



RESEARCH ARTICLE

Environmental Conditions in Estuaries of the Southeast United States: Long-Term Trends and Seasonal Drivers

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Due to their location at the intersection of marine and freshwater ecosystems, estuaries are subject to the impacts of global change from both the ocean and land. Recent evidence has demonstrated numerous changes to environmental conditions within estuarine ecosystems, from increasing temperatures to changes in primary production, among others. We utilized long-term, high-temporal-resolution data on water temperature, salinity, dissolved oxygen, and chlorophyll-a concentrations in 3 National Estuarine Research Reserves in the southeast United States to characterize trends and seasonal drivers of estuarine water quality. We document spatiotemporal variability in long-term trends and seasonal patterns, with ubiquitous increases in water temperature over our study period (1995–2022) mainly driven by changes during winter months (December to February), concurrent with slight reductions in dissolved oxygen through time. We also document strong spatiotemporal variability in trends in salinity and chlorophyll-a concentration both across and within estuaries. Understanding the changes in biophysical conditions in estuarine ecosystems is critical to ensure our ability to predict the ecosystem functions and services estuaries can provide as climate conditions continue to change.

Introduction

Estuaries are sentinel ecosystems that deliver critical ecosystem services and functions, including providing habitat for diverse biotic communities, linking aquatic and marine ecosystems, and serving as nurseries for numerous economically important finfish and shellfish [1–5]. In recent decades, water quality in many estuaries has experienced substantial changes owing to the impacts of a diverse set of local, regional, and large-scale drivers. Documented changes in estuarine conditions include rising water temperatures [6], change in freshwater flow or salinity regimes [7], altered precipitation patterns [8], modified primary productivity [9], increased organic matter loads [10], hypoxia [11], eutrophication [12], harmful algal blooms [13], and impacts associated with sea level rise [14]. In addition, these drivers can work synergistically to put estuarine environments and their associated biota under stress [15].

In order to assess the magnitude of change or the effect of any particular driver, it is necessary to have baseline information [16]. In the context of changing environmental conditions in estuaries, long-term monitoring data allows for establishing baselines as well as quantifying spatial and temporal variability associated with ecosystem processes over time. In these dynamic environments, data collected over short periods of time cannot be used for robust ecosystem assessments because many ecological processes unfold at decadal (or longer) time scales and due to the potential for nonlinear relationships among environmental

variables that may not lead to changes on shorter time scales [17]. For example, in the Neuse River Estuary and Chesapeake Bay on the Atlantic coast of the United States, control of pH differs spatially and both local and large-scale drivers influence long-term trends as well as episodic tropical cyclone events [18]. Similarly, in assessing variability of phytoplankton at different spatial and temporal scales, long-term data enabled the detection of a shift in controlling processes in numerous estuarine ecosystems [19]. In the San Francisco Estuary, the largest estuary on the west coast of the United States, long-term monitoring data revealed seasonally varying relationships between several water quality variables including temperature and inflow [20]. These examples provide evidence that long-term monitoring data can unravel underlying processes and mechanisms that impact critical ecosystem functions.

Estuaries of the Atlantic coast in the southeast United States are typically characterized by the presence of vast salt marsh platforms (often dominated by the emergent plant *Spartina alterniflora*), high primary productivity, and moderate to high tidal ranges [21]. Similar to other parts of the world, many of the estuaries in this region are facing threats due to recent global changes (e.g., temperature increases and sea level rise), which interact with local and regional impacts (e.g., anthropogenic development, subsidence, and shoreline armoring). In recent years, coastal areas in the southeast United States have experienced warming, declines in coastal upwelling and primary productivity, substantial sea level rise, increased nutrient

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loading, reductions in salinity due to increased precipitation, and longer dry periods interspersed with extreme precipitation events [22]. Although these trends reflect large-scale changes in this region, responses to local and regional drivers can vary across different estuarine systems. Spatial variation within a region can determine the distribution and patchiness of biotic communities, and different life stages of fishes and invertebrates use habitats characterized by specific hydrodynamics and vegetation types. For example, juvenile penaeid shrimps prefer vegetated marshes compared to other estuarine habitats [23,24], so changes in emergent vegetation due to marsh drowning can have cascading effects on biota. Thus, it is important to assess trends in environmental conditions at multiple locations in order to effectively predict the impacts of these changes on species with broad geographic distributions.

The National Estuarine Research Reserve (NERR) System was established in 1972 by the U.S. Coastal Zone Management Act to protect unique estuarine ecosystems for research, education, and training. In 1995, the Reserve System initiated a coordinated effort to collect continuous, high-frequency water quality data with the goal of monitoring short-term variability and long-term changes in estuarine conditions [25]. This System-Wide Monitoring Program (SWMP) generates standardized, quality-controlled data on numerous water quality parameters at multiple stations in each of 30 NERR sites across the United States. Measured parameters include water temperature, salinity, dissolved oxygen (DO), pH, conductivity, turbidity, and chlorophyll-a (chl-a), among others,

which collectively total tens of millions of data points annually. These datasets have already proven useful in assessing tidal marsh resilience to sea level rise [26], examining changes in ecosystem metabolism following hurricane events [27], exploring the relationship between DO oscillations with tidal phases [28], documenting a shift from benthic to pelagic control of primary production [29], and quantifying trends in nutrient concentrations and variability [14], among numerous other investigations.

In Georgia (GA) and South Carolina (SC), 3 NERR sites [North Inlet–Winyah Bay (NI-WB) and ACE Basin, SC, and Sapelo Island, GA] encompass a total area of approximately 50,000 hectares [30] and vary in their degree of anthropogenic impact [14,31]. Numerous ecologically and economically important fish and shellfish species use these estuaries, as either full-time residents or seasonal transients, including Atlantic Menhaden (*Brevoortia tyrannus*), sciaenid species (*Sciaenops ocellatus*, *Micropogonias undulatus*), mullets (*Mugil curema* and *Mugil cephalus*), sturgeon (*Acipenser oxyrinchus oxyrinchus*), penaeid shrimp (*Penaeus aztecus* and *Penaeus setiferus*), and blue crabs (*Callinectes sapidus*), among many others [32–36]. These Reserves also serve as critical habitat for numerous shorebirds and marsh birds, reptiles, and mammals [37–39]. Given this region’s level of vulnerability to sea level rise [40,41] and degree of rapid suburban development [42], it is important to examine long-term trends and establish baselines for water

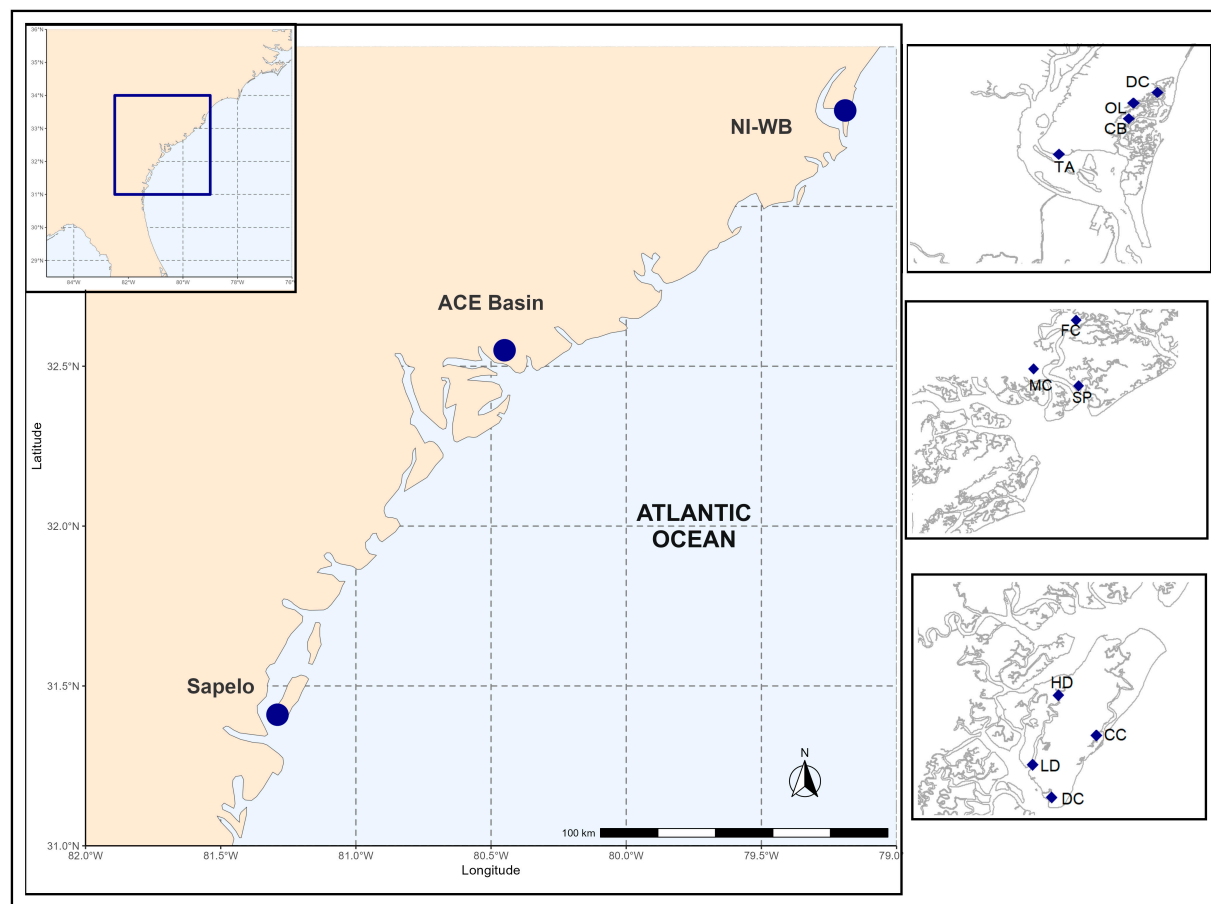


Fig. 1. Map of study site, showing southeast United States region (inset, top left), the location of 3 focal NERRs in SC and GA, and SWMP stations within each Reserve (right panels, ordered by latitude). SWMP station acronyms for NI-WB are as follows: DC, Debidue Creek; OL, Oyster Landing; CB, Clambank Landing; and TA, Thousand Acre; for ACE Basin: FC, Fishing Creek; MC, Mosquito Creek; and SP, St. Pierre; for Sapelo Island: HD, Hunt Dock; CC, Cabretta Creek; LD, Lower Duplin; and DC, Dean Creek.

quality parameters in order to understand how climate change and local stressors are impacting estuarine environments.

It has been nearly 2 decades since the last region-wide assessment of water quality was conducted using these high-frequency, decadal-scale time series [43], although shorter-term studies in individual Reserves have been conducted using SWMP data. Buzzelli et al. [44] analyzed 9 years of data (1993–2001) collected from 2 stations in the NI-WB NERR and found substantial variation in seasonal hydrography, chl-a, and dissolved materials between river-dominated and ocean-dominated sites. Dunn et al. [14] similarly observed differences between the North Inlet and Winyah Bay systems in terms of trends in eutrophication and primary production. In the Sapelo Island NERR in coastal GA, analysis of 1.5 months of SWMP data was conducted to detect diel and seasonal variation in water quality parameters (temperature, DO, pH, and salinity; [45]). One of the main strengths of these datasets is their standardized collection, sample processing, and quality assurance/quality control (QA/QC) protocols, making data from different locations directly comparable. Thus, the goal of this study is to leverage the power of NERR SWMP datasets to investigate long-term trends and seasonal variability in temperature, salinity, DO, and chl-a within estuaries of the southeast United States.

Materials and Methods

Study area

Our study sites were 3 National Estuarine Research Reserves (NERRs) located in SC and GA: NI-WB and Ashepoo-

Combahee–Edisto (ACE) Basin in SC and Sapelo Island in GA (Fig. 1). Each of these 3 Reserves are within the Carolinian biogeographic region, which is characterized by expanses of tidal marshes protected by barrier islands. NI-WB encompasses an area of ~10,000 hectares and is made up of 2 connected estuarine systems characterized by distinct dynamics. North Inlet (33.33 N, 79.17 W) is a small, ocean-dominated, tidally well-mixed, and high-salinity system, dominated by *S. alterniflora* [34]. Conversely, Winyah Bay (33.29 N, 79.26 W) is a relatively large, coastal plain estuary that has more freshwater influence from a large, modified watershed [46]. The ACE Basin (32.50 N, 80.45 W) is the largest of the 3 Reserves with an area of ~40,000 hectares, with forested upland dominated by pines and hardwoods and lowland dominated by tidal salt marshes punctuated by oyster reefs and numerous creeks. This site is one of the largest undeveloped estuaries on the east coast of the United States [47]. This Reserve receives relatively large inputs of freshwater (approximately 8,000 km² drainage basin) from one of the longest free-flowing blackwater rivers in the United States, the Edisto River [48]. Sapelo Island is the smallest of the 3 Reserves (~2,500 hectares) and is located at the convergence of Doboy Sound and the Duplin River [49]. Conditions in the Reserve are strongly influenced by the Duplin River watershed that drains into Duplin River estuary, a tidally dominated system that converges with Doboy Sound from the north. The hydrodynamics of Doboy sound are influenced by the Altamaha River, which brings freshwater during

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Table 1. Name, location, and period of data collection of each of the SWMP stations within each focal NERR, as well as median values for temperature, salinity, DO, and chl-a from each time series

Reserve	Station	Location	Time series duration	Median temperature (°C)	Median salinity	Median DO (mg l ⁻¹)	Median chl-a (µg l ⁻¹)
North Inlet–Winyah Bay	Clambank Creek	33.33390 N 79.19295 W	2001–2022	20.74	33.75	6.03	4.99
	Debidue Creek	33.36013 N 79.16744 W	1998–2022	20.71	33.04	6.21	5.54
	Oyster Landing	33.36602 N 79.18888 W	1996–2022	20.62	33.14	5.91	7.19
	Thousand Acre	33.29917 N 79.25604 W	1995–2022	20.05	6.57	6.70	7.49
ACE Basin	Fishing Creek	32.63593 N 80.36556 W	2002–2022	21.16	8.46	5.40	8.06
	Mosquito Creek	32.5558 N 80.4380 W	2002–2022	21.58	17.87	5.87	7.5
	St. Pierre	32.52800 N 80.36144 W	1995–2022	21.44	29.05	5.85	3.95
Sapelo Island	Cabretta Creek	31.43866 N 81.23875 W	2004–2022	21.51	31.55	6.28	8.86
	Dean Creek	31.39483 N 81.26986 W	2004–2022	22.17	26.27	4.75	4.22
	Hunt Dock	31.47869 N 81.27311 W	1999–2022	22.14	25.02	5.40	4.93
	Lower Duplin	31.41786 N 81.29594 W	1999–2022	21.62	27.00	6.18	9.5

ebb tide in this system, and as a result, Doboy Sound behaves as a well-mixed estuary [50]. All 3 Reserves encompass estuarine habitats that are relatively pristine but also include areas with clear signatures of anthropogenic degradation.

Within each Reserve, multiple SWMP stations were selected for this study—4 each from NI-WB and Sapelo Island, and 3 from ACE Basin (Table 1 and Fig. 1), for a total of 11 stations. The tidal amplitude for the Sapelo Island stations is ~3 m [51], in ACE Basin the tidal range is ~2 m, while in NI-WB sites the mean tidal range is 1.4 m [34]. Two of the 3 sites in ACE Basin (Mosquito Creek and Fishing Creek) and 1 site in NI-WB (Thousand Acre) are meso-haline, while the other 8 sites are typically polyhaline (Table 1).

SWMP data processing

Our study focuses on 4 water quality parameters: temperature, salinity, DO, and chl-a. Time series data for each of these variables were retrieved from the NERR System Centralized Data Management Office (CDMO) [52]. We included only stations with >10 years of continuous data on record. We excluded data points flagged as “suspect data” via the standard CDMO QA/QC protocol. Temperature, salinity, and DO data are collected in situ at 15-min intervals using data sondes (Yellow Springs Instruments). Here, these high-temporal-resolution data were aggregated into weekly mean values for model fitting. The start of each time series varied based on the parameter and when the station was established (Table 1), but in all cases, we retrieved data through December 2022 for analysis. Chl-a grab samples are collected monthly at each site during the tidal ebb, so we used monthly aggregated data collected near low tide to describe primary production (monthly means). Chl-a time series extended back to 2003, at the earliest. For retrieval and processing of these data, the SWMP and SWMPExtension packages [53,54] were used. Additional technical details describing SWMP data collection methodologies are available in the studies of Buskey et al. [25] and Dunn et al. [14].

Data analysis and statistical modeling

We used generalized additive models (GAMs) to evaluate long-term monthly trends and intra-annual seasonality in water quality. GAMs are regression-type models that are flexible in terms of underlying assumptions about the structure and distribution of the data, in contrast to linear regression models where the data must meet certain assumptions (e.g., linear relationship between response and predictor, and residuals with a Gaussian distribution). GAMs offer relaxed parameter assumptions and allow the data to determine the shape of the model via basis functions [55]. As such, GAMs are effective in capturing nonlinear relationships and are flexible enough to include linear terms, smoothing terms, and interactions within a single model [56]. As ecological relationships are often nonlinear with variability occurring at different time scales (e.g., long-term change and seasonal cycles), this technique is suitable for environmental time series analyses [55], and GAMs are increasingly being used to analyze data from water quality monitoring programs [20,57,58].

We built a set of models to systematically investigate the environmental conditions within the Reserves at different spatial or temporal scales. We fit 3 sets of models with individual objectives to examine (a) long-term trends and seasonality, (b) long-term trends at the monthly scale to identify when conditions are changing within years, and (c) spatial variability in

the long-term trends within each of the 3 estuarine systems. The use of separate models simplifies interpretation of the results and is justified by the unique objectives of each model. In the first model, we inspected long-term trends and seasonal patterns (Eq. 1) of each variable by using the weekly mean values (monthly mean value of chl-a) for each station. In constructing the model, we used a smooth term for both year and numeric month (with the basis function set as cyclical for month). In the second model (Eq. 2), we investigated long-term trends broken down by months to be able to quantify which month(s) is driving any observed changes over time. In this model, we used a smooth-factor interaction for year and month in which months were added as a linear term (first predictor) and then are included inside the smoothing term of year as a “by” variable. Months were included as a linear term in the model to take into account the variation among months; otherwise, the model will assume the same mean for all months [56]. Finally, to incorporate spatial variability among the stations within each Reserve, in the next model (Eq. 3) we added site as an additional linear predictor. This model allows us to

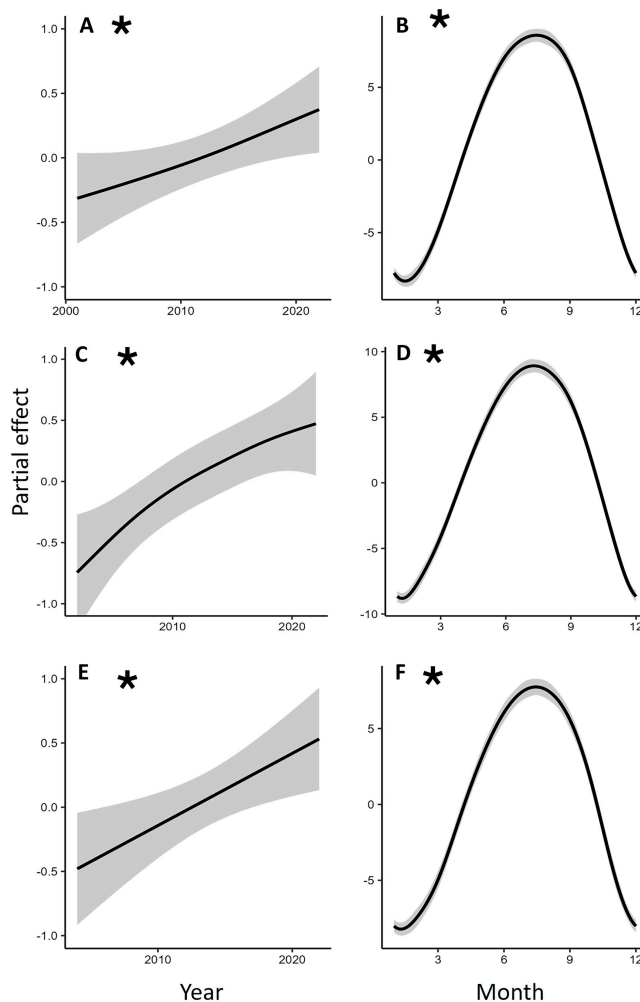


Fig. 2. Partial effect plots of model 1 investigating the long-term trend (A, C, and E) and seasonal pattern (B, D, and F) in temperature (°C) across the Reserves. A single representative SWMP station from each Reserve is shown: (A and B) Clambank Creek, NI-WB; (C and D) Fishing Creek, ACE Basin; and (E and F) Cabretta Creek, Sapelo Island. The shaded gray region is the 95% confidence interval. Statistically significant trends are indicated by asterisk (*).

investigate how environmental conditions within a given Reserve are changing through time and across space.

In all models, to derive the shape of the smoothing term, we used the restricted maximum likelihood (REML) selection procedure as it is recommended for use in GAMs [59]. From each GAM model output, effective degrees of freedom (EDFs) are used as a measure of “wiggleness” or nonlinearity in the trend, with higher EDF indicating more nonlinearity. Specifically, $EDF = 1$ is equivalent to a linear relationship, $1 < EDF \leq 2$ is a weakly nonlinear relationship, and $EDF > 2$ suggests a highly nonlinear relationship. We used model 1 for estimating the rate of change (year^{-1}) for each parameter; this was only conducted for models with EDF between 1 and 2. We set the α level to 0.05 for delineating “statistically significant” trends, but we also interpreted our findings based on the partial effect plots generated by the models. The partial effect plots visualize the long-term, monthly, and seasonal trends, and in cases when $P > 0.05$ but partial effect plots indicated a trend (increasing, decreasing, or stable), we also noted that trend. All analyses were performed, and models were constructed using *mgcv* package [59] in R version 4.3.3 [60].

The generic forms of each generalized additive model are as follows:

$$\text{Model 1: } gam(r \sim s(x) + s(y, bs = 'cc')) \quad (1)$$

$$\text{Model 2: } gam(r \sim m + s(x, by = 'm')) \quad (2)$$

$$\text{Model 3: } gam(r \sim h + m + s(x, by = 'm')) \quad (3)$$

where r is the response variable of interest (temperature, salinity, DO, or chl-a), s is the smoothing function, x is the year as numerical predictor, y is the month coded as numerical predictor (1 to 12), m is the month coded as a factor (January to December), and h is the sites within each Reserve coded as a

factor. To provide an estimate of the rate of long-term change in each parameter, we calculated the slope for the term “year” only for models in which the long-term trend was approximately linear (model 1 smooth term for “year” < 2).

Qualitative approach to assess holistic water quality change across Reserves

To understand the degree to which environmental conditions writ large at each SWMP station changed through time, we utilized nonmetric multidimensional scaling (nMDS). This is an ordination technique that is effective at compressing complex, multivariate datasets into a reduced number of dimensions [61]. nMDS is often used for visualizing ecological communities of many species [62], but here, we generated an nMDS ordination based on SWMP station-level mean annual values of our 4 focal parameters (water temperature, salinity, DO, and chl-a concentration). Thus, the 4 station means for a given year can be considered equivalent to annual species abundances within the traditional nMDS community ecology framework, and points closer together within the ordination space can be considered more similar than points further apart. Within the nMDS, we then drew vectors between consecutive years for each station to visualize the trajectory through time of our multivariate water quality metric. This qualitative analysis allowed us to visually investigate the temporal variation in environmental conditions at a single SWMP station, at all stations within each Reserve, and across all 3 of our focal estuaries.

Results

Temperature

Temperature showed an increasing trend across all of the Reserves as well as the expected strong seasonality (Fig. 2). All temperature time series trends were approximately linear ($1 \leq EDF < 2$), and the estimated rates of change in water temperature

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Table 2. Generalized additive model statistical output from model 2 estimating the monthly long-term trend for temperature. Monthly long-term trend column reports output of the interaction between the smoothing function of year and month. Significance level was set at $\alpha = 0.05$.

Reserve	Site	Deviance explained	P value	Monthly long-term trend
North Inlet–Winyah Bay	Clambank Creek	86.9	<0.001	Significant increasing trend in December and February
	Debidue Creek	85.9	<0.001	Significant increasing trend in December and February
	Oyster Landing	85.7	<0.001	Significant increasing trend during December to February and April
	Thousand Acre	87.1	<0.001	Significant increasing trend in September, November, December to February
ACE Basin	Fishing Creek	85.9	<0.001	Significant increasing trend in December and February
	Mosquito Creek	88.1	<0.001	Significant increasing trend in December to March
	St. Pierre	85.7	<0.001	Significant increasing trend in December, March, April, and October
Sapelo Island	Cabretta Creek	85.7	<0.001	Significant increasing trend in November and December
	Dean Creek	84.5	<0.001	Significant increasing trend in February and March
	Hunt Dock	84.7	<0.001	Significant increasing trend in December and February
	Lower Duplin	84.0	<0.05	Significant increasing trend in December and February

range from 0.03 to 0.09 °C year⁻¹ (Table S1). The increasing trend is mainly driven by rising temperatures during the winter months of December to February (Table 2 and Fig. S1), although some increase during fall months (September to December) was also apparent for Sapelo Island and NI-WB (Table 2 and Fig. S1). Little spatial variation exists between stations within a Reserve in terms of temperature trends, based on the nearly identical amount of deviance explained between fitted models 2 and 3 (Table 2 and Table S2).

Salinity

We documented variable long-term trends in salinity across and within Reserves. Of 11 sites across the 3 estuaries, 4 sites exhibited a decreasing salinity trend (3 sites at Sapelo Island and 1 site at NI-WB), 5 sites demonstrated an increasing trend (all sites in ACE Basin and 2 sites in NI-WB), and 2 sites were temporally stable (Table 3 and Fig. 3). Long-term trends were generally nonlinear, so we were unable to estimate a long-term slope for salinity. Over a seasonal cycle, across the Reserves, salinity minima were documented during the start of the spring (~April) while the highest salinities are typically observed in late summer and early fall (Fig. 4). Some sites within ACE Basin and NI-WB showed considerable variation as a function of riverine input such that including site as a predictor (model 3) substantially improved model fit (Table S3).

Long-term monthly trends in salinity also differ among sites within Reserves. For the NI-WB Reserve, Clambank and Debidue Creek both showed visible decreasing trends in most months (Fig. S2). Oyster Landing showed a substantial increase during September and mixed trends for other months. At Thousand Acre, a visible increasing trend was observed during the months of October and November, with minimal changes during other months. At Sapelo Island, Cabretta Creek showed mixed trends—a significant ($P < 0.05$) decreasing trend during February, August, September, and November; significant ($P < 0.05$) increase in December; and stable in October (Table 4). Dean Creek exhibits a visible decreasing trend in most months, with the months of April, May, and June likely driving the long-term trend (Fig. S2 and Table 3). The Hunt Dock and Lower Duplin stations showed decreasing trends for all months (Fig. S2). In the ACE Basin Reserve, an increasing overall trend at Fishing Creek was driven by May and June as well as fall months (September to November; Fig. S2), while at the Mosquito Creek site, we observed a visible increasing trend for summer months (Fig. S2), and at St. Pierre an increasing overall trend (Table 3), which is most likely driven by changes in spring months, March, April, and May (Fig. S2).

Dissolved oxygen

Across estuaries, we documented a long-term decreasing trend (−0.03 to −0.01 mg/l year⁻¹ for stations with an approximately linear trend; Table S1) in DO (Fig. 4), which is mostly driven by declines in winter months, December to February (Fig. S3). Strong seasonality was also documented with lowest values in summer and maxima in winter (Fig. 4). There was little spatial variation among sites within estuaries (Table S4).

Chlorophyll-a

Chl-a time series trends differed among estuaries. At NI-WB and Sapelo Island sites, we observed a long-term increase in chl-a (Table 5 and Fig. 5), with much of the increase occurring during warm season months (June to October; Fig. S4). For the few sites

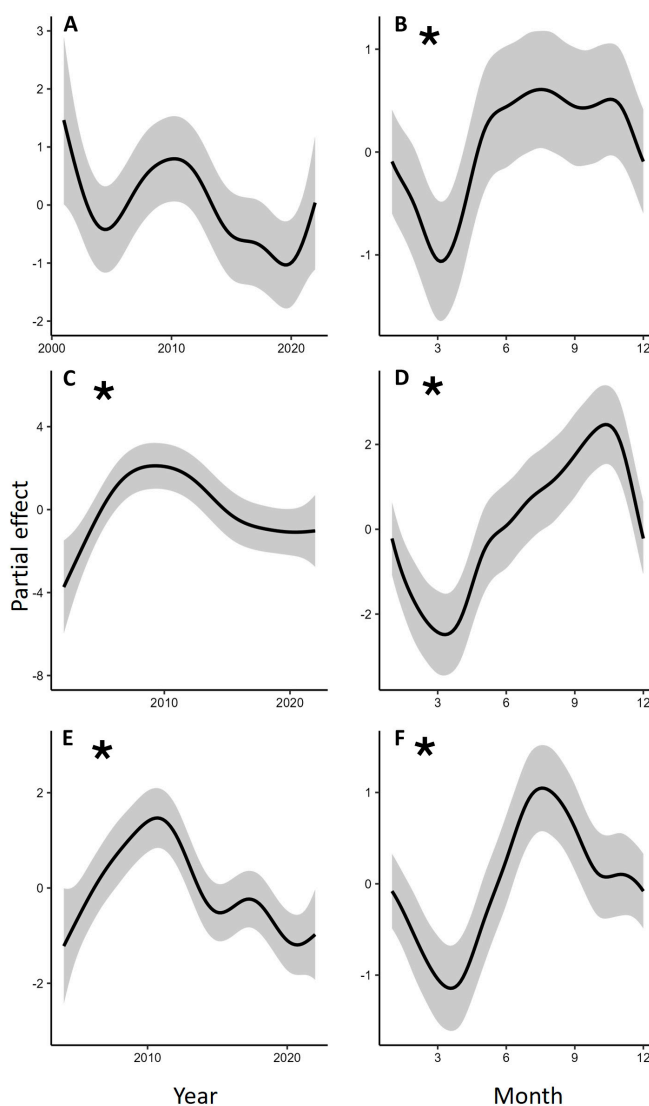


Fig. 3. Partial effect plots of model 1 investigating the long-term trend (A, C, and E) and seasonal pattern (B, D, and F) in salinity across the Reserves. A single representative SWMP station from each Reserve is shown: (A and B) Clambank, NI-WB; (C and D) Fishing Creek, ACE Basin; and (E and F) Cabretta Creek, Sapelo Island. The shaded gray region is the 95% confidence interval. Statistically significant trends are indicated by asterisk (*).

that exhibited an approximately linear trend, rates of change ranged from 0.002 to 0.60 μg/l year⁻¹ (Table S1). Conversely, trends in chl-a at ACE Basin sites are highly variable, with Mosquito Creek showing a decreasing trend, Fishing Creek showing high inter-annual variability, and St. Pierre showing an increasing temporal trend (Table 5 and Fig. S4). The seasonal pattern in chl-a mimics the pattern of temperature with high values documented in summer months (July and August) and production minima in winter months of January and February (Fig. 5). Differences among sites within each Reserve were minimal (Table S5).

Holistic evaluation of estuarine conditions through time

Our multivariate water quality metric captured substantial variability at the station level, Reserve level, and across the region (Fig. 6) over the period 2003–2022. Three SWMP stations in

Table 3. GAM statistical model output from model 1 for salinity. These models account for seasonal variation in modeling the long-term trend. The reported *P* value is based on the smooth function of the year term. Trends that are significant are highlighted in bold, and description of the long-term trend is based on visual observation of the partial plots from GAM model 1.

Reserve	Sites	Deviance explained	<i>P</i> value	Long-term trend
North Inlet–Winyah Bay	Clambank Creek	25.4	<0.001	Decreasing
	Debidue Creek	10.4	>0.05	Stable
	Oyster Landing	10.2	0.004	Increasing
ACE Basin	Thousand Acre	27.8	0.004	Increasing
	Fishing Creek	37.2	<0.05	Increasing
	Mosquito Creek	21.1	0.047	Increasing
Sapelo Island	St. Pierre	22.4	0.007	Increasing
	Cabretta Creek	33.7	<0.05	Stable
	Dean Creek	26.6	0.004	Decreasing
	Hunt Dock	20.1	>0.05	Decreasing
	Lower Duplin	27.2	>0.05	Decreasing

particular exhibited high temporal variation and separated from the other stations in ordination space; the remaining 8 stations largely overlapped. The 3 stations exhibiting both high temporal variation within a site and differences relative to other stations (NI-WB Thousand Acre, ACE Basin Fishing Creek, and ACE Basin Mosquito Creek) are characterized by a higher degree of riverine input compared with the remaining stations, which are ocean dominated. Parameter scores within the ordination largely back up this finding, as high values of salinity and chl-a overlaid on the ocean- and river-dominated stations, respectively (Fig. 6).

Interesting patterns also arise in terms of temporal synchrony across stations. For example, at ocean-dominated stations across Reserves, 2020 was a year of relatively lower salinity and higher primary productivity, exhibited by the station trajectories heading toward the southwest in that year (i.e., more negative values on both axes; Fig. 6). Conversely, 2011 exhibited higher salinity conditions at most of these stations. The year 2003 was characterized by lower primary production, particularly for riverine-dominated stations, with those points located toward the northwest within their respective station trajectories.

Discussion

Based on their location at the confluence of marine and freshwater ecosystems, estuaries are subject to the impacts of global change from both the oceanic and terrestrial realms. Recent evidence has demonstrated the warming of surface waters in estuaries globally [63], and even relatively “pristine” estuaries are subject to the effects of global climate change such as sea level rise [14]. In this study, we document spatiotemporal variability in long-term trends and seasonal patterns in multiple biophysical parameters among and within 3 estuaries in the southeast United States. We leverage high-frequency data collected over 2 to 3 decades through the National Oceanic and Atmospheric Administration NERR SWMP effort and document rising water temperatures across this region mainly driven by increases

during winter months (December to February). Likely associated with this long-term annual increase in temperature is a widespread decrease in DO concentrations, also occurring mainly during the cold weather period. In addition, we identify variable trends in salinity, with substantial spatial variability in 2 of the 3 estuarine systems, and an increase in concentrations of chl-a in 2 of the 3 estuaries. Finally, our holistic, qualitative assessment of water quality elucidated variation in the time series trajectories of ocean- and river-dominated locations. These decadal-scale changes in environmental conditions have wide-ranging implications for estuaries broadly, including shaping habitat use by biotic communities, modulating trophodynamics and community structure, and altering ecosystem functions and services provided by estuarine ecosystems.

Trends in temperature

Increasing water temperatures in coastal zones have been documented globally [7,63,64], and increases in winter temperatures are a key driver of that change in some regions [65–68]. In the United States, the Chesapeake Bay [69], San Francisco Estuary [6], Narragansett Bay [70], and Gulf coastal plain estuaries [71] have all experienced warming winter water temperatures during the past half century. Here, we have shown that estuaries of the South Atlantic Bight can be added to this list of coastal ecosystems experiencing warming waters. Several climatic cycles such as the North Atlantic Oscillation (NAO) and El Niño–Southern Oscillation (ENSO) are strongly linked with temperature patterns at interannual and decadal scales [72], and in the southeast United States, multiple climate indices can be important determinants of long-term temperature trends [22]. Abiotic conditions (including temperature) can be a critical driver of estuarine community dynamics [73]. Winter water temperature in particular is a key determinant of population density for numerous species, which utilize estuaries as nursery habitats, including striped bass *Morone saxatilis* [74] and white shrimp *P. setiferus* [75], among others. In addition, cold winter water temperatures

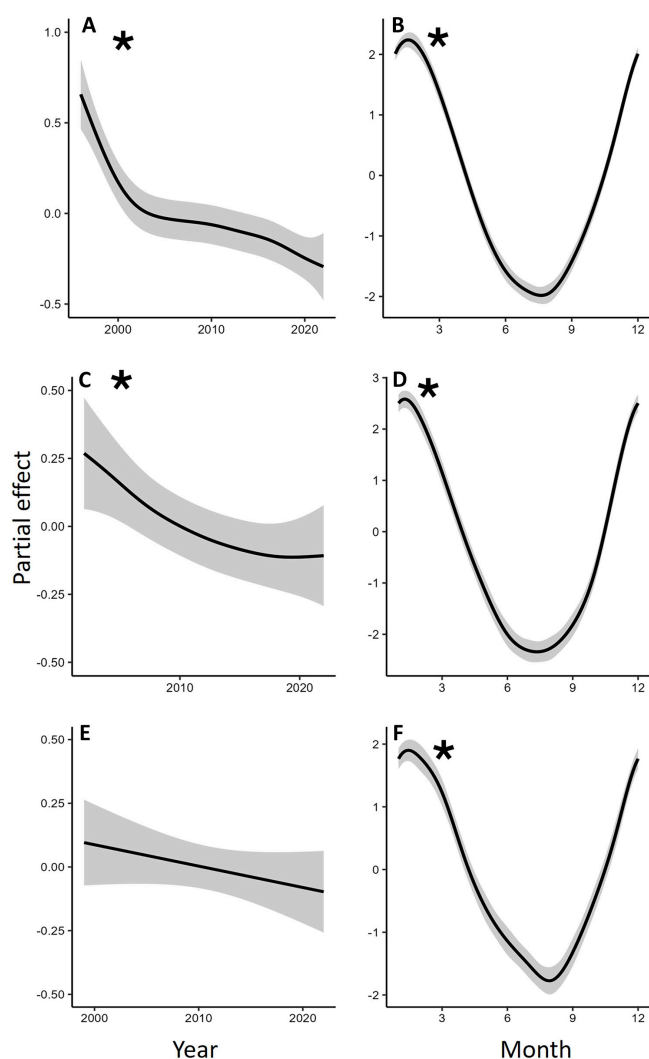


Fig. 4. Partial effect plots of model 1 investigating the long-term trend (A, C, and E) and seasonal pattern (B, D, and F) in DO (mg l^{-1}) across the Reserves. A single representative SWMP station from each Reserve is shown: (A and B) Oyster Landing, NI-WB; (C and D) Fishing Creek, ACE Basin; and (E and F) Lower Duplin, Sapelo Island. The shaded gray region is the 95% confidence interval. Statistically significant trends are indicated by asterisk (*).

can serve as a barrier to the expansion of low-latitude species into more temperate regions, including both natives (e.g., gray snapper *Lutjanus griseus*; [76]) and invasives (e.g., green porcelain crab *Petrolisthes armatus*; [77]). Finally, water temperature is a key indicator for numerous estuarine-dependent species, so changing temperatures can impact ingress or egress from these nursery habitats. Thus, changes in temperature conditions, and particularly the annual minima experienced during the cold season, can have wide-ranging implications for ecosystem function and the delivery of ecosystem services such as habitat provision.

Trends in salinity

The lack of a uniform trend in salinity conditions across the region is most likely due to the influence of local drivers such as freshwater inflow, precipitation, and degree of modification within the drainage of an individual sampling station. ACE Basin exhibited increasing salinities between 1979 and 2005 [33], and that trend

appears to continue through 2022. Conversely, stations within the NI-WB system are variable compared to the other 2 estuarine Reserves. In NI-WB, 3 ocean-dominated stations located <4 km from each other exhibited contrasting salinity trends, with Clambank Creek decreasing, Oyster Landing increasing, and Debidue Creek station temporally stable. Nonetheless, each of these 3 sites remains polyhaline with mean salinities of >30 (Table 1). One station in NI-WB and 2 stations in ACE Basin are river dominated as evidenced by the long-term median salinity values (Table 1). There has been a long-term decrease in riverine discharge from the Pee Dee River, which provides ~90% of freshwater input to Winyah Bay [34]. This reduction in freshwater flow may contribute to the increasing salinities observed at the Thousand Acre sampling station in NI-WB. Generally, upstream portions of these estuaries are subject to changes in abiotic conditions associated with freshwater input from rivers and experience more interannual variability than ocean-dominated sites, as we demonstrate based on multivariate trajectories of water quality (Fig. 6).

We document increased salinity levels across the region during the period 2008–2012 (Fig. 3), which coincided with intense La Niña conditions. La Niña is associated with reduced precipitation in the southeast United States and is linked to drought conditions across the northern hemisphere [78]. In addition, the southeast United States is experiencing substantial rises in sea level [79], which can result in both increases in salinity [80] and contribute to changes in nutrient availability [14]. Because global scale climatic variables influence local salinity regimes via atmospheric teleconnection [81], the anticipated increase in frequency and intensity of ENSO events [82,83] is likely to continue to impact observed salinities in estuaries. This can have critical consequences for estuarine foundation species and their associated fauna, such as the diverse community found on oyster reefs. In the southeast United States, the estuarine salinity gradient is a key driver of oyster reef community structure and function [84]; our results suggest that reefs in this region may be tending toward the community dynamics associated with higher salinity conditions.

Trends in DO

Across our study region, DO concentrations showed a uniform decreasing trend as well as a clear seasonal pattern. Nonetheless, we documented higher median values of DO in NI-WB and ACE Basin NERRs compared to the mean value observed during the period of 2005–2009 [30], and DO values at these 11 stations generally do not fall below the thresholds for hypoxia or anoxia for extended periods. Decreasing trends in DO have also been observed in Corpus Christi Bay [85], the Nassau River Estuary [86], the Pearl River estuary [87], Chesapeake Bay [12,88], Indian River Lagoon [10], and Waquoit Bay [29]. In all of these estuaries, increased nutrient loading from the upstream watershed is identified as the primary cause of reductions in DO, and they can experience seasonal, episodic, or prolonged hypoxia. Some of our study sites, in contrast, receive minimal anthropogenic nutrient input from their watersheds and thus rarely experience hypoxic or anoxic conditions. These relatively pristine conditions make the Reserves an ideal natural laboratory to understand the magnitude of change in other more impacted ecosystems. While the reductions in DO that we document are likely linked to increasing temperatures, there are other simultaneous processes that can regulate the dynamics

Table 4. GAM statistical output from model 2 of the monthly long-term trends for salinity. Monthly long-term trend column reports output of the interaction between smoothing function of year and month. Significance level was set at 0.05

Reserve	Sites	Deviance explained	P value	Monthly long-term trend
North Inlet–Winyah Bay	Clambank Creek	17.7	>0.05	All months showed visible decreasing trend
	Debidue Creek	10.1	>0.05	All months showed visible decreasing trend
	Oyster Landing	8.7	<0.05	Significant increasing trend in September
	Thousand Acre	22.8	>0.05	Most months showed visible increasing trend
ACE Basin	Fishing Creek	39.8	<0.001	Significant increasing trend in August and November
	Mosquito Creek	16.1	>0.05	Visible decreasing trend for all months
	St. Pierre	18.2	<0.001	Significant increasing trend in May
Sapelo Island	Cabretta Creek	38.5	<0.001	Significant decreasing trend in February, August, September, November, increasing trend in December, stable in October
	Dean Creek	27.6	<0.001	Significant decreasing trend in February, May
	Hunt Dock	25.6	>0.05	Most months showed visible decreasing trend
	Lower Duplin	27.8	<0.05	Most months showed visible decreasing trend

Table 5. GAM statistical model output for chl-a model 1. These models account for seasonal variation in modeling the long-term trend. The reported P value is based on the smooth function of the year term. Trends that are significant are highlighted in bold, and description of the long-term trend is based on visual observation of the partial plots from GAM model 1.

Reserve	Sites	Deviance explained	P value	Long-term trend
North Inlet–Winyah Bay	Clambank Creek	38.7	<0.001	Increasing
	Debidue Creek	48.8	<0.001	Increasing
	Oyster Landing	48.0	<0.001	Increasing
	Thousand Acre	20.4	0.01	Increasing
ACE Basin	Fishing Creek	30.8	<0.001	No change, high interannual variation
	Mosquito Creek	19.5	<0.001	Decreasing
	St. Pierre	26.3	<0.001	Increasing trend with high interannual variation
Sapelo Island	Cabretta Creek	39.9	0.006	No overall change
	Dean Creek	11.1	0.203	Increasing
	Hunt Dock	36.5	0.08	Increasing
	Lower Duplin	24.4	0.003	Increasing

of DO in estuaries including tidal flux and mixing [89] as well as residence time [90,91], which we could not investigate as NERR SWMP does not collect data on these parameters.

Trends in chl-a

Our finding of substantial spatial variation in chl-a trends aligns with previous work [92–94] documenting the potential for local-scale factors to impact primary production in estuarine waters. For the NI-WB and Sapelo Island Reserves, we show increasing concentrations of chl-a during the warmest months of the year (June to September). Additional recent evidence of increasing chl-a concentrations comes from an analysis of SWMP data over the period 2002–2019 [14], although that study did not identify

the seasonal drivers of trends as we do here. Increases in chl-a have also been observed in tidal marshes along the mid-Atlantic coast of the United States over approximately the same period as our study [95]. Conversely, a long-term study in an estuary in the northeast United States (Narragansett Bay, Rhode Island) demonstrated a nearly 50% decline in phytoplankton biomass between the mid-20th Century and present, in addition to a shift toward earlier spring phytoplankton blooms of nearly 5 d per decade [96]. Those changes were attributed to lower nitrogen availability due to weakened water column stratification and reduced nutrient loading from anthropogenic sources [96]. The SWMP stations utilized here are relatively shallow and typically well mixed, and many of their associated watersheds have comparatively low levels of development. Both of these factors potentially contribute to

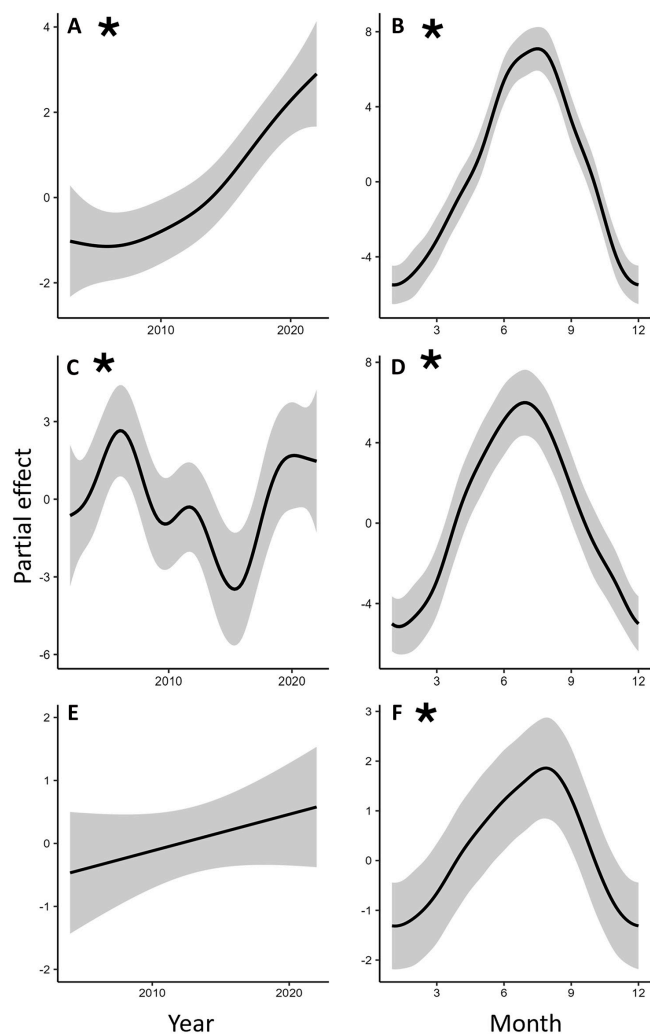


Fig. 5. Partial effect plots of model 1 investigating the long-term trend (A, C, and E) and seasonal pattern (B, D, and F) in chlorophyll a across the Reserves. A single representative SWMP station from each Reserve is shown: (A and B) Oyster Landing, NI-WB; (C and D) Fishing Creek, ACE Basin; and (E and F) Dean Creek, Sapelo Island. The shaded gray region is the 95% confidence interval. Statistically significant trends are indicated by asterisk (*).

the differences we observed in chl-a trends in the southeast compared to the decline reported from Narragansett Bay.

Conclusions

Our analysis of long-term, high-temporal-resolution biotic and abiotic data from 3 estuaries in the southeast United States provides clear evidence of the impacts of climate change in coastal ecosystems. We documented a region-wide increasing trend in temperature driven by changes in winter months (December to February) with a concurrent decrease in DO. Salinity trends were characterized by substantial spatial variability in 2 of the 3 Reserves and strong nonlinear temporal trends throughout the Reserve. Chl-a showed an increasing temporal trend in 2 Reserves, mostly observed during warm months. These documented changes in environmental conditions provide strong evidence of climate change throughout the region. These impacts can alter interactions between different components of estuarine ecosystems, which serve as a critical

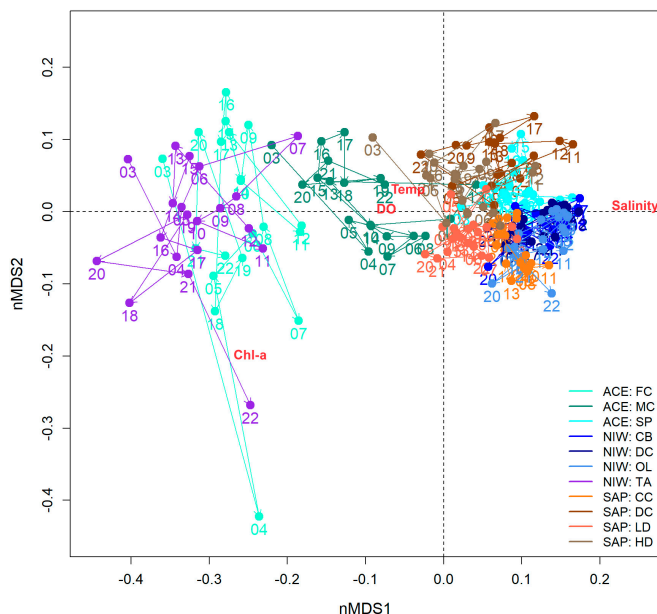


Fig. 6. nMDS visualization of holistic water quality trajectories, showing the multivariate response [based on annual means of temperature (Temp), salinity, DO, and chl-a concentration] for each SWMP station over the period 2003–2022. Note: Dean Creek and Cabretta Creek stations cover the period 2005–2022. Number labels on points indicate the last 2 digits of the associated sampling year, and red text shows location of ordination scores for each water quality parameter. Station codes are as in Fig. 1, and 2-D stress = 0.06.

nursery habitat for numerous ecologically and economically important fauna. The implications of these changes for the flora and fauna that utilize estuaries requires continued investigation, particularly because phenological responses to environmental changes can be taxon specific [97,98]. The baseline information provided here can serve as a useful standard to measure against due to the intensification of changes associated with anthropogenic warming (e.g., sea level rise; [79]).

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Author contributions: The study was conceived and designed by R.P.D. N.M. and R.P.D. analyzed the data. N.M. wrote the first draft of the manuscript, and both authors contributed to subsequent versions.

Competing interests: The authors declare that they have no competing interests.

Data Availability

The System-Wide Monitoring Program data are accessible from the Centralized Data Management Office of the National Estuarine Research Reserve System at www.nerrsdata.org.

Supplementary Materials

Figs. S1 to S4
Tables S1 to S5

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