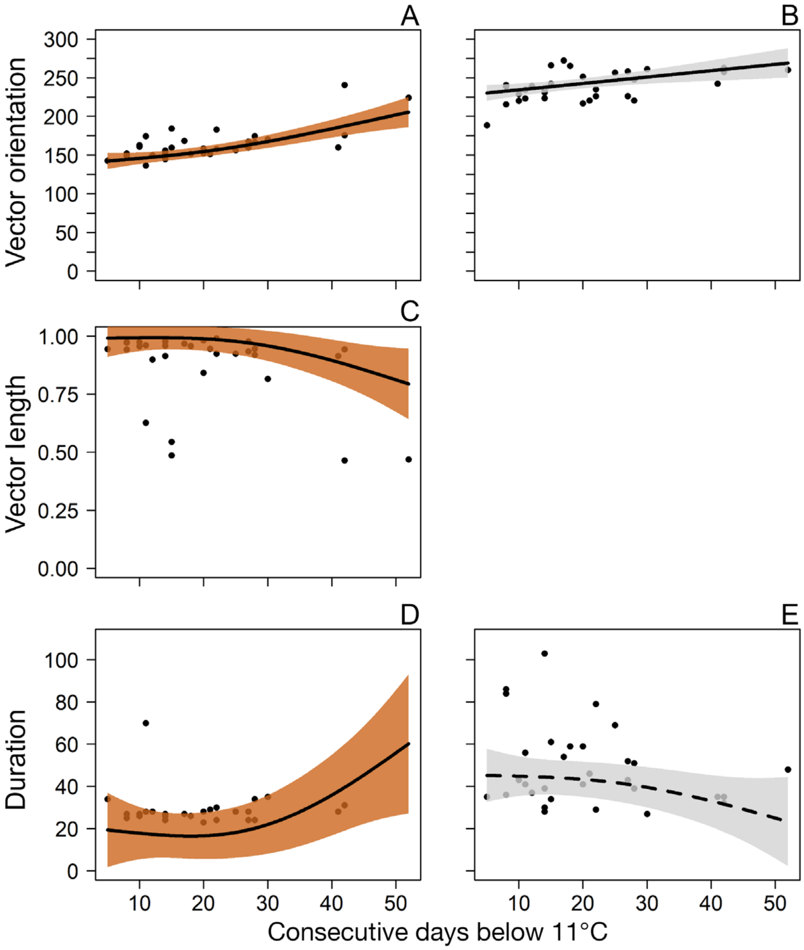

Fig. 6. GAM prediction of (A,B) mean vector orientation (timing), (C) mean vector length (synchrony), and (D,E) duration (75–25% ingress) across simulated values of consecutive days below 11°C for brown shrimp (left panels) and white shrimp (right panels). For white shrimp synchrony, consecutive days below 11°C was not retained in the final model, so we did not predict this phenology metric for this species. In all plots, points: observed values from the time series; solid lines: significant model prediction; shading: 95% confidence intervals; dashed line: model prediction based on a non-significant variable

Interannual variability in the phenology of juvenile penaeid shrimp habitat use is well explained by *in situ* environmental conditions during and just prior to their estuarine nursery phase, particularly for brown shrimp. For this species, all 3 phenology metrics showed a strong relationship with mean salinity during the nursery period (April–July). Increased salinity during estuarine residency increases both the abundance and growth of juvenile brown shrimp (Saoud & Davis 2003, Rozas & Minello 2011, Glover et al. 2023), and we document a positive relationship with timing (occurred later in the year) as salinity increased, especially above 32 psu. Brown and white shrimp move with preferred salinity conditions (Doerr et al. 2016), so it is plausible that juvenile brown shrimp appear later in the tidal creek habitat sampled here because they are avoiding the low-salinity conditions that lead to sub-optimal growth and survivorship until salinity conditions increase. Many mobile species of fishes and invertebrates have demonstrated the ability to shift their habitat use in response to salinity, and as a result, salinity is commonly shown to shape estuarine nekton communities (Greenwood 2007, Hollweg et al. 2020). Unlike nekton, sessile organisms like the eastern oyster *Crassostrea virginica* are unable to move in response to favorable conditions. However, this species can delay gametogenesis and spawning until salinities increase to a level required for survival of early life stages, resulting in a shift in phenology corresponding to salinity conditions (Gregory et al. 2023). Although we were not able to incorporate the salinity conditions experienced by spawning adult shrimp in the coastal ocean into these analyses, like the example provided by the eastern oyster, these conditions may also play a key role in the timing of nursery habitat use by juvenile shrimp. In the North Inlet estuary, brown shrimp nursery habitat use is most synchronized, and the duration is lowest when salinity is ~32 psu. This indicates that individuals are recruiting to these habitats when they are able to take advantage of the rapid growth associated with high salinities, thereby decreasing their duration of nursery habitat use.

While not supported as an important predictor for timing or duration of white shrimp, nursery habitat salinity did have a significant negative relationship with white shrimp synchrony. White shrimp tend to favor lower (more moderate) salinities than brown shrimp (Rozas & Minello 2011, Fowler et al. 2018), and their abundance in tidal creeks appears less correlated to *in situ* salinity than that of brown shrimp (Schlenker et al. 2023). Generally, our results indicate that salinity is a dominant factor influencing the phenology of brown shrimp nursery habitat use and plays a less substantial role in determining the synchrony of nursery habitat use by white shrimp. Anthropogenic climate and land use changes will alter salinity regimes in estuarine systems, with increases in salinity expected in regions where upstream freshwater use and sea level rise are major disturbances to the system (Mulamba et al. 2019). Other estuaries are predicted to decrease in salinity as increases in precipitation and the magnitude of major cyclonic events alter flow regimes in coastal watersheds (Paerl et al. 2019). In systems where storm events create more varied salinity, nektonic species like shrimp may be able to move to more favorable habitats, thereby altering both their distribution and timing of habitat use within a system. It is difficult to predict the directionality of salinity change in the North Inlet estuary, but the strong connection of this variable to phenology indicates that shifts in salinity will lead to shifts in the phenology of estuarine habitat use for both brown and white shrimp and potentially impact the phenology of other nekton species with similar life histories that use these systems as nurseries.

In addition to salinity, winter water temperatures have a significant relationship with brown shrimp timing, synchrony, and duration. In particular, the number of consecutive days below 11°C was retained in the final models for all 3 phenology metrics. This temperature threshold has been previously linked to decreased white shrimp abundance due to winter mortality, and resource managers currently use an 8°C temperature threshold to inform fishery management decisions (Fowler et al. 2018). Our findings indicate that similar to the effect on white shrimp abundance, sustained water temperatures below 11°C has an effect on the phenology of brown shrimp estuarine nursery habitat use. The number of consecutive days below 11°C was retained in the synchrony and duration models over any other winter water temperature variable examined here, indicating its significance in shaping the distribution of brown shrimp estuarine nursery habitat across a year. Retention of consecutive days below 11°C in our model describing the timing of habitat use provides strong evidence that brown shrimp are sensitive to winter water temperatures in the range of those that affect white shrimp. Because of the demonstrated relationship between severe winter temperatures (below 8° and 11°C) and white shrimp abundance (Fowler et al. 2018), we anticipated a relationship between these severe winter temperatures and phenology as well. However, only consecutive days below 11°C was retained as a significant predictor in the model of timing for white shrimp, where it showed a positive relationship (delay) in the timing of their nursery habitat use. This suggests that severe winters affect all portions of the year class equally (both earlier and later recruits), such that the overall abundance decreases and mean timing is delayed but the distribution of individuals (i.e. synchrony and duration) remains unaffected. Continued use of a winter water temperature threshold to determine the opening and closing of white shrimp harvest seasons in South Carolina is well supported by our results, and consideration of the 11°C threshold as well as the inclusion of winter water temperature in the management of brown shrimp could be considered. Additionally, as winter water temperatures continue to increase with climate change, the number of days below 11°C will continue to approach 0 (Fig. S1A,B), likely resulting in earlier timing of estuarine habitat use for both white and brown shrimp.

The current latitudinal distribution of penaeid shrimp exemplifies the range of environmental conditions to which individuals are capable of acclimating. Brown shrimp in Texas estuaries, relatively far south in their range, are showing decreased abundance and growth in relation to increasing summer temperatures (Olsen et al. 2022). In lower Chesapeake Bay (northern range extent of both species), white and brown shrimp have been increasing in abundance since 1991; however, white shrimp are 10-fold more abundant than other penaeids (Tuckey et al. 2021). Rising water temperature may be weakening the historical range boundary for white shrimp into Chesapeake Bay; however, brown shrimp, which require high salinities, may not be able to expand as widely in this typically lower salinity system as white shrimp. In South Carolina, white shrimp nursery habitat use may be changing in duration and synchrony since 1984 because of a similar weakening of the constraint caused by warming winters, but our statistical models show weak or no relationship between any of the water temperature variables we examined and the duration and synchrony of white shrimp nursery habitat use. Winter water temperature showed a much stronger relationship to brown shrimp phenology. Brown shrimp exhibit plasticity in their reproductive strategy along their latitudinal range, transitioning from pulsed, well-synchronized bouts of spawning to continuous, less-synchronized reproduction as latitude decreases and growing season increases (van de Kerk et al. 2016). As winter water temperatures in the southeastern USA begin to resemble more closely that of regions farther south, it is possible that the reproductive strategy of penaeid shrimp in South Carolina may more closely resemble the continuous spawning observed in subtropical extents of their range.

Because phenological responses to changing environmental conditions are species-specific (Prather et al. 2023), it is difficult to predict what individual or synergistic effects any 2 variables will have on the phenology of white and brown shrimp and, therefore, their overlap in nursery habitat use. The potential increase in estuarine salinity associated with climate and land use change described above may be advantageous for brown shrimp whose phenology is closely linked to higher salinity but disadvantageous to white shrimp that favor more moderate salinities as juveniles. The timing of both species' estuarine habitat use is likely to shift earlier as fewer days with water temperatures below 11°C occur. For brown shrimp, the increase in synchrony and lower duration in tidal creeks predicted with fewer days below 11°C may constrict the temporal distribution of their nursery habitat use. On the other hand, reduced synchrony and increased duration of white shrimp nursery habitat use from 1984–2022 suggest that the temporal distribution of their estuarine nursery period has the potential to continue expanding. This suggests that the earliest use of nursery habitat by white shrimp may start to overlap with the more synchronized pulse of brown shrimp recruitment. This would decrease the temporal partitioning of tidal creek nursery habitats for these 2 species that rely on similar resources. While not directly studied here, the prey available to juvenile white and brown shrimp, including short-lived benthic invertebrates, may also be experiencing changes in phenology as a result of climate change (Little et al. 2017), and foraging by penaeid shrimp can shape benthic infauna communities (Beseres Pollack et al. 2011). Earlier timing of habitat use by brown shrimp may lead to misalignment with their abundant prey sources, and when paired with an increase in temporal overlap with white shrimp, could lead to increased competition between these 2 species (Carter & Rudolf 2019). In addition, due to their role as both predator and prey in estuarine ecosystems, changes in shrimp phenology will likely have broader implications for the population dynamics of numerous other species.

A few aspects of our study warrant additional discussion. First, while shrimp abundance was used to calculate the phenology metrics discussed in this study, phenology and abundance are distinct from one another and should be interpreted carefully. For example, an increase in the timing (later date) of white shrimp nursery habitat use does not necessarily indicate a change in abundance. In addition, due to the time-series nature of this study, the linear models (Fig. 2) are at risk of the effect of temporal autocorrelation. However, we tested for this effect using a Durban-Watson (DW) test on the residuals of 1000 bootstrapped iterations of each linear model and found no evidence of temporal autocorrelation (DW ~ 2, $p > 0.05$). Intertidal habitats are highly dynamic, especially in a system like the North Inlet Estuary, where complete turnover occurs every 2–3 tidal cycles (Dame et al. 1986). As such, the abiotic conditions and ecological community in our sampling location are distinct between sampling periods and years, leading to the lack of temporal autocorrelation. Finally, while the timing, duration, and ingress of brown shrimp appear substantially different in the years 2002, 2004, 2006, 2008, and 2011, we did not find compelling evidence that these data points were statistical outliers. Specifically, Cook's distances were always <0.3. In addition, using the 3× and 4/n 'rules of thumb' to identify outliers, various subsets of the years 2002–2011 appeared potentially questionable but were not consistent across response variables. When re-running each of the 5 models after removing the potential outlier years above, only the 25% ingress period exhibited a change in the results of the trend analysis, and that new result was marginal ($p = 0.045$) with a low goodness of fit ($R^2_{adj} = 0.1$). Each of the points in question corresponded to years with very low abundance of brown shrimp. Because of this, we believe later cohorts entering the estuary have a higher than usual influence on the phenology of this species in a given year (see later 75% ingress; Fig. 2A). Thus, we believe these years to be biologically meaningful and demonstrate the high level of natural variation in these populations rather than an artefact of sampling methodology.

The phenology of nursery habitat use by brown and white shrimp is strongly influenced by environmental conditions, which will continue to change as a result of anthropogenic climate and land use changes (Sanger et al. 2015, Dunn et al. 2023). The suite of environmental variables studied here better explained brown shrimp phenology than that of white shrimp, indicating other external conditions are impacting the observed shifts in estuarine habitat use for white shrimp. These could potentially include offshore water temperature, atmospheric pressure, tidal range, and food availability. This study highlights the importance of long-term monitoring data for identifying trends in phenology change and supports other studies that have suggested phenological responses to climate change will likely be taxon-specific even amongst closely related species (Prather et al. 2023). Some of the observed changes in juvenile phenology may be the result of changes occurring in preceding life stages (spawning adults, eggs, larvae); further study of the reproductive phenology of adults, larval shrimp survival in nearshore waters, the ingress of post larvae, and the environmental cues associated with these phenomena could help illuminate life-stage-specific phenology shifts in order to better understand the relationships between stages in species with complex life histories. Similarly, our study focused on the phenology of penaeid shrimp use of tidal creek habitats specifically. However, juvenile shrimp take advantage of multiple habitat types within estuarine seascapes, so it is important to also understand how habitat utilization may be changing across estuarine habitats to determine if phenological shifts are specific to this particular habitat type or reflect more widespread changes throughout the estuarine nursery period. This study is an important step in understanding the effects that changing environmental conditions will have on a key life history stage of penaeid shrimp, on estuarine-dependent communities as a whole, and on the nursery role of estuarine habitats.

Data availability. Environmental data and phenological metrics are available in Zenodo database at https://doi.org/10.5281/zenodo.14206339.

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