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# Multi-decade declines of white shrimp *Penaeus setiferus* size in open water estuarine habitats of the southeastern US

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## ABSTRACT

Warming temperatures can alter the life histories of marine organisms, including shifting body sizes, the timing of migratory cues, and habitat use. The Atlantic white shrimp *Penaeus setiferus* (hereafter white shrimp) is an ecologically important species supporting significant fisheries in the southeastern USA. White shrimp move across the estuarine-oceanic continuum, from small shallow estuarine habitats as juveniles to nearshore oceanic waters as adults. Using six separate fisheries-independent datasets spanning estuarine creeks, estuarine sounds, and nearshore habitats, we investigated long-term trends in salinity, water temperature, and shrimp sizes across South Carolina and Georgia, USA, over more than 30 years. Salinity only increased significantly for estuarine sound sampling in South Carolina, but not for other habitats; however, temperature increased significantly in all three habitats. We also documented concurrent changes in the sizes of white shrimp that were especially evident in estuarine sounds during the fall, with shrimp size declining linearly at an average rate of 5 mm decade<sup>-1</sup>. Concurrently, adult sizes in coastal waters remained unchanged across surveys and seasons. One potential mechanism for these observed changes is that warming water temperatures are altering shrimp growth patterns and shifting the phenology of their offshore migrations, leading to reduced sizes of shrimp sampled in estuarine sounds, but additional research is needed to test this hypothesis. This serves as a case study of the potential impacts of more than three decades of changing climate and highlights the utility of long-term fisheries-independent datasets for conducting integrated ecological assessments.

## 1. Introduction

Increased temperatures associated with climate warming impact marine animals in ways that can alter growth rates leading to changes in body size, shortened development times, and changes in migration cues (O'Connor et al., 2007; Daufresne et al., 2009; Sheridan and Bickford, 2011; Langan et al., 2021). Shifts in the size distributions of marine organisms can have cascading effects at the population and community levels, including impacts on fecundity (Koops et al., 2004) and trophic interactions (Romanuk et al., 2011). Much of the research on climate-induced shifts in population demographics has focused on mature individuals (Daufresne et al., 2009; Wootton et al., 2022), but an integrative understanding of population size demographics across a species' life cycle can help inform the mechanisms underlying observed shifts in body size.

Fisheries are a key ecosystem service impacted by climate-driven changes in the marine environment (Galappaththi et al., 2022). With the direct economic connection associated with fisheries, significant financial resources are sometimes invested in monitoring and understanding key species, leading to the availability of high-resolution long-term time series data for some marine populations (Boenish et al., 2020). As a result, these organisms can serve as sentinels for better understanding the impacts of long-term environmental change on marine and estuarine fauna more broadly, and these datasets capture gradual and subtle changes that can be overlooked at shorter timescales.

The Atlantic white shrimp *Penaeus setiferus* (hereafter white shrimp) has long supported one of the largest commercial fisheries in the southeastern US (NOAA, 2025) and is captured in many long-term monitoring programs (e.g., Kimball et al., 2020; Kendrick et al., 2021; Schlenker et al., 2023). In South Carolina and Georgia alone, white

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shrimp constitute the highest valued commercial fishery, averaging annual landings of 2.4 million kg valued at more than \$16 million annually since 2010 (NOAA, 2025). While white shrimp continue to account for large portions of overall landed seafood in the southeastern US, recent years have been characterized by a decline in fall landings (Kendrick et al., 2021). In addition to their commercial importance, white shrimp are a key food source to numerous vertebrate and invertebrate consumers in coastal environments (Hettler, 1989; Scharf and Schlicht, 2000), and their sizes impact their role as both predators (Oh et al., 2001) and prey (Mace and Rozas, 2018). Understanding how climate warming may contribute to changes in body size, and thus potentially commercial landings, of white shrimp is important not only for developing effective management strategies, but also as a test case for documenting how climate change is impacting estuarine organisms.

White shrimp use multiple habitats in estuarine and nearshore environments throughout their approximate one-year life cycle. During the spring, mature adult white shrimp typically spawn in the coastal ocean and produce pelagic larvae that develop offshore before migrating into estuarine systems where they settle in small, shallow estuarine creeks (Weymouth et al., 1933; Anderson et al., 1949; Lindner and Anderson, 1956; Wenner et al., 2005). In these meso- or polyhaline tidal creeks, juvenile shrimp continue to grow through the summer and early fall (Weymouth et al., 1933; Bauer, 2018; Batchelder et al., 2024). Juvenile shrimp then migrate out of creeks and into larger, deeper, open water habitats (e.g., bays or sounds) as sub-adults (Fowler et al., 2018; Kendrick et al., 2021). Sub-adults continue to grow and develop before egressing out of the estuary into nearshore habitats as adult shrimp during the late fall, winter, or spring period (DeLancey et al., 2005). This spatial and temporal partitioning of habitat use by white shrimp across the estuarine-oceanic continuum facilitates the use of habitat-specific

sampling to capture distinct life stages (Fig. S1).

The goal of this study is to assess the patterns and drivers of long-term (30+ years) trends in white shrimp size demographics across the estuarine-oceanic continuum, integrating multiple shrimp life stages (i.e., juvenile, subadult, and adult). The specific objectives include: 1) Test for systematic (i.e., monotonic) trends in water temperature and salinity; 2) Test for systematic and non-linear trends in the sizes of white shrimp across multiple shrimp life stages; and 3) Determine how water temperature and salinity may relate to trends in shrimp size. These findings are intended to help understand how environmental conditions affect white shrimp size and to provide resource managers with contemporary information on population demographics to ensure effective management strategies for this multi-million dollar fishery.

## 2. Materials & methods

This study examined salinity, water temperature, and white shrimp size data from six separate fishery-independent research and monitoring programs conducted by state natural resource agencies and universities in the southeastern US (Fig. 1, Table S1; described in more detail below). Each of the six survey time series represents more than 30 years of sampling efforts. These six surveys collected white shrimp across three distinct life stage-habitat combinations: 1) juveniles in estuarine creeks, 2) sub-adults in open water estuarine bays and sounds (hereafter, estuarine sounds) and 3) adults in nearshore/coastal ocean waters (hereafter, coastal waters). For all surveys, measurements of water temperature and bottom salinity were collected *in-situ* at each sampling site. Catches from each survey were identified to species, and a subset of white shrimp individuals were measured for total length (TL, mm). When necessary, alternative measurements (e.g., cephalothorax length)

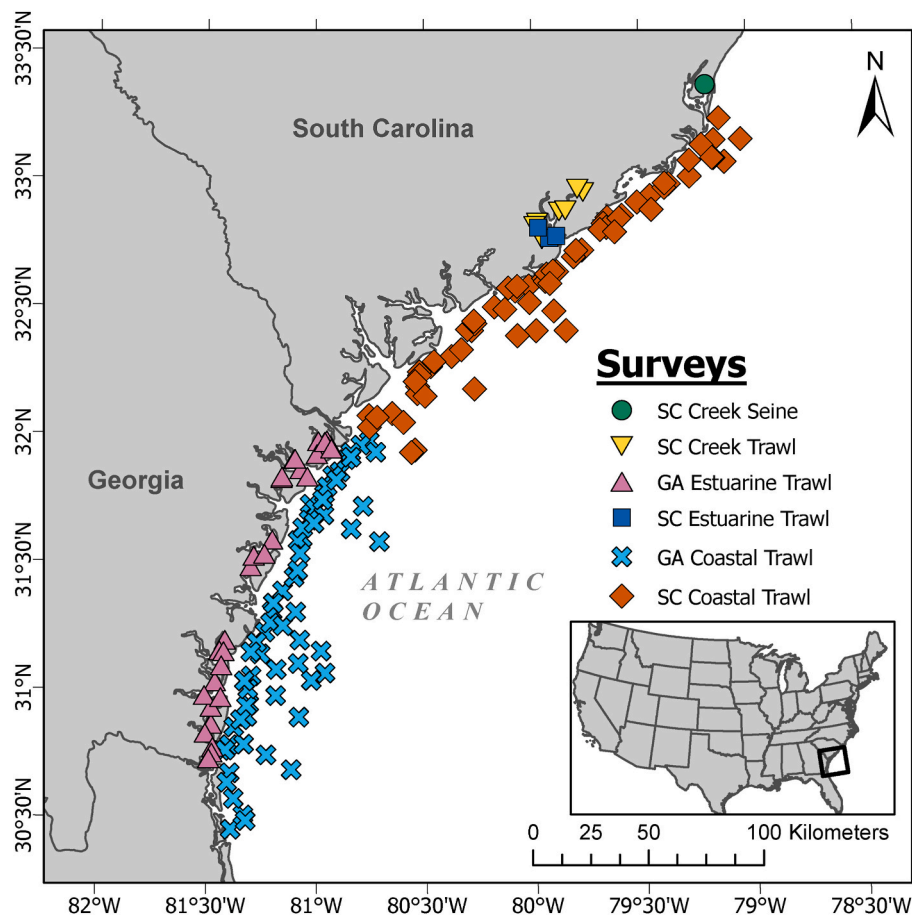


Fig. 1. Sampling locations of the six fishery-independent monitoring surveys used in these analyses.

were converted to total length prior to data analysis.

### 2.1. Surveys

The Creek Trawl survey (1979–2021; hereafter, SC Creek Trawl) was conducted by the South Carolina Department of Natural Resources (SCDNR) monthly from May–September at seven fixed stations in tidal creeks of the Ashley River and Wando River watersheds of the Charleston Harbor estuary (Fig. 1; Table S1). The typical depth of creeks sampled was 0.5–1.5 m. A 3-m head rope length otter trawl net with 6.4-mm heavy delta mesh was towed for 5 min at approximately 1.5 knots behind a 17-ft outboard vessel towards the mouth of the creek near low tide. The TL of up to 50 haphazardly chosen individual white shrimp were collected from each catch.

The Creek Seine survey (1984–2021; hereafter, SC Creek Seine) was conducted by researchers from the University of South Carolina's Baruch Marine Field Laboratory (Fig. 1) at a single station biweekly around low tide using a 15.2 m × 1.2 m × 6 mm mesh nylon bag seine (1984–2003, 2012–2021) or high tide using a 6 mm mesh block net (2003–2011) to collect nekton in a salt marsh intertidal tidal creek system (Allen et al., 2017; Kimball et al., 2023). Typical water depth at time of sampling ranged from 0.3 to 1.5 m. The cephalothorax lengths of up to 100 (1984–2011) or 30 (2012–2021) haphazardly chosen individual white shrimp were collected from each catch. For use here, white shrimp cephalothorax length was converted to TL using the following regression based on sampling from this survey (Batchelder et al., 2024):

$$\text{Total Length} = (2.249 * \text{Cephalothorax Length}) + 4.27133$$

The Estuarine Trawl Survey (1979–2021; hereafter, SC Estuarine Trawl) was conducted by the SCDNR at three fixed stations monthly in the Charleston Harbor estuary and the Ashley River, a tributary of the Charleston Harbor (Kendrick et al., 2021). Since 2002, this survey's gear has been standardized to one 6-m headrope otter trawl net with 2.54-cm stretch mesh and a 9-mm tickler chain towed from a 52-ft stern-rigged trawler for 15 min at approximately 2 knots. The typical depth of the stations sampled ranged from 5 to 10 m. The TL of up to 50 haphazardly chosen individual white shrimp were collected from each catch. All data collected prior to 2002 have been standardized to this single 6-m otter trawl towed for 15 min.

The Georgia Ecological Monitoring Trawl Survey (1979–2021; hereafter, GA Estuarine Trawl) was conducted by the Georgia Department of Natural Resources using a 12.2-m flat shrimp net with 4.8-cm stretch-mesh webbing throughout the body and bag towed at approximately 2 knots behind a 54-ft stern-rigged trawler for 15 min (Page, 2012). Monthly samples were collected at 36 total fixed stations (Fig. 1) in and around the following estuarine sounds (listed from south to north): Cumberland, St. Andrew, St. Simons, Sapelo, Ossabaw, and Wassaw. Typical depths sampled ranged from 5 to 10 m. The TL of up to 30 haphazardly chosen individual white shrimp were collected from each catch.

The SC Coastal Trawl Survey (1986–2021; hereafter, SC Coastal Trawl) and Georgia Coastal Trawl survey (1986–2021; hereafter, GA Coastal Trawl) were conducted by the SCDNR as part of the Southeast Area Monitoring and Assessment Program (SEAMAP) (SEAMAP-SA Management Plan, 2020). These surveys sample, for the purpose of this analysis, coastal waters (i.e., nearshore and offshore habitat consisting mostly of sandy and muddy bottom) in state and federal waters off the coasts of South Carolina and Georgia, respectively (Fig. 1). The surveys sampled at depths from 5 to 10 m. Samples were collected aboard a 75-ft trawler by towing a pair of 23-m mongoose-type Falcon trawls at approximately 2 knots for 20 min. Cruises were conducted each year in spring (mid-April to the end of May), summer (mid-July to mid-August), and fall (late September to mid-November). The TL of up to 50 haphazardly chosen individual white shrimp were collected from each catch.

### 2.2. Data management & analyses

Season was defined as the meteorological season in which a sampling event took place (spring = March–May, summer = June–August, fall = September–November, and winter = December–February, with January and February falling into the next calendar year). Sampling efforts were not always conducted in all seasons. This is due, in part, to the lack of shrimp in some habitats during some times of the year (e.g., juvenile white shrimp are not generally present in estuarine creeks during the winter or spring). Season-specific exclusions of surveys from size-based analyses occurred if an average of less than 30 white shrimp were measured. Environmental data were included in analyses where available. Mean shrimp sizes within each survey were calculated as the geometric mean of white shrimp total lengths for each meteorological season within each year. All analyses were conducted using the R statistical program version 4.3.2 (R Core Team, 2023).

All analyses were conducted separately for each survey within each season. To test for systematic changes in water temperature, salinity, and mean shrimp size, Kendall rank correlations (tau) and associated Sen slopes, which are analogous to  $R^2$ , and slopes from ordinary least squares regressions, respectively, were calculated for each dataset. This approach is robust to missing data, temporal autocorrelation, and non-normality (Carlaw and Ropkins, 2012).

We then fit generalized additive models (GAMs; Wood, 2011) using restricted maximum likelihood to data describing the geometric mean white shrimp sizes in each season of each year, with year as an independent smoothed variable with degrees of freedom allowed to vary up to a maximum of four (i.e.,  $k = 4$ ). GAM modeling was conducted using the R package 'mgcv' (Wood, 2023).

Additional analyses were then performed to better understand patterns and drivers of trends during the fall season. The fall was selected due to strength of patterns observed, the availability of data across habitats and surveys, and the importance of the fall to the commercial shrimping industry (Kendrick et al., 2021). To visualize temporal trends in fall white shrimp size, we first constructed kernel density distribution plots of raw white shrimp lengths (Wickham, 2016).

To determine how water temperature and salinity relate to patterns of shrimp size in the fall, we developed generalized linear mixed models (GLMM) using the R package 'lme4' (Bates et al., 2015) incorporating 1) shrimp size as the dependent variable; 2) year, water temperature, and salinity as fixed (independent) effects; and 3) station, month, year, and month nested within year as potential random effects. Because the SC and GA Coastal Trawl Surveys used a stratified fixed station sampling design, stratum location was used in place of station as a random effect in the models for these surveys. Additionally, because the SC and GA Coastal Trawl Surveys were conducted seasonally rather than monthly, month was not included as a random effect. The SC Creek Seine survey is conducted at a single location, so station was not included as a random effect in the models for that survey. Model selection was conducted starting with a global model including all predictors, with the model showing the lowest AIC score being presented. In instances where two or more models performed similarly (delta AIC < 2), the model with the fewest parameters is presented as the top model but similarly performing models that included both temperature and salinity were also investigated.

To investigate how salinity and water temperature synergistically influence the sizes of fall white shrimp, the GLMM with the lowest AIC score that also contained an interaction term between salinity and water temperature was then chosen for *post-hoc* marginal means analyses using the 'emmeans' package (Lenth, 2024). In all instances, the model used was either the top model or within 2 AIC scores of the top model. This approach allowed us to evaluate the effects of salinity on fall white shrimp sizes at three water temperature categories: medium (temperatures between one standard deviation above, and one standard deviation below mean temperature), low (temperatures at or lower than one standard deviation below mean water temperature), and high

(temperatures at or above one standard deviation above mean water temperature) across the time series (Table S2).

### 3. Results

#### 3.1. Trends in environmental data

Salinity exhibited significant systematic increases in spring and winter for the SC Estuarine Trawl, but not for other habitats or seasons (Fig. 2, Table 1, Fig. S2). Conversely, at least one survey exhibited a significant trend of increasing water temperatures for each of the four seasons, though considerable variation among surveys was apparent (Fig. S3). Summer water temperatures showed significant systematic increases for the SC Creek Seine, the GA Estuarine Trawl, and the SC Coastal Trawl while fall water temperatures showed significant systematic increases for the SC Creek Seine, the GA Estuarine Trawl, and the GA Coastal Trawl (Fig. 2, Table 1). Winter data were only available for three surveys, with the SC Estuarine Trawl and the GA Estuarine Trawl both showing significant systematic increases in winter water temperature, while there was no systematic change in winter water temperature detected for the SC Creek Seine (Fig. 2, Table 1). In the spring, the GA Estuarine Trawl showed a significant systematic increase in water temperature, but the GA Coastal Trawl was characterized by a significant systematic decrease in water temperature, and the remaining surveys showed no significant change in water temperature (Fig. 2, Table 1).

#### 3.2. Trends in shrimp size

Multiple surveys showed evidence of a change in the mean size of white shrimp in the fall, while the other seasons were characterized by more stability in white shrimp sizes. In the summer, the two estuarine creek surveys both showed significant change, but the direction of change was not consistent. While the SC Creek Trawl showed declines in shrimp size, the SC Creek Seine showed increases in shrimp size (Fig. 3, Table 1). In the fall, the SC Creek Trawl, the SC Estuarine Trawl, and the GA Estuarine Trawl all showed significant systematic decreases in shrimp size (Fig. 3., Table 1). In the winter, the SC Estuarine Trawl and the GA Estuarine Trawl both showed significant decreases in shrimp size (Fig. 3, Table 1). In the spring, the GA Estuarine Trawl was the only

survey to show significant changes, revealing decreases in shrimp size (Fig. 3, Table 1).

The systematic changes in seasonal white shrimp sizes assessed using Kendall correlations were largely supported through the use of GAMs designed to identify non-linear changes. In the summer, the SC Creek Trawl and the SC Creek Seine both showed significant curvilinear trends, but none of the estuarine or coastal surveys were significant (Fig. 4, Table 2). In the fall, the SC Creek Trawl, the SC Estuarine Trawl, and the GA Estuarine Trawl all showed significant declines in shrimp size, with linear trends for the SC and GA Estuarine Trawls, and slightly curvilinear trends for the SC Creek Trawl (Fig. 4, S4, Table 2). Neither the SC Creek Seine nor the Coastal Trawl Surveys showed significant trends (Fig. 4, S4, Table 2). In the winter, the SC Estuarine Trawl displayed significant declines in shrimp size, but the GA Estuarine Trawl model was not significant (Fig. 4, Table 2). These were the only winter surveys to encounter a sufficient number of individual white shrimp to conduct size analyses. In the spring, only the GA Estuarine Trawl Survey showed a significant decline in white shrimp size, while the remaining surveys showed no significant change in white shrimp size over time (Fig. 4, Table 2).

#### 3.3. Environmental effects on fall shrimp size

Length frequency density distributions of white shrimp sizes in the fall supported the results of Kendall correlations and GAMs. These visualizations used the raw sizes of all shrimp encountered (rather than geometric mean, as in the models), and therefore illustrated how the significant changes in shrimp sizes occurred over time. Specifically, there were declines in white shrimp sizes for the SC Creek Trawl, the SC Estuarine Trawl, and the GA Estuarine Trawl in the fall (Fig. 5). The observed changes in the SC Creek Trawl were due to reductions in abnormally large white shrimp encountered early in that survey. The changes in the two estuarine sound surveys were characterized by a gradual loss of the largest shrimp on the right tails of the length frequency distributions. Neither mean size nor length frequencies appear to exhibit a change through time for either of the two Coastal Trawl surveys (Figs. 4 and 5, Table 1). Mixed-models were developed to determine how water temperature and salinity relate to shrimp size in the fall. For all six surveys, the top GLMM or a similarly-performing model (i.e., delta AIC < 2) contained salinity, water temperature, and an interaction

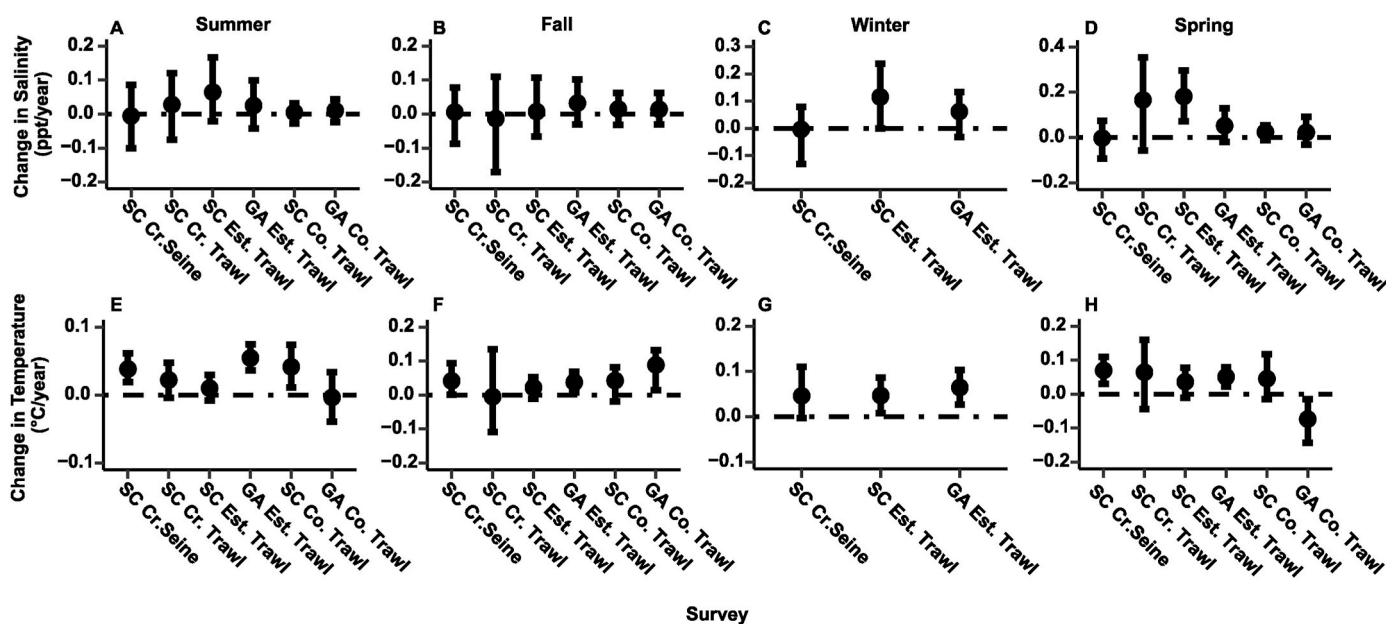


Fig. 2. Sen slopes from Kendall correlations to assess seasonal systematic trends in salinity (A-D, top) and water temperature (E-H, bottom) for each of the surveys. Bars denote standard error around the Sen slopes. Summer = Jun–Aug, Fall = Sep–Nov, Winter = Dec–Feb, Spring = Mar–May.

**Table 1**  
Results of Kendall correlation tests showing Kendall rank correlation coefficient (Tau), Sen slopes (Slope), intercepts (Int.), and p-values for assessing systematic trends. Significant model results are shown in bold.

Survey	Date Range	Season	Salinity			Water Temperature			White Shrimp Total Length					
			p-value	Slope	Tau	p-value	Slope	Int.	Tau	p-value	Slope	Int.	Tau	
SC Creek Trawl	1980–2021	Summer	0.649	0.028	-39.61	0.050	0.104	0.022	-14.75	0.175	0.037	-0.259	564.19	0.224
		Fall	0.751	-0.013	42.62	-0.051	0.792	-0.005	36.66	-0.043	0.011	-0.393	846.91	-0.383
		Winter	-	-	-	-	-	-	-	-	-	-	-	-
SC Creek Seine	1984–2021	Spring	0.115	0.166	-313.94	0.269	0.263	0.064	-103.15	0.193	0.007	0.261	-466.34	0.309
		Summer	0.870	-0.006	44.09	-0.020	0.001	0.038	-48.97	0.383	0.763	-0.043	151.36	-0.036
		Fall	0.831	0.006	21.80	0.026	0.048	0.042	-61.63	0.225	-	-	-	-
SC Estuarine Trawl	1979–2021	Winter	0.953	-0.004	40.79	-0.009	0.064	0.046	-81.32	0.225	-	-	-	-
		Spring	0.940	-0.002	35.13	-0.010	0.002	0.070	-120.44	0.356	-	-	-	-
		Summer	0.140	0.065	-103.44	0.157	0.209	0.010	8.39	0.134	0.675	0.065	-24.08	0.045
GA Estuarine Trawl	1975–2021	Fall	0.812	0.007	12.42	0.027	0.251	0.022	-21.22	0.124	< 0.001	-0.565	1242.97	-0.475
		Winter	0.050	0.115	-204.04	0.208	0.017	0.047	-82.65	0.254	0.028	-0.305	717.29	-0.230
		Spring	0.002	0.181	-337.89	0.347	0.113	0.038	-51.77	0.176	0.788	0.036	56.28	0.031
SC Coastal Trawl	1989–2021	Summer	0.493	0.025	-20.86	0.072	< 0.001	0.055	-80.50	0.538	0.703	-0.029	177.12	-0.040
		Fall	0.428	0.032	-36.72	0.083	0.015	0.038	-52.04	0.253	< 0.001	-0.434	989.04	-0.491
		Winter	0.173	0.062	-97.21	0.140	0.001	0.065	-116.26	0.329	0.019	-0.221	553.77	-0.241
GA Coastal Trawl	1989–2021	Spring	0.760	0.005	24.73	0.041	0.011	0.051	-83.72	0.311	0.029	-0.145	417.82	-0.223
		Summer	0.427	0.015	3.86	0.101	0.178	0.043	-63.56	0.169	0.833	0.037	77.01	0.028
		Fall	-	-	-	-	-	-	-	-	0.884	0.018	112.60	0.020
SC Coastal Trawl	1989–2021	Winter	0.212	0.024	-14.60	0.163	0.133	0.045	-70.68	0.195	0.972	-0.003	158.92	-0.007
		Spring	0.527	0.010	14.30	0.081	0.783	-0.003	35.53	-0.036	0.549	0.085	-19.50	0.077
		Fall	0.486	0.014	5.31	0.089	0.034	0.089	-154.49	0.266	0.168	-0.109	369.85	-0.173
SC Coastal Trawl	1989–2021	Winter	-	-	-	-	-	-	-	-	-	-	-	-
		Spring	0.292	0.023	-12.92	0.135	0.019	-0.074	168.60	-0.299	0.208	-0.100	351.15	-0.161

between salinity and water temperature (Table 3 & S3). Additionally, there were significant differences in the effects of salinity on the sizes of white shrimp across low, medium, and high water temperature categories in the two estuarine sound surveys and the two coastal surveys (Fig. 6, S5), though the direction of those effects differed by habitat. In estuarine sounds, shrimp size increased as a function of salinity more rapidly at low water temperatures (i.e., steeper slope) than at warmer water temperatures (Fig. 6, S5). In the coastal ocean, salinities were relatively stable such that the impacts of water temperatures were variable (Fig. 6, S5). Conversely, there were no significant differences in the effects of salinity on the sizes of white shrimp in the fall at different water temperature regimes for the SC Creek Trawl and the SC Creek Seine, with sizes of white shrimp generally increasing with increasing salinity (Fig. 6, S5).

#### 4. Discussion

Organismal body size is a key predictor of numerous ecological processes (Woodward et al., 2005) and interacts with temperature to determine organismal fitness (Kingsolver and Huey, 2008). Analysis of more than three decades of fishery-independent monitoring data from six independent surveys representing nearly 20,000 sampling events across ~500 km of coastline revealed significant changes in the size of white shrimp sampled at multiple points in their complex life cycle. To our knowledge, this is the first examination of the long-term impacts of climate change on size demographics integrated over multiple life stages and habitats for a nekton species with a complex estuary-ocean life history strategy. In addition, we demonstrate increasing trends in water temperatures across three coastal habitats. Together, these results reflect underlying changes in the habitat-specific demographics exhibited by white shrimp, an ecologically and economically important species. These changes may be explained by shifting phenology, changes in the timing of migrations between habitats along the estuarine-oceanic continuum, changes in habitat-specific growth rates, or more likely, some combination thereof. Furthermore, this study demonstrates the value of long-term fishery-independent monitoring programs to address regional- and decadal-scale ecological questions, as well as improves our understanding of the habitat- and life stage-specific impacts of climate change on estuarine organisms.

##### 4.1. Trends in environmental data

Except for indications of increasing salinities in the spring and winter for the SC Estuarine Trawl, there was relatively little systematic change detected in salinity. In coastal and estuarine systems of SC, salinity can be influenced by a suite of drivers, including river discharge, climatic conditions, and tidal stage (Mathews and Shealy, 1982; Dame et al., 2000), but spatio-temporal variability in salinity is high, as shown from decadal-scale salinity trends from a subset of the estuaries sampled here (Mallick and Dunn, 2024). Given the relative stability of salinity in the coastal ocean and the sensitivity of point salinity measurements to ephemeral influences, the relative lack of systematic long-term change in salinity is unsurprising.

Conversely, although not uniform across seasons and surveys, water temperatures tend to show systematic increases. This aligns with the increases in global sea surface (Levitus et al., 2000; Belkin, 2009; Lima and Wethey, 2012; Cheng et al., 2023) and estuarine temperatures (Prum et al., 2024) documented in recent decades. Warming waters are known to alter life history patterns by increasing metabolic rates of poikilothermic organisms (Hansen et al., 2006; O'Connor et al., 2007), altering phenologies (Batchelder et al., 2024), influencing the timing of cues leading to migrations (Parmesan and Yohe, 2003), and quickening the onset of reproductive maturity (Daufresne et al., 2009; Sheridan and Bickford, 2011). Shifts to an earlier onset of warm seasons and a significant reduction in the number of cold events exacerbate the impacts of general warming trends in coastal systems (Lima and Wethey, 2012).

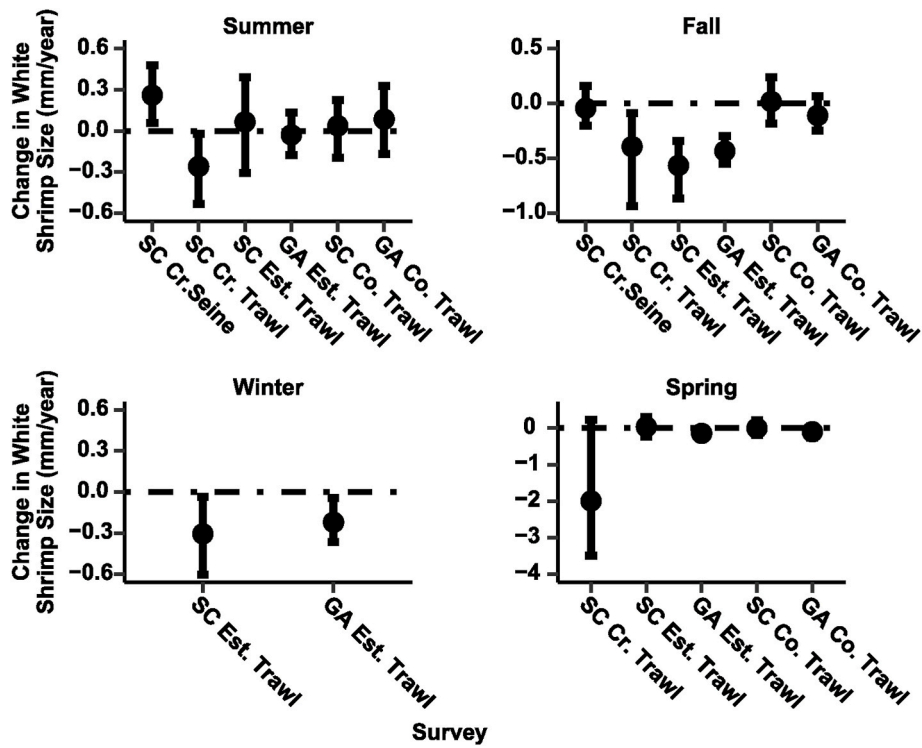


Fig. 3. Sen slopes from Kendall correlations to assess seasonal systematic trends in white shrimp sizes for each of the surveys. Bars denote standard error around the Sen slopes. Summer = Jun–Aug, Fall = Sep–Nov, Winter = Dec–Feb, Spring = Mar–May.

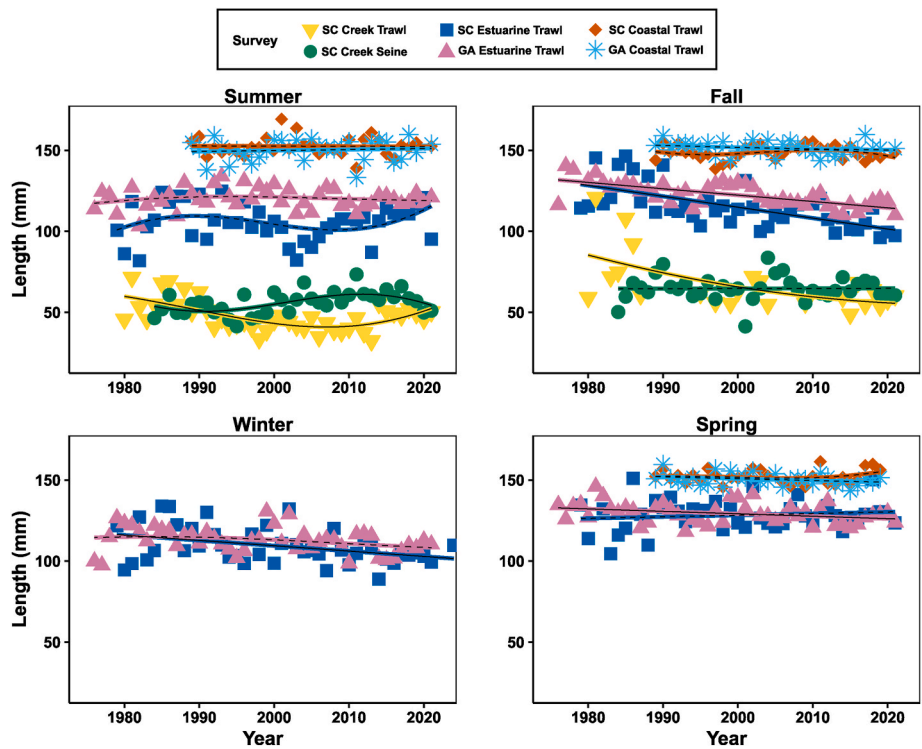


Fig. 4. Generalized Additive Models to assess non-linear trends in white shrimp size (mm TL). Solid lines indicate significant models, dashed lines indicate non-significant models.

This has led to altered migratory phenology in coastal marine organisms, involving longer residence times in coastal systems (Langan et al., 2021), including for white shrimp (Batchelder et al., 2024). These changes in environmental conditions (including water temperature, salinity, and other abiotic parameters) within coastal ecosystems will

alter the distribution of species, as already observed in some marine regions (Pinsky et al., 2013). In addition to altered spatial distributions, key demographic parameters can be impacted by climate change, including organismal body size as previously demonstrated for marine fishes (Genner et al., 2010) and as we show here for white shrimp.

**Table 2**

Results of generalized additive models (GAMs) assessing non-linear trends in seasonal (summer, fall, winter, spring) white shrimp size. Significant model results are shown in bold.

Survey	Season	p-value	% Deviance Explained	Estimated DF
SC Creek Trawl	<b>Summer</b>	<b>&lt; 0.001</b>	<b>44.1</b>	<b>2.687</b>
	<b>Fall</b>	<b>0.009</b>	<b>38.0</b>	<b>1.517</b>
	Winter	–	–	–
	Spring	–	–	–
SC Creek Seine	<b>Summer</b>	<b>0.002</b>	<b>37.6</b>	<b>2.695</b>
	Fall	0.953	0.01	1
	Winter	–	–	–
	Spring	–	–	–
SC Estuarine Trawl	Summer	0.128	17.1	2.627
	<b>Fall</b>	<b>&lt; 0.001</b>	<b>42.1</b>	<b>1</b>
	<b>Winter</b>	<b>0.011</b>	<b>14.5</b>	<b>1</b>
	Spring	0.447	1.53	1
GA Estuarine Trawl	Summer	0.493	6.92	1.957
	<b>Fall</b>	<b>&lt; 0.001</b>	<b>47.9</b>	<b>1</b>
	Winter	0.118	11.0	1.622
	<b>Spring</b>	<b>0.029</b>	<b>10.4</b>	<b>1</b>
SC Coastal Trawl	Summer	0.900	0.05	1
	Fall	0.336	15.9	2.401
	Winter	–	–	–
	Spring	0.472	11.8	2.041
GA Coastal Trawl	Summer	0.628	0.79	1
	Fall	0.310	5.86	1.181
	Winter	–	–	–
	Spring	0.114	8.41	1

#### 4.2. Trends in shrimp size

Our results support previous studies demonstrating that shrimp are highly affiliated with certain habitats at different stages in their life cycle (Williams, 1955, Baker et al., 2014), and also builds on this knowledge by showing decadal-scale shifts in the sizes of shrimp within individual habitats and across multiple seasons. Of the surveys we examined, the greatest number showing change in white shrimp sizes, as well as the greatest magnitude of change, occurred in the fall when sub-adult white shrimp begin moving offshore to overwinter as adults (Kendrick et al., 2021). This includes the non-linear trend from the SC Creek Trawl and the linear trends from the SC and GA Estuarine Trawls that collectively suggest a shared regional tendency for declining sizes of estuarine shrimp in the fall. The two surveys sampling open water estuarine habitats in the winter, a period when sub-adult shrimp continue moving offshore, also showed significant declines in size. There was a relative lack of systematic change in shrimp sizes for the spring and summer seasons. This includes a lack of change in size for shrimp collected from nearshore oceanic environments, indicating that the sizes of mature shrimp are not declining.

The presence of anomalously large fall white shrimp in the SC Creek Trawl survey in the early 1980s, followed by their disappearance in later decades likely drives the observed significant trend in that fall survey. The presence of these shrimp may have been related to several significant winter cold snaps and associated white shrimp kills in the Charleston Harbor watershed in the late 1970s and early 1980s (SCDNR unpublished data), although similar cold snaps occurred in the late 1980s that did not result in anomalously large shrimp. The reduced densities of white shrimp in estuarine creek systems following these

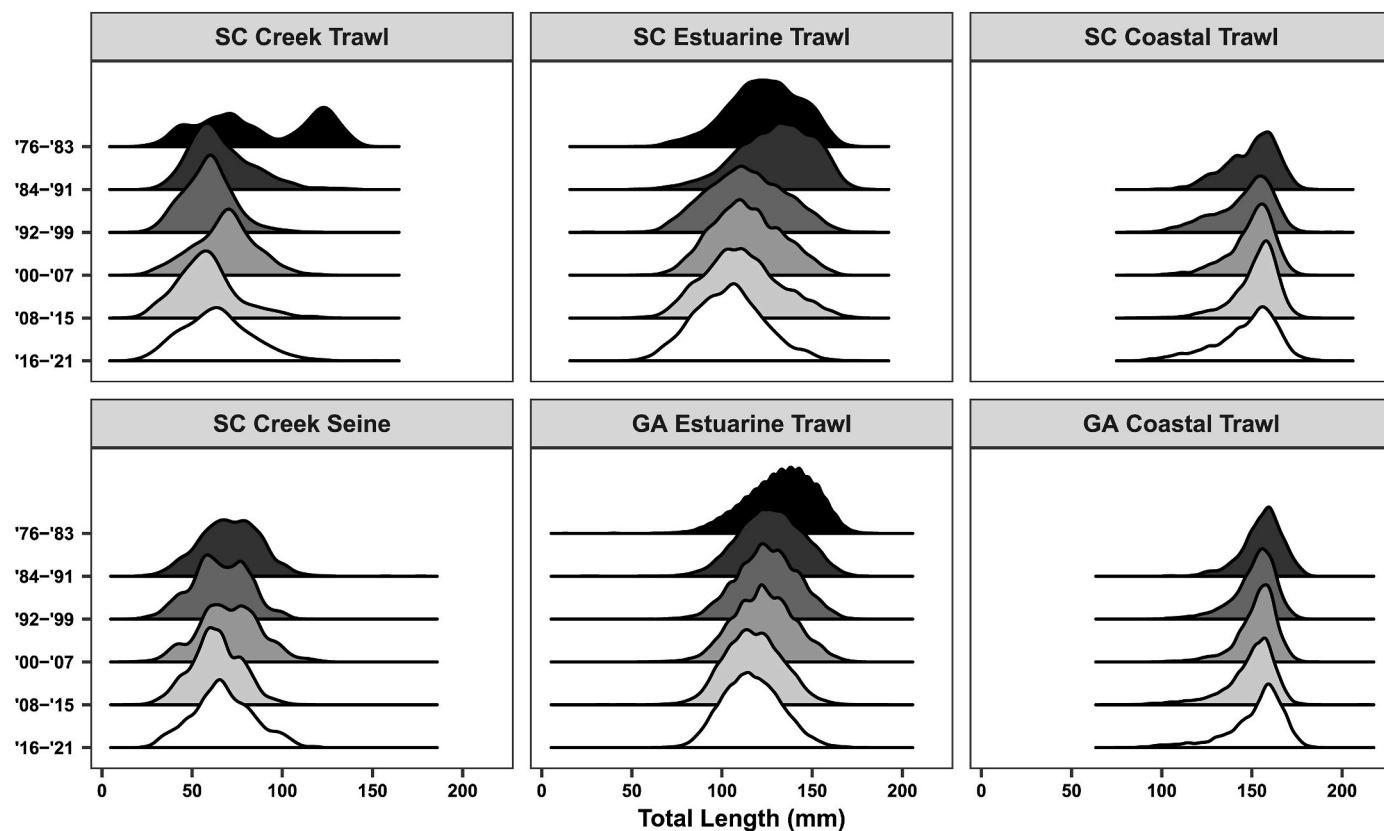


Fig. 5. Length frequency kernel density distributions of white shrimp sizes (mm TL) in the fall (Sep–Nov) for each of the surveys across time periods.

**Table 3**

Results of model ranking for generalized linear mixed-effects models (GLMMs) investigating how water temperature and salinity relate to patterns of fall white shrimp size. Models ranked using AIC; top models and those within 2 AIC scores are shown in bold.

Survey	Model	AIC
SC Creek Trawl	<b>Length ~ Sal. + Temp. + (1   Yr/Mon) + (1   Station)</b>	<b>34,038</b>
	<b>Length ~ Sal. * Temp. + (1   Yr/Mon) + (1   Station)</b>	<b>34,039</b>
	Length ~ Temp. + (1   Yr/Mon) + (1   Station)	34,040
	Length ~ Sal. + (1   Yr/Mon) + (1   Station)	34,048
SC Creek Seine	Length ~ (1   Yr/Mon) + (1   Station)	34,048
	<b>Length ~ Sal. + Temp. + (1   Yr/Mon)</b>	<b>83,872</b>
	<b>Length ~ Sal. + (1   Yr/Mon)</b>	<b>83,872</b>
	<b>Length ~ Sal. * Temp. + (1   Yr/Mon)</b>	<b>83,873</b>
	Length ~ Temp. + (1   Yr/Mon)	83,906
SC Estuarine Trawl	Length ~ (1   Yr/Mon)	83,913
	<b>Length ~ Sal. * Temp. + (1   Yr/Mon) + (1   Station)</b>	<b>704,433</b>
	Length ~ Sal. + Temp. + (1   Yr/Mon) + (1   Station)	705,354
	Length ~ Temp. + (1   Yr/Mon) + (1   Station)	705,606
	Length ~ Sal. + (1   Yr/Mon) + (1   Station)	705,817
GA Estuarine Trawl	Length ~ (1   Yr/Mon) + (1   Station)	706,047
	<b>Length ~ Sal. * Temp. + (1   Yr/Mon) + (1   Station)</b>	<b>785,292</b>
	Length ~ Sal. + Temp. + (1   Yr/Mon) + (1   Station)	785,396
	Length ~ Sal. + (1   Yr/Mon) + (1   Station)	785,427
	Length ~ Temp. + (1   Yr/Mon) + (1   Station)	787,126
SC Coastal Trawl	Length ~ (1   Yr/Mon) + (1   Station)	787,188
	<b>Length ~ Sal. * Temp. + (1   Yr) + (1   Station)</b>	<b>154,984</b>
	Length ~ Sal. + Temp. + (1   Yr) + (1   Station)	155,162
	Length ~ Temp. + (1   Yr) + (1   Station)	155,167
	Length ~ Sal. + (1   Yr) + (1   Station)	155,203
GA Coastal Trawl	Length ~ (1   Yr) + (1   Station)	155,209
	<b>Length ~ Sal. * Temp. + (1   Yr) + (1   Station)</b>	<b>181,115</b>
	Length ~ Sal. + Temp. + (1   Yr) + (1   Station)	181,217
	Length ~ Temp. + (1   Yr) + (1   Station)	181,291
	Length ~ Sal. (1   Yr) + (1   Station)	181,389
	Length ~ (1   Yr) + (1   Station)	181,427

mortality events may have facilitated faster growth of shrimp in these systems, potentially leading to the larger shrimp collected in the SC Creek Trawl survey during this time period. Changing climate has resulted in fewer extreme cold events (Lima and Wethey, 2012), which can cause large mortality events in white shrimp. Without these bottlenecks, abundances of white shrimp in estuarine creeks could increase, which could result in reduced growth due to density-dependent competition (Dunn et al., 2024).

The SC and GA Estuarine Trawls were each characterized by gradual, linear declines in white shrimp sizes for fall over the duration of the time series. These linear decreases in white shrimp sizes in the two surveys of estuarine sounds over the course of four decades suggest that the driver of this decrease is not related to a specific episode such as a disease outbreak or an anomalous weather event. Black gill, for example, is a condition known to affect penaeid shrimp that greatly increased in prevalence in the late 1990s (Frischer et al., 2017) that can reduce respiratory capacity (Burnett and Kendrick, 2024), increase mortality (Lightner et al., 1975; Overstreet and Hawkins, 2017), make shrimp more susceptible to predation (Gooding et al., 2020), and is most prevalent in white shrimp in the fall (Kendrick et al., 2021). However, if black gill were driving the observed reduction in white shrimp size, we would expect to see this reflected through non-linear trends designed to be captured in the GAM approach. Rather, the linear decreases in white shrimp sizes observed in this study suggest more continuous factor(s) (e. g., gradual environmental change) contributing to the observed patterns.

In contrast to the estuarine sounds, shrimp sizes from coastal waters showed no change over the study period. This finding contrasts with previous findings for poikilothermic animals that climate warming leads to declines in the size of mature animals (Daufresne et al., 2009), showing that the size of mature white shrimp in coastal ocean environments is not changing. A study from the same region of another commercially important species, the Atlantic blue crab *Callinectes sapidus*, has similarly shown no evidence for climate-induced reductions in the size of mature individuals (Thienes et al., 2025). Previous research has indicated that heavy commercial pressure on an exploited stock can lead to reduced size of adults (Beverton and Holt, 1957; Jennings et al., 1999; Shin et al., 2005), but the stable sizes of adult white shrimp in nearshore and offshore habitats does not suggest that commercial fishing pressure has changed sufficiently enough to alter the size of adult white shrimp over the past 30+ years along the southeastern US Atlantic coast. It is currently unclear what roles fishing pressure, and environmental factors other than water temperature and salinity, may play in determining the size of mature white shrimp in the southeastern US.

#### 4.3. Environmental effects on fall shrimp size

Model results examining the influences of salinity and water temperature for the two creek systems in our study showed increasing size with increasing salinity, but no difference in the effect of salinity across different temperature categories. The North Inlet estuary, where the SC Creek Seine was conducted, is an ocean-dominated, well-mixed, and high salinity system, which receives freshwater input almost exclusively from local rainfall in a small, largely forested watershed (Allen et al., 2014). In contrast, the SC Creek Trawl was conducted in estuarine creeks of the Charleston Harbor estuary, which are characterized by lower salinities, in part due to riverine input and larger watershed areas. Previous research has indicated that combinations of low salinity and low water temperature together can negatively impact white shrimp growth (Perez-Velazquez et al., 2013). Though the influences of salinity and water temperature on the sizes of white shrimp in the fall in the SC Creek Trawl and SC Creek Seine were similar, the time series for these surveys showed declines in average fall white shrimp sizes in the SC Creek Trawl and no changes in the SC Creek Seine. However, declines in white shrimp size in the SC Creek Trawl were largely driven by abnormally large shrimp encountered early in that survey, as described previously.

When examining open water estuarine habitats, the mixed-effects models in our study showed that the influence of salinity decreased with increasing water temperatures. In years with cooler fall temperatures, salinity is likely a larger driver of the sizes of white shrimp in estuaries, and in warmer years, the salinity regime is likely less influential in determining the distribution of white shrimp sizes in estuarine sounds. This is especially important given the increases in fall water temperatures detected in the GA Estuarine Trawl survey, suggesting that the influence of salinity on fall white shrimp sizes may be weakening over time as temperatures increase. High water temperatures can also reduce dissolved oxygen levels which can negatively impact white shrimp growth (Rosas et al., 1998) and reduce respiratory capacity in shrimp with black gill (Burnett and Kendrick, 2024).

Conversely, environmental conditions in the coastal ocean tended to be less variable than those in estuarine creeks or sounds, as coastal habitats are not as influenced by the tides, and the tremendous volume of water in coastal environments buffers against drastic swings in water temperatures and salinities. The narrow range of observed salinities in both the SC and GA Coastal Trawls likely prevented us from observing a consistent relationship between water temperature or salinity on white shrimp size.

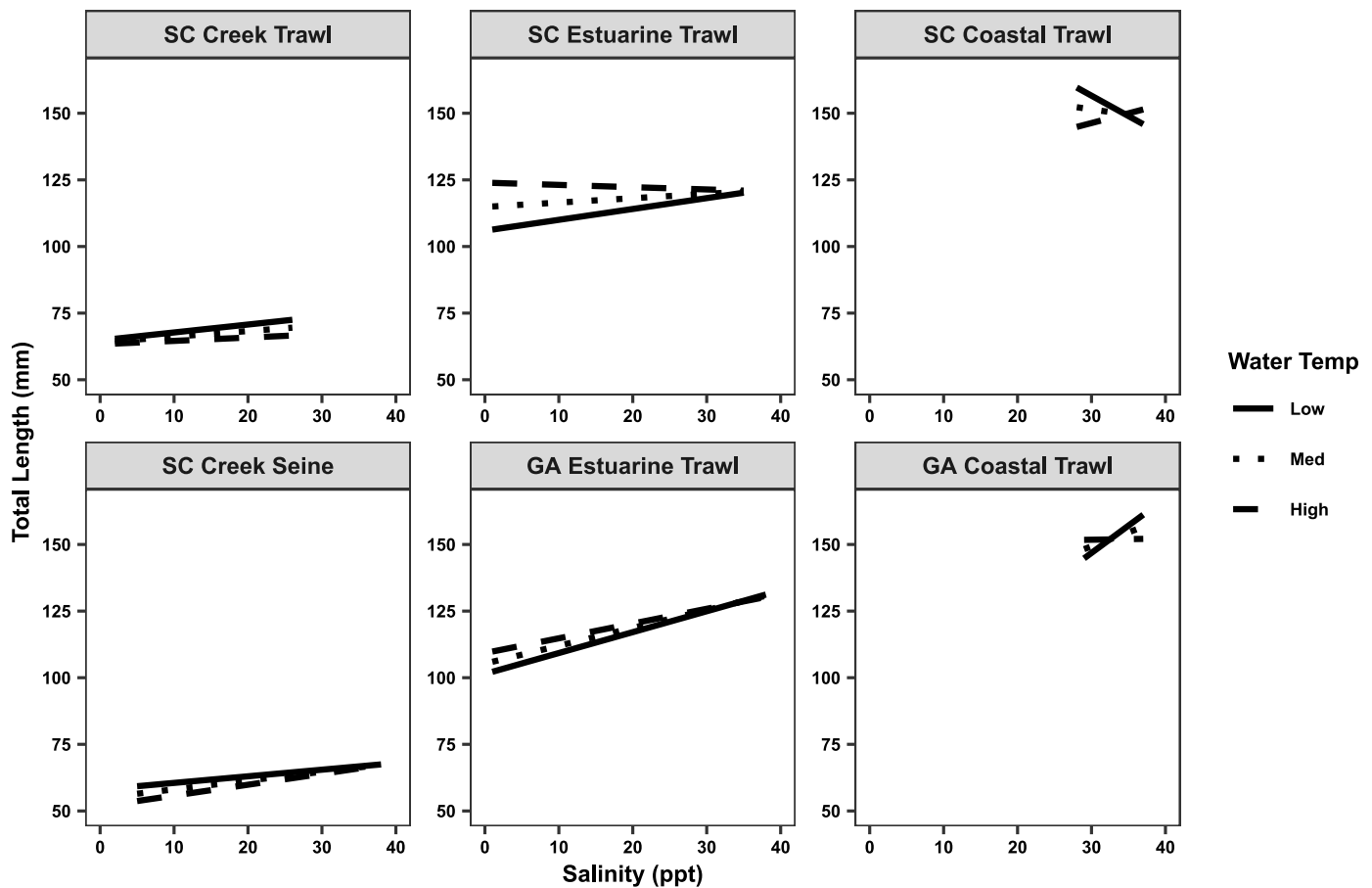


Fig. 6. Post-hoc marginal means analyses using highest ranking models for each survey assessing the interaction of salinity and water temperature on fall white shrimp size (mm TL). Low water temperature = mean water temperature - 1 SD; medium (Med) water temperature = mean water temperature; High water temperature = mean water temperature + 1 SD.

#### 4.4. Potential mechanisms

The juxtaposition of long-term declines in white shrimp sizes in estuaries and the stability of white shrimp sizes in coastal oceans might be explained by altered phenology and migration schedules. Animal migration patterns are influenced by a combination of endogenous and exogenous factors (Fudickar et al., 2021), with endogenous factors often preparing an animal for migration and exogenous factors cueing the migration event. In penaeid shrimp, migratory behavior is influenced by an interaction of body size, salinity, and water temperatures (Manzano-Sarabia et al., 2007; Bauer, 2018). Our findings of declining body size in estuarine sounds, but stable sizes in coastal environments, may be explained by adult white shrimp reaching an appropriate body size, or other life history milestone, earlier over the duration of the time series and then egressing from the estuary, leading to declines in mean size. This explanation is supported by the reduced number of larger white shrimp seen in our estuarine surveys in the fall (i.e., general shortening of the right tails of the length frequency distributions). Decreasing water temperatures are thought to serve as a cue for migration initiation in shrimp (Bauer, 2018), but our results show a tendency for increasing fall water temperatures. Warming fall temperatures are thus unlikely to be cueing earlier egress from the estuary, suggesting that endogenous factors due to higher growth rates, for instance, may contribute to shifts in migration phenology. For example, white shrimp nursery habitat utilization phenology has changed over the same period studied here, with juvenile white shrimp populations exhibiting less synchrony in their timing of nursery habitat use as well as a longer nursery habitat duration (Batchelder et al., 2024). Our results provide support for the hypothesis that observed changes in

environmental conditions, especially early in the white shrimp life cycle, may be contributing to shifts in growth and migration phenology, leading to declining mean size of estuarine white shrimp in the fall. Additional research is needed to test this hypothesis and to better understand how both endogenous and exogenous factors relate to shrimp migration from estuarine to coastal waters.

As changing climate continues to alter environmental conditions in marine ecosystems, shifts in migratory patterns and phenology of estuarine and marine organisms are expected to follow (Asch, 2015; Thaxton et al., 2020). These changes have the potential to alter size demographics (as we suggest here for white shrimp), as well as absolute body size at the individual level (Sheridan and Bickford, 2011). Understanding changes in size demographics is critical because, along with temperature, organismal size affects nearly all physiological and ecological processes, providing fundamental restrictions on fitness (Kingsolver and Huey, 2008). As a result, these shifts in size demographics can have cascading effects on reproductive output, biomass, and commercial availability. Therefore, understanding how changing environmental conditions impact ecologically and commercially important species can allow managers to make more proactive and informed decisions regarding management strategies.

#### CRediT authorship contribution statement

**Graham A. Wagner:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Robert P. Dunn:** Data curation, Funding acquisition, Writing – review & editing. **Matthew E. Kimball:** Data curation, Funding acquisition, Writing – review & editing. **Bruce W. Pfirmann:** Data curation, Writing – review

& editing. **Michael R. Kendrick:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2025.109375>.

### Data availability

Data will be made available on request.

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