Hot and fresh: evidence of climate-related suboptimal conditions for seagrass in a large Gulf coast estuary

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## Abstract

Climate change is an existential threat to natural resources that sustain human health and the environment. In Tampa Bay, Florida (USA), seagrass coverage has declined since 2016 by nearly a third (11,518 acres), despite sustained reductions of nitrogen loads supportive of light environments for growth. Changing physical water quality conditions related to climate change may be stressing seagrasses beyond their optimal growth ranges, requiring an assessment to determine if this decline can be linked to climate stress. Three ambient water quality datasets of varying sampling design and coverage were evaluated to characterize physicochemical environments in Tampa Bay and the potential relationships with seagrass change. Over the last fifty years, Tampa Bay has become hotter and fresher with water temperature increasing by 0.03 - 0.07 C per year and salinity decreasing by 0.04 - 0.2 PSU per year. These changes varied spatially and seasonally, with the most dramatic changes observed in the upper bay during the summer months. Simple linear models provided limited evidence that recent seagrass declines are associated with hotter and fresher conditions. Trends in warming and increased precipitation in the region are likely to continue, further creating suboptimal conditions for seagrasses in Tampa Bay. These results should compel resource managers to consider the likelihood that reduced resilience of estuarine resources due to shifting ecological baselines driven by additional climate change drivers will complicate long-standing management paradigms. While conventional management approaches that focus on limiting nutrient loads should be continued, their future effectiveness may be confounded by other cliamte change driveres and warrant additional, complementary interventions to maintain ecosystem health into the future.

## 1 Introduction

The monitoring and management of seagrasses in coastal environments has received substantial attention at a global scale. Seagrasses are fundamental indicators of coastal ecosystem health (Roca et al. 2016; Orth et al. 2017), while also serving as foundational species that provide numerous ecosystem services (Fourqurean et al. 2012; Orth et al. 2020; Orth and Heck 2023). Seagrasses have been in global decline with rapid development of coastal environments, particularly in the latter half of the 20th century with accelerating losses estimated at a rate of 110 km yr since the 1980s (Waycott et al. 2009; Dunic et al. 2021). These losses are comparable to, if not more significant than, other interconnected critical coastal environments such as mangroves and salt marshes (Duarte et al. 2008), which threatens the natural and economic services that these habitats provide. Losses have been attributed to numerous stressors including decline in light environments with nutrient enrichment, sedimentation, and physical disturbance primarily from human activities (Duarte 1995; Margaret O. Hall et al. 1999; Orth et al. 2006; Burkholder et al. 2007). Furthermore, natural disturbances such as storm events and disease have also been implicated (Robblee et al. 1991; Tomasko et al. 2020). Contemporary management actions and interventions aimed at mitigating loss and ultimately supporting restoration require adaptive approaches to address the effects of multiple stressors that have contributed to seagrass decline (Dunic and Côté 2023).

The sustained coverage or restoration of seagrasses in stressed coastal environments requires management actions that support vegetative growth, reproduction, and coverage expansion. A long-standing approach adopted by numerous management entities has been the control of external nutrient inputs in systems where excessive algal growth has created poor light environments for seagrasses (Boesch et al. 2001; Greening and Janicki 2006; Greening et al. 2014; Han and Liu 2014). There are limited examples of successful recovery of seagrass through control of nutrient inputs alone, primarily because of the difficulty in identifying and regulating both point and diffuse non-point sources. Notable exceptions include Tampa Bay on the west coast of Florida (Greening et al. 2014) and the much larger Chesapeake Bay on the east Atlantic US coast (Lefcheck et al. 2018), where both showed significant increase in seagrass areal coverage through sustained and long-term reductions in external nutrient loads. Cooperation among management, regulatory, public, and private sectors were critical aspects of both examples (Sherwood et al. 2016; Tango and Batiuk 2016). In other cases, the reversal of seagrass losses through nutrient reductions alone may not be possible because of system hysteresis, where the path to recovery is not the same as the path to decline (Maxwell et al. 2016). Complementary management actions, in addition to nutrient reductions, are needed in these situations. Management actions with other ecosystem co-benefits are much more effective in estuaries that are stressed but not past critical thresholds that produce an alternative ecosystem state.

Climate change has complicated the understanding of ecosystem response to conventional stressors, presenting new challenges and expectations for how ecological resources will respond to management actions (Statham 2012; Sherwood and Greening 2013). In addition to sea-level rise, the most anticipated effects of climate change in coastal environments are increasing temperature and alteration of precipitation patterns. These changes will profoundly alter physicochemical habitats, creating suboptimal or uninhabitable conditions for many species (Madeira et al. 2012; Lefcheck et al. 2017; Hensel et al. 2023). Lefcheck et al. (2017) evaluated interactive effects of water clarity and rising temperatures on seagrasses with over 30 years of data in Chesapeake Bay. The effects of decreased water clarity for seagrasses in shallow habitats were exacerbated by acute warming related to climate change, demonstrating a concerning synergy of multiple stressors. Moreno-Marín et al. (2018) produced similar results using a multifactorial experiment that considered temperature, light, and nutrient (nitrogen) availability for North Sea eelgrass (*Zostera marina*). Species shifts are also expected to occur as changing physical conditions decrease the competitive advantages of historically abundant species. Again in Chesapeake Bay, the abundance of widgeongrass (*Ruppia maritima*) has been mediated by nutrient reductions, while also outcompeting and replacing formerly dominant eelgrass (*Zostera marina*) given higher tolerance to increased temperatures (Hensel et al. 2023). Changing frequency and severity of precipitation patterns may further alter the distribution and abundance of seagrasses by pushing species outside of optimal salinity tolerance ranges (Rasheed and Unsworth 2011; Webster et al. 2021). These changes may produce hypersaline conditions under periods of prolonged drought or more freshwater conditions with increased storm events. Seagrasses may respond differently under individual or multiple stressors (Lefcheck et al. 2017; Zhang et al. 2023), suggesting place-based assessments of response to climate change provide valuable insights for managers responsible for maintaining ecological resources.

In Tampa Bay, Florida, seagrasses are a primary indicator of bay health that have been the focus of management efforts over the last thirty years (Sherwood et al. 2017). Through successful reduction of external nitrogen loads, seagrasses have recovered from a low, system-wide coverage in the 1980s to an all-time high in 2016 of 41,655 acres (16,857 ha, Greening and Janicki 2006; Greening et al. 2014). Seagrass distribution and abundance has been dynamic throughout this period, overall responding positively to increases in water clarity with nutrient load reductions, while also demonstrating more short-term variability in response to regional climate events (Greening and Janicki 2006). Since 2016, seagrass areal cover has decreased by nearly 1/3 despite relatively stable water quality with adequate light penetration that has been historically shown to support growth (Janicki and Wade 1996; Beck 2020a). Factors that have influenced this recent decline are unknown and the effects of climate change drivers on physical water quality conditions have been implicated as potential stressors. Following global trends, recent work has demonstrated a broad long-term trend of increasing water temperature in Tampa Bay, although at a relatively coarse scale (Nickerson et al. 2023). Changing salinity has not been well-described, nor have potential links of changing salinity and temperature with recent seagrass change. Tampa Bay is rich with historical data that can be used to evaluate long-term trends and to develop models that can explain relationships of seagrass change with water quality conditions. This information can fill a critical knowledge gap that can inform regional management activities, while also demonstrating the confounding effects of climate change with ecosystem response to conventional stressors.

This paper describes a comprehensive assessment of long-term trends in water temperature and salinity in the Tampa Bay estuary over the last fifty years. Three datasets of varying sampling designs and temporal coverage were used to assess the primary hypothesis that Tampa Bay is trending towards hotter and fresher conditions that are likely stressing seagrasses beyond their optimal tolerance ranges, particularly in upper bay segments where marginal light environments exist. This hypothesis was generated from preliminary assessments of datasets used herein and discussions with the regional scientific and management community, despite information in the primary literature suggesting the contrary for salinity (e.g., Costa et al. 2023). This analysis was supported by 30-year seagrass datasets describing approximate biennial coverage of all seagrasses, annual transect monitoring describing cover of individual species, and synoptic seagrass data collected with routine biotic and water quality surveys. Specific focus was on the periods prior to and after 2016, when seagrasses recovered baywide and then declined despite water quality conditions remaining relatively stable. Our primary goal was to relate recent seagrass changes to climate stressors to provide a motivating example for the management community in the Tampa Bay region that a shifting ecological baseline presents new challenges beyond the known success story of long-term bay recovery. The results are also provided as a cautionary example of the subtle but increasing role of climate-related stressors on the resiliency of estuarine systems at the tropical-temperate boundary, necessitating the need to resassess existing management paradigms and adaptively manage to accommodate current and anticipated future conditions.

## 2 Methods

### 2.1 Study area

Tampa Bay is the largest open-water estuary in Florida covering 400 mi (1,036 km) and the second largest in the Gulf of Mexico. The watershed covers an additional 2,200 mi (5,872 km) with the Hillsborough, Alafia, Manatee, and Little Manatee rivers that contribute to a majority of freshwater inflow to the bay. Tampa Bay straddles the tropical and temperate boundary of central Florida characterized by warm, humid conditions and a distinct rainy season during the summer (Morrison et al. 2006). El Niño weather events have also been associated with prolonged periods of heavy rainfall contributing to seagrass reductions through increased stormwater nutrient loads (Schmidt and Luther 2002; Greening and Janicki 2006; Morrison et al. 2006). The watershed is heavily developed and includes over 3 million people (Todd et al. 2023) with 42% of the land as urban or suburban contributing substantial inputs of wastewater and stormwater runoff that can stress bay resources (Beck et al. 2023). The geology of the watershed is rich in phosphates and mining activities have greatly altered the landscape, with notable spills and releases of wastewater that have affected water quality and biological resources (Garrett et al. 2011; Beck et al. 2022). Important subtidal habitats include seagrasses, hard bottom, tidal flats, and oyster reefs, where a majority of management efforts have historically focused on restoring and maintaining seagrass cover (Sherwood et al. 2017). Additional native habitats include intertidal wetlands (mangroves, salt marshes, salt barrens) and pine forests, oak hammocks, and freshwater wetlands present in upland habitats (Robison et al. 2020). Losses of native uplands and potentially restorable habitats to development in the watershed from 1990 to 2020 have been estimated at 188,429 acres (76,254 ha, Beck et al. 2023).

Tampa Bay is divided into distinct sub-segments defined by physical and natural boundaries to assist with water quality management activities (Lewis III et al. 1985): Old Tampa Bay (OTB) in the northwest; Hillsborough Bay (HB) in the northeast; Middle Tampa Bay (MTB); and Lower Tampa Bay (LTB) that connects to the Gulf of Mexico (Figure [1](#fig-map)a). Old Tampa Bay and Hillsborough Bay have historically had the most degraded water quality primarily from direct external nutrient inputs from wastewater and stormwater (Greening et al. 2014). Hydrologic conditions vary between the two, such that Hillsborough Bay receives a majority of direct surface water inflow from the Hillsborough and Alafia rivers, whereas Old Tampa Bay receives much less inflow with a majority from multiple small tributaries and manmade flood control conveyances (Janicki Environmental, Inc. 2023). Notably, Old Tampa Bay has restricted circulation from multiple land bridges associated with causeways that traverse the bay (Sherwood et al. 2015; Luther and Meyers 2022). Recurring seasonal harmful algal blooms of the dinoflagellete *Pyrodinium bahamense* have contributed to exceedances of the chlorophyll-a regulatory standard in Old Tampa Bay (Lopez et al. 2023). By comparison, water quality conditions in Middle Tampa Bay and Lower Tampa Bay are generally better than the upper two bay segments primarily from more frequent water exchanges with the Gulf of Mexico and lower nutrient loading (Janicki Environmental, Inc. 2023). All bay segments are relatively shallow, with a baywide mean depth of approximately 3 m. Light penetration typically reaches bottom habitats under current conditions, although seagrasses were historically limited by high phytoplankton production that affected light environments prior to wastewater and stormwater regulation, particularly in Old Tampa Bay and Hillsborough Bay (Greening et al. 2014; Johansson and Janicki Environmental, Inc. 2015).

### 2.2 Seagrass change in Tampa Bay

The long-term recovery of seagrass habitats in Tampa Bay is a nationally-recognized success story that demonstrates application of a successful management paradigm through the EPA-administered National Estuary Program (Greening and Janicki 2006; Greening et al. 2014; Sherwood et al. 2017). From 1988 to 2016, seagrasses increased 79% to 41,655 acres (16,857 ha), surpassing the regional management goal of restoring coverage to 95% of a benchmark 1950s coverage. The greatest areal coverage expansions were observed in the upper bay segments (OTB, HB, and MTB; Figure [2](#fig-seagrasschg)a). Throughout this same period, external nitrogen load estimates decreased by about 2/3 from a peak 1970s estimate of 8.9 x 10 kg/year, largely from advanced wastewater treatment upgrades and in part from the cumulative effects of habitat restoration and additional stormwater control projects implemented in the watershed (Greening et al. 2014; Beck et al. 2019). These reductions in nutrient loadings resulted in large scale reductions in chlorophyll concentrations and light attenuation in the water column, creating favorable environments for seagrass growth.

From 2016 to present, dramatic losses of seagrasses have been observed in Tampa Bay, despite nutrient loading and light attenuation remaining relatively stable (Figure [2](#fig-seagrasschg)a). Total cover in Tampa Bay has decreased by 28% (11,518 acres/4,661 ha) from the 2016 peak to a total baywide coverage of 30,137 acres (12,196 ha). Losses have been most pronounced in Old Tampa Bay (62%; 6,963 acres/2,818 ha loss) and Hillsborough Bay (80%; 1,599 acres/647 ha loss). The current estimate for Old Tampa Bay of 4,183 acres (1,693 ha) is the lowest ever recorded in that bay segment since mapping efforts began in the 1980s. Coverage in Middle Tampa Bay decreased by 20% (1,926 acres/779 ha loss), whereas coverage in Lower Tampa Bay has remained stable, with only a 2% loss that is likely within the range of mapping error for the coverage estimates.

### 2.3 Seagrass data

Two primary sources of data have been used to track seagrass change over time in Tampa Bay. The Southwest Florida Water Management District (SWFWMD) has estimated areal coverage of seagrasses approximately biennially since the late 1980s (Figure [2](#fig-seagrasschg)a, available at <https://data-swfwmd.opendata.arcgis.com/>). These maps are created by photointerpretation of aerial images obtained at the end of the growing season, typically during November-February. No species information is provided. A more detailed, but spatially-specific, data source is the Tampa Bay Interagency Seagrass Monitoring Program (Figure [2](#fig-seagrasschg)b, <https://tampabay.wateratlas.usf.edu/seagrass-monitoring/>). Annual transect surveys have been conducted since 1998 at 62 fixed locations in Tampa Bay, many of which were chosen to target seagrass beds of interest (Johansson 2016; Sherwood et al. 2017). This dataset provides species information on cover-abundance, frequency occurrence, and condition, collected at fixed meter marks along a transect extending from the shoreline to the deepwater edge of the seagrass bed. Although the areal maps provide the standard for assessment of restoration goals, the transect data allow inter-annual comparison at greater temporal resolution, particularly for the recent period of interest when seagrasses have declined. As such, the transect data were used below for comparison with temperature and salinity changes for the major bay segments. Additional sources of seagrass data are described in the next section.

### 2.4 Water quality data

Several datasets with distinct sample designs are available to assess long-term changes in water temperature and salinity in Tampa Bay. These datasets were evaluated individually to assess trends and relationships with seagrass change to provide a weight-of-evidence approach for potential causal relationships driving the recent decline. First, the Environmental Protection Commission (EPC) of Hillsborough County has collected discrete water quality measurements monthly at 45 stations in the major bay segments since the late 1970s (Figure [1](#fig-map)b). These data are used for regulatory assessments for the federally-recognized nutrient Total Maximum Daily Load and state Reasonable Assurance determination in Tampa Bay. Water quality samples are collected at each station from surface water grabs (e.g., nutrients, biological, and chemical constituents) or *in situ* measurements of physical parameters (e.g., salinity, temperature) collected at the surface, mid-depth, and bottom. Most analyses herein used only bottom water measurements given the shallow depth and mixed water column of most of Tampa Bay (Weisberg and Zheng 2006). Time of sampling can vary, although most samples are collected from mid-morning to early afternoon. Compared to the additional datasets described below, the monitoring stations are generally in deeper water beyond where seagrasses occur along the shallow margins of the bay. The data were obtained using the tbeptools R package that imports the data directly from a stable web address provided by the EPC (Beck et al. 2021).

The second dataset used to evaluate water quality trends was available from the Florida Fish and Wildlife Conservation Commission (FWC). The Fisheries Independent Monitoring (FIM) program administered by FWC provides monthly surveys of the entire nekton community in Tampa Bay, including species richness and abundance, using multiple gear types that target different habitats. A stratified sampling design is used to select sites for 21.3 meter center-bag seines that target shallow habitats (<1.5 m) where seagrasses are predominantly found in Tampa Bay and includes the longest consistent sampling protocol (1996 to present, Figure [1](#fig-map)c). Seines were deployed (1) parallel to bay shorelines in shallow waters (<1.5 m) and (2) offshore into the prevailing current at least 5 m from the shoreline to sample approximately 140 m of bay bottom (Schrandt et al. 2021). In addition to collecting fish and selected invertebrates, *in situ* physical measurements for water temperature and salinity are collected at the bag, and at the surface and at 1 m intervals to the bottom. Only measurements from the bottom were used. Seagrass data are also provided for each site, with information on species and cover. Total percent cover for all species at a site was used for comparison with temperature and salinity measurements. Sites exclusively with macroalgae were not included in the analysis. All FIM data were provided from FWC staff upon request.

The third and final dataset evaluated was from the Pinellas County Department of Environmental Management (PDEM). Surface waters in Pinellas County have been monitored since the 1990s, although a consistent stratified random sampling designed has only been used in Tampa Bay since 2003 primarily to support robust statistical assessments for regulatory stormwater permit reporting. Data were obtained by request to PDEM staff for the western portion of Old Tampa Bay where sampling occurred from 2003 to present (Figure [1](#fig-map)d, also available at <https://wateratlas.usf.edu/>). We focused primarily on OTB for the analysis of the PDEM data given the length of record, consistency of sampling, and relative loss of seagrass compared to the other bay segments. Four distinct spatial zones in OTB are used to stratify the random selection of sample points that typically include 4 sample points per month in each zone. Water quality samples at each site are similar to those collected by EPC but can occur in shallower locations. Seagrass presence/absence is also recorded at each site and all sites were defined as “seagrass” if only seagrass species were identified (any with macroalgae were excluded) and “no seagrass” if bare sediment was observed.

All of the organizations that provided water quality datasets participate in the Southwest Florida Regional Ambient Monitoring Program (Sherwood et al. 2016). This *ad hoc* group meets quarterly to ensure similar standards and methods are used for the collection and processing of surface water quality monitoring data in the region. Split-samples evaluated by each organization are also compared to assess precision between different laboratories. As such, the water quality measurements used herein are considered comparable, relative to the different sampling designs used by each program.

### 2.5 Trend analysis

The first goal of the analysis was to describe spatial and temporal trends in water temperature and salinity using the three water quality datasets described above. This assessment provided an indication of the extent of change in Tampa Bay as context for understanding potential relationships with seagrass change. An assumption was that any changes in physical characteristics in Tampa Bay were driven by interannual changes in weather conditions related to long-term (multi-decadal) climate change drivers. For comparison to water quality conditions, daily air temperature (Tampa International Airport [TIA] National Weather Service site) and precipitation (SWFWMD area-weighted watershed summaries) were used to characterize regional conditions for the period of record covered by the water quality samples (i.e., 1975 to present for the EPC data). The rnoaa R package (Chamberlain and Hocking 2023) was used to obtain the TIA temperature data. Regional precipitation summaries were obtained directly from the SWFWMD (https://www.swfwmd.state.fl.us/resources/data-maps/rainfall-summary-data-region). Only rainfall data for the wet season (June to September) were evaluated for trends, whereas the complete record was used to calculate the Standardized Precipitation Index (SPI, Beguería et al. 2013) to identify periods of time when rainfall significantly deviated from the long-term average (using the *spei* R package, Beguería and Vicente-Serrano 2023). Annual hydrologic loading data to Tampa Bay beginning in 1985 were also obtained for comparison to annual precipitation (Janicki Environmental, Inc. 2023). All climate and loading data were evaluated annually with simple linear regression trends to assess change over time. Water temperature and salinity trends using the EPC, FIM, and PDEM data were similarly evaluated by averaging the monthly data each year for each bay segment. Linear trends for these data were evaluated based on averages of all stations and months within each year and bay segment, which allowed for comparable statistical power between datasets with different sampling designs.

Formal trend tests were used to assess station-level changes in water temperature and salinity in the EPC data. These analyses also provided a detailed spatial assessment of trends because the EPC data is the only dataset of the three where the same sites have been sampled over time. Seasonal Kendall trend tests were used to evaluate the monotonic change for temperature and salinity from 1975 to present at each water quality station (Hirsch et al. 1982; Millard 2013). The change per year was also evaluated for each parameter based on the slope estimates returned by each test. Kendall tests were also used to evaluate changes over time for each month across years to determine when the trends were most pronounced seasonally (e.g., all January estimates across years, all February estimates, etc.). The percentage of stations in each bay segment with significantly increasing temperature or decreasing salinity trends were evaluated for each month.

### 2.6 Quantifying potential stress

The second goal of the analysis was to evaluate if seagrass changes were linked to long-term changes in water temperature and salinity, with particular attention on differences between bay segments and the time periods before and after 2016 (pre/post seagrass recovery). The conceptual model for evaluating these changes describes the niche space where seagrass growth and reproduction is hypothesized to be greatest within optimal ranges for forcing factors that are present in the environment (Hutchinson 1957; Vandermeer 1972). In the simplest form, this can conceptualized as a bell curve with optimal conditions defined within a range of values for a single parameter (e.g., minimum and maximum temperatures where a species is typically observed), where reduced growth or mortality is observed outside of these ranges. Because both water temperature and salinity were evaluated, the same model can be conceptualized in two-dimensional space ([Figure 3](#fig-concept)). Seagrass growth can be limited when temperature is below or above the optimum range, when salinity is below or above the optimum range, or when both temperature and salinity conditions are outside of the optimum range. Based on the results of the trend tests, we hypothesized that seagrasses are likely stressed by both high temperature and low salinity (bottom right, [Figure 3](#fig-concept)). Although the optimal niche space can be defined in multiple dimensions for many parameters, we focus on water temperature and salinity given that other dominant forcing factors, i.e., light availability, have generally not been limiting for growth in recent years.

A fundamental challenge describing niche space is identifying the boundaries for optimal conditions. In Tampa Bay, three dominant seagrass species occur: *Halodule wrightii* (shoal grass), *Syringodium filiforme* (manatee grass), and *Thalassia testudinum* (turtle grass) (Lewis III et al. 1985). These species co-occur often in mixed beds throughout the bay, although some differences in abundance are observed across salinity ranges. Shoal grass is tolerant of a wide range of salinity (Lirman and Cropper 2003), but is more abundant in oligo/mesohaline portions of Tampa Bay. Conversely, turtle grass is less tolerant of low salinity and is more abundant in more euryhaline conditions near the mouth of Tampa Bay. Reported salinity ranges for each of these species varies depending on location, season, and other co-occurring factors like temperature (Phillips 1960; McMillan and Moseley 1967; Zieman 1975; Lewis III et al. 1985), although most studies place lower limits of salinity in the range of 15-25 ppt. Optimal temperature ranges are similar between these temperate-tropical species, with reduced growth observed at temperatures above 30 C (Zieman 1975; Lewis III et al. 1985).

Because of the uncertainty in defining *in situ* thresholds for optimal temperature and salinity ranges, multiple thresholds were evaluated to describe the potential for stress and how it may be related to changes in seagrass. Distinctions were not made between species, primarily due to lack of consensus between studies and likely site-specific ranges that affect seagrass growth in Tampa Bay. First, we developed metrics of potential temperature and salinity stress by quantifying the maximum number of continuous days each year when temperature was above or salinity was below a given threshold. This approach assumed that stress could be observed based on duration of exposure (i.e., maximum number of continuous days each year) relative to a threshold that may or may not be outside of the optimum range for seagrasses. These metrics were quantified from the monthly long-term observations in the EPC data. To quantify daily counts each year, a continuous prediction of temperature and salinity over time at each of 45 stations was estimated using Generalized Additive Models (GAMs) fit to temperature or salinity with a single predictor for decimal year (Wood 2017). The smoothing spline for decimal year had sufficient knots to capture the seasonal signal within each year and the long-term inter-annual trends. Model fit for each station was considered sufficient to calculate daily predictions to assess potential stressor metrics (Figure S5, R ranged from 0.85 to 0.95 for temperature models, 0.71 to 0.96 for salinity models, Tables S1, S2).

Counts of the maximum continuous number of days each year that temperature was above or salinity was below a threshold were obtained from the daily GAM predictions. This was done at each of the 45 stations in the EPC data using temperature thresholds of 29, 30, and 31 C and salinity thresholds of 15, 20, and 25 ppt. The number of days when both temperature was above and salinity was below the thresholds was also estimated as a combined potential stress measure. Stressor metrics were further aggregated across stations in each bay segment using a mixed-effects regression model where the annual stressor counts for stations in a bay segment were fit against year (1975 to 2022) using a random intercept for station (Zuur et al. 2009; Bates et al. 2015). This produced an overall assessment of how the stressor metrics have changed over time by bay segment, including counts for temperature, salinity, and both relative to the thresholds.

### 2.7 Links to seagrass

For comparison to seagrass, the annual metrics calculated from the EPC data were referenced to approximate periods of time between the annual seagrass transect surveys, as opposed to the calendar year for describing trends. Transect surveys are typically done in the late summer during peak growing season. The average sampling date for each year across the subset of transects in each bay segment was estimated and the stressor metrics were referenced accordingly. For example, if the average transect date for a bay segment was September 15th in 2009 and Oct 1st in 2010, the 2010 stressor counts were based on all days between the two average dates. This was repeated for all years from 1998 to 2022 when transect data were available. Bay segment stressor metrics were calculated as the average counts in each “transect year” from all stations in each segment. The stressor metrics were compared to frequency occurrence (all species) each year by bay segment. Generalized Linear regression Models (GLMs) were used to evaluate frequency occurrence in response to the independent variables, where the latter were the stressor metrics for temperature, salinity, both, bay segment, and time period (recovery pre-2016, decline post-2016). Two models were evaluated, one with the temperature and salinity metrics together and another with the both metric. Interactions were included between temperature, salinity, and time period or the both metric and time period, depending on the model. Bay segment was included as a main effect without interactions. The most parsimonious models were identified by forward and backward selection of the independent variables and comparison with AIC values (Sakamoto et al. 1986; Venables and Ripley 2002). All models excluded Lower Tampa Bay because of minimal seagrass change over time.

Separate models were constructed to provide an additional weight-of-evidence for the FIM and PDEM temperature and salinity datasets relative to seagrass change. These models used direct measurements of salinity and temperature as independent variables because the stressor metrics could not be calculated using the sampling designs from these monitoring programs. GLMs were used for the FIM data to evaluate seagrass percent cover using continuous temperature and salinity as independent variables. Interactions with time period and a main effect for bay segment were also included as above. GLMs for the PDEM data were constructed similarly, except only Old Tampa Bay was evaluated (no bay segment interaction) and the seagrass response variable was presence/absence (i.e., a binomial distribution was used) to model the probability of observing seagrass. Model input data were further subset to include only months from July to November to describe seagrasses during the growing season and to reduce potential seasonal effects.

## 3 Results

### 3.1 Temperature and salinity trends

Long-term meteorological data showed increasing trends for air temperature and precipitation ([Figure 4](#fig-meteowqraw)). Mean annual air temperature has increased by 0.04 C per year (p < 0.005, 0.51). Mean annual air temperature in 1975 was 22.1 (+/-0.17 st. err.) C, whereas current mean annual air temperature in 2022 was 24.1 (+/-0.17 st. err.) C, showing an overall increase in the period of record of 2 C. Similarly, total precipitation during the rainy season has increased by 1.91 mm per year, although the model was not significant (p = 0.14, 0.03). Removing September from the rainy season showed a significantly increasing trend of 2.4 mm per year (p < 0.05, = 0.07). Using this model, total precipitation in 1975 was 559.1 (+/-30.72 st. err.) mm, whereas current total precipitation in 2022 was 671.7 (+/-30.72 st. err.) mm, showing an overall increase in the period of record of 112.7 mm. Increasing trends in total annual hydrologic load from 1985 to present mirrored total annual precipitation, although the linear model was not significant. The SPI showed notable anomalies in precipitation, with pronounced rainy periods in the early 1980s, late 1990s, 2005, and 2015-2020.

Increasing water temperature and decreasing salinity generally followed the meteorological trends for all three *in situ* datasets (EPC, FIM, and PDEM, [Figure 4](#fig-meteowqraw), Tables [1](#tbl-temptrndtab), [2](#tbl-saltrndtab), Figures S1, S2, S3). Note that for tables [1](#tbl-temptrndtab) and [2](#tbl-saltrndtab), comparable time periods were evaluated between the datasets when possible given the different sample sizes, and therefore power, to detect trends. The strongest trends were observed for the EPC dataset, which had the longest record from 1975 to 2022. The top and bottom water temperature or salinity changes were similar across bay segments likely because of the relatively shallow water depths and minimal stratification in Tampa Bay ([Figure 4](#fig-meteowqraw)). Trends in water temperature were similar across bay segments with significant increases varying from 0.03 to 0.04 C per year, with a total increase of 1.4 (OTB) to 2.0 (HB) C from 1975 to present ([Table 1](#tbl-temptrndtab)). Salinity trends were similar between bay segments, although overall salinity was predictably higher for bay segments closer to the Gulf of Mexico. Only Old Tampa Bay and Lower Tampa Bay had significantly decreasing trends, with decreases of 0.06 (OTB) and 0.04 (LTB) ppt per year, with a total decrease of 2.7 (OTB) and 2.1 (LTB) ppt from 1975 to present. As expected, intra-annual variability of water temperature was much higher than salinity consistent with larger seasonal variation in temperature ([Figure 4](#fig-meteowqraw)). This variation may also be related to differences among the monitoring stations in each segment because the averages combine monthly and spatial variation. Significant increasing temperature trends were also observed for the FIM dataset from 1996 to present in OTB and from 2004 to present in OTB and HB ([Table 1](#tbl-temptrndtab)). No significant temperature or salinity trends were observed in the other bay segments for the FIM and PDEM datasets from 1996 to present nor from 2004 to present (Figures S2, S3). However, the EPC dataset showed significant increasing temperature across all time periods and bay segments. Salinity trends from the EPC dataset were not significant from 1996 to present, but were significantly decreasing from 2004 to present in all bay segments ([Table 2](#tbl-saltrndtab)).

The EPC dataset was also used to provide detailed information on station-level trends from 1975 to present ([Figure 5](#fig-kendall), see Figure S4 for 1998 to 2022). All stations had significantly increasing temperature and decreasing salinity from 1975 to present, excluding one station in HB that did not have significantly decreasing bottom salinity (Figure [5](#fig-kendall)a). Seasonally, most stations had more significant trends in the summer, early fall period for both temperature and salinity (Figure [5](#fig-kendall)b, c), although some variation was observed between bay segments. Temperature trends were more often observed in the summer, early fall for the upper bay segments (OTB, HB), whereas the lower bay segments (MTB, LTB) had more seasonally homogeneous trends. Seasonal trends in salinity did not vary as much between segments, although OTB and LTB had more stations with significantly decreasing trends than the other bay segments.

### 3.2 Stressor metrics

Linear mixed-effects models for the EPC data showed similar trends in each bay segment for the number of days when temperature was above different thresholds. All of the temperature models for each of the three thresholds (29, 30, 31 C) showed significantly increasing trends for each bay segment, with the largest slope of 1.4 days per year in OTB when temperature was above 29 C (Table S3). The estimated slopes for the number of days when temperature was above 30 C varied from 0.9 days per year in LTB to 1.1 days per year in MTB. Likewise, the average number of days when temperature was above 30 C at the beginning and end of the period of record varied from 8 (OTB, HB) to 21 (LTB) days in 1975 to 55 (HB) to 63 (LTB) days in 2022 (Table S5, see Table S6 for 1998 to 2022). Trends for the other two temperature thresholds were similar.

The salinity models were less similar between bay segments compared to the temperature models, primarily because of the natural variation in salinity along the bay’s longitudinal axis (Tables S3, S4). None of the bay segments had significantly increasing number of days per year when salinity was below 15 ppt. The only significant model for MTB was the number of days when salinity was below 25 ppt, which was increasing at a rate of 0.7 days per year. Both HB and OTB had significantly increasing number of days per year when salinity was below 20 and 25 ppt, although the slopes varied such that the rates in OTB were nearly double those in HB. The number of days per year when salinity was below 25 ppt in OTB increased by 2 days per year, whereas the number of days in HB increased by 0.9 days per year from 1975 to present. Likewise, the average number of days per year when salinity was continuously below 25 ppt at the beginning and end of the period of record was 128 (OTB) and 131 (HB) days in 1975 and 171 (HB) and 219 (OTB) days in 2022 (Table S5, see Table S6 for 1998 to 2022).

The number of days when both temperature was above and salinity was below a threshold also varied by bay segment. Four models were significant for OTB, seven for HB, four for MTB, and none for LTB (Table S3). The number of days when temperature was above 29 C and salinity was below 25 ppt had the largest slopes of 1.4, 1.2, and 0.7 days per year for OTB, HB, and MTB, respectively. Likewise, the average number of days when both temperature was above 29 C and salinity was below 25 ppt from the beginning to the end of the period of record varied from 6, 12, and 1 day(s) in 1975 to 72, 68, and 34 days in 2022 for OTB, HB, and MTB, respectively.

[Figure 6](#fig-mixeff) provides visual examples of the mixed-effects models for the estimated number of days over time for each bay segment from 1975 to present when temperature was above 30, salinity was below 25 ppt, and when both occurred (see Figure S6 for 1998 to 2022). Temperature trends were similar among segments, whereas the number of days when salinity was below the threshold decreased with proximity to the Gulf of Mexico ([Table 3](#tbl-mixdaytab)). The number of days when both temperature was above and salinity was below the threshold generally followed the trends for the number of days when salinity was below the threshold. These thresholds were used for comparison to seagrass changes described below, based primarily on the statistical strength of the trends and the variance of counts across stations within each bay segment (points in [Figure 6](#fig-mixeff)). That is, more restrictive thresholds did not provide sufficient counts of days per year to more rigorously develop seagrass response models and the chosen thresholds were based primarily on statistical considerations.

### 3.3 Seagrass response

Linear models to assess the potential effects of temperature and salinity on seagrass change provided modest evidence that seagrass loss after 2016 was influenced by climate stressors. The most parsimonious model for the EPC data included the temperature and salinity metrics as potentially important for explaining inter-annual variation in seagrass frequency occurrence (Adj. R = 0.59, F = 12.82, df = 9, 65, p < 0.005). An interaction of the metrics with time period was also observed, with notable differences by predictor (Figure [7](#fig-sgmod)a, [Table 4](#tbl-modtab)). For the period prior to 2016, frequency occurrence of seagrass increased as the number of days where temperature was above 30 increased, whereas no relationship was observed after 2016. However, the interaction between time period and temperature was not significant, suggesting no difference between time periods. The opposite trend was observed for the number of days when salinity was below 25 ppt, where no relationship was observed prior to 2016 and a decreasing relationship was observed after 2016 (interaction term between salinity and time period was marginally significant, p < 0.1, Figure [7](#fig-sgmod)a, [Table 4](#tbl-modtab)). The interaction between the temperature and salinity metric was included in the most parsimonious model (marginally significant, p < 0.1), although the direction of the relationship of temperature with time period or salinity with time period did not noticeably change using different conditional values for salinity or temperature, respectively. The second model for the EPC data that evaluated the number of days when both temperature was above and salinity was below the threshold was also significant (Adj. R = 0.6, F = 29.17, df = 4, 70, p < 0.005), although the interaction term with time period was not included in the most parsimonious model, suggesting no effect of this metric in describing seagrass change after 2016 ([Table 4](#tbl-modtab)). Note that [Figure 7](#fig-sgmod) shows model predictions for OTB only, although the shape of the relationships do not change for other bay segments other than as additive shifts of the curves up or down (i.e., no interactions of bay segments with the other predictors were in the original models).

The most parsimonious model for the FIM dataset also showed potential temperature and salinity associations with seagrass change after 2016, although explanatory power was lower than the EPC models likely due to larger spread of the data (Adj. R = 0.12, F = 32.75, df = 7, 1659, p < 0.005). Increases in temperature and decreases in salinity were both associated with reductions in percent cover after 2016, whereas no relationships were observed prior to 2016 (p < 0.05 and p < 0.1 for the interactions between temperature or salinity with time period, respectively, Figure [7](#fig-sgmod)b, [Table 4](#tbl-modtab)). The interaction between salinity and temperature was not included as a significant term in the final FIM model. Lastly, the most parsimonious model for the PDEM dataset only included time period as a marginally significant variable and the overall model fit was not significant ([Table 4](#tbl-modtab)).

## 4 Discussion

Global increases in temperature and precipitation related to climate change have contributed to widespread alteration of the structure and functioning of natural environments (Osland et al. 2015; Oliver et al. 2018). At a local scale, these changes have been demonstrated herein for Tampa Bay where the evaluation of long-term trends in water temperature and salinity showed clear changes mirrored by long-term changes in air temperature and precipitation. Over the previous fifty years, Tampa Bay has consistently trended towards hotter and fresher conditions, where water temperature has approximately increased by 0.03 - 0.07 C per year and salinity has decreased by 0.04 - 0.2 ppt per year. These changes were demonstrated in three long-term datasets with different sampling methods and periods of record. Understandably, the trends were most consistently observed in the dataset with the longest period of record (EPC) covering nearly fifty years of monthly observations, with the most dramatic changes occurring during the summer rainy season at locations farther from the mouth of the Bay. These long-term changes manifested into consistent trends in select stressor metrics; the continuous number of days each year when temperature was above and/or salinity was below defined thresholds consistently increased across the period of record. Notably, bottom and surface trends for water temperature and salinity in the EPC dataset were similar, suggesting that any potential stress on biotic resources related to these factors are likely occurring throughout the water column.

Similar regional, long-term changes in coastal waters and estuaries have been observed by others (Nickerson et al. 2023; Shi and Hu In review). Nickerson et al. (2023) evaluated sea surface trends at a larger spatial scale for Tampa Bay, the West Florida Continental Shelf, and the adjacent Gulf of Mexico. Temperature trends were similar for Tampa Bay (the EPC dataset was also used), although the power to detect trends decreased for shorter time periods, as verified herein with the FIM and PDEM datasets. Nickerson et al. (2023) also noted that temperature increases in Tampa Bay were most pronounced in the winter, which somewhat conflicts with our results showing distinct increases in the summer, particularly for the upper bay segments (OTB and HB). However, our assessment evaluated trends at individual EPC stations and bay segments, whereas Nickerson et al. (2023) evaluated the EPC data as an average for the entire bay for consistency of comparison to their larger spatial area and model domain. These differences are understandable given the analysis goals and methods for data synthesis. Our results showing increases in temperature and decreases in salinity for OTB and HB for the summer months are likely related to hydrodynamic characteristics of these segments relative to MTB and LTB that flush more regularly with the Gulf of Mexico. These upper bay segments are more affected by hydrologic inflows (HB), lack of circulation (OTB), or thermal stress related to more rapid warming with shallower depths. Additionally, Shi and Hu (In review) provided a recent assessment of a 2023 heatwave in south Florida, supported by a 20-year trend assessment that suggested estuaries were warming at nearly double the rate of the Gulf of Mexico. The upper limit of our warming estimate for Tampa Bay is comparable.

Our relatively simple modeling approach provided some evidence that climate-related stressors impart some effect on recent seagrass losses in Tampa Bay. The models did not provide a consistent, nor statistically powerful, explanation that increasing temperature and decreasing salinity were key (or the sole) drivers. However, evaluating all models together does suggest a pattern that demonstrates the value of considering multiple datasets and models to explain noisy patterns and compounding ecological processes. Model results for the EPC and FIM datasets both suggested that increasing temperature and decreasing salinity were associated with potential seagrass loss post-2016, described primarily using separate interaction terms of temperature or salinity with time period. For the EPC model, the interaction term was not significant for temperature, whereas the interaction was marginally significant for the salinity metric such that a negative association was observed post-2016 as compared to pre-2016 where frequency occurrence of seagrass declined with the increasing number of days when salinity was below 25 ppt. Likewise, the FIM models had a significant interaction term for the association of temperature with time period and a marginally significant interaction term for the association of salinity with time period, such that percent cover of seagrasses showed a decline with increasing temperature and decreasing salinity post-2016. An important distinction between the EPC and FIM models is that the former evaluated the number of days above/below thresholds each year to quantify increases in annual stress associated with temperature and salinity, whereas the latter evaluated observed temperature and salinity values at the time of seagrass sampling. As such, both models attempted to describe the role of these stressors on potential seagrass change, but use different independent variables given the different sampling designs of each monitoring programs. The FIM model also used water quality measurements collected at the same locations where seagrasses were observed, whereas the EPC model provided a general characterization of seagrass transect data with water quality at stations farther from shore. These differences highlight challenges describing noisy relationships in long-term ecological datasets, while also demonstrating the utility of our weight-of-evidence approach to describe these relationships.

An additional caveat of our models was the use of “thresholds” to define potential stressor metrics for temperature and salinity on an annual time scale. Our choice to use 30 C and 25 ppt for temperature and salinity was primarily a statistical consideration given a consistent increase over time in the number of days when these thresholds were crossed, as shown by the mixed-effects linear models for each bay segment. That is, sufficient change and variation in the independent variables for the models of seagrass change were needed to statistically describe potential relationships. These thresholds are likely not ecologically significant since most of the reported values in tropical and sub-tropical environments suggest that the limits of the ecological niche for seagrasses are higher for temperature and lower for salinity (Phillips 1960; McMillan and Moseley 1967; Zieman 1975; Lirman and Cropper 2003). Because we did not see a dramatic increase in the number of days each year when the thresholds were crossed at more stressful values (i.e., higher temperature, lower salinity), conditions in Tampa Bay in recent years are generally within the ecological niche for seagrasses. This does not suggest that these factors are unimportant, both currently and in the future. Our models suggested that temperature and salinity are potentially associated with seagrass loss and the consistent long-term trend in temperature and salinity imply that these conditions are likely to become more stressful in the future, further confounding seagrass recovery efforts in the region. Moreover, the GAMs used to model continuous temperature and salinity at each EPC monitoring station likely did not fully describe the current extent of stress given that extreme low or high values were not often captured by the daily modeled predictions (Figure S5). Regardless of the above limitations, climate stressors are likely to affect Tampa Bay’s seagrass ecology in the future, as suggested by our results.

Additional limitations of our model may relate to an incomplete description of factors influencing seagrass growth. This relates to the inclusion of additional drivers as well as issues related to correlation/causation. For the former, the primary management paradigm in Tampa Bay for the past three decades has relied on the role of nutrients, external nitrogen inputs in particular, in affecting light environments for seagrass growth (Greening et al. 2014; Sherwood et al. 2017). As such, light attenuation or water clarity could have been included in our models to more completely describe factors influencing growth, i.e., the residual differences after accounting for light attenuation could additionally be explained by temperature or salinity. Our use of time period (pre-/post-2016) as a categorical variable partially addressed this issue. Modeling seagrass change as related to temperature or salinity for the entire record would have shown a spurious correlation of both with seagrass given the long-term recovery of seagrass. Thus, time period was necessary to control for these confounding relationships. Additionally, light attenuation has been relatively consistent since 2016 and within the limits estimated to be supportive of seagrass growth in Tampa Bay, particularly in OTB where the most loss occurred (Janicki and Wade 1996; Beck 2020a). This suggests that other factors are influencing seagrass growth and the inclusion of light attenuation in the models was likely not critical for describing the roles of temperature and salinity. A final consideration for our models relates to how seagrasses may influence their environment, particularly for the PDEM and FIM datasets where temperature and salinity were measured at the same locations as seagrass. For example, temperature may simply be higher in locations where seagrasses are present and can absorb solar radiation, i.e., seagrasses may be influencing their environment rather than the environment influencing seagrasses. This explanation cannot be ruled out with the existing datasets, although the trend analyses and models suggest that climate-related stressors driving seagrass loss is a more likely scenario. This is especially true for water temperature trends captured by the EPC dataset which includes deeper, fixed sites adjacent to shallow seagrass flats.

The seagrass loss in Tampa Bay since 2016 is a notable phenomenon that is not limited to our study area (Lizcano-Sandoval et al. 2022). Losses have been observed throughout southwest Florida during this time period, including Sarasota Bay directly south of Tampa Bay and Charlotte Harbor further south. These regional losses suggest that large-scale stressors are driving these changes, leading us to our initial hypothesis that climate-related stressors could partially explain the change in Tampa Bay. Based on our results, the losses elsewhere may potentially be explained by temperature and salinity and are worth exploring in other southwest Florida coastal regions and estuaries where long-term datasets exist. Additional factors that could explain these changes are also likely co-occurring with climate stress, some of which are unique to Tampa Bay and others that are more likely pervasive. For Tampa Bay, annual summer/fall blooms of the toxic dinoflagellate *Pyrodinium bahamense* have occurred in OTB since 2008 (Usup et al. 1994; Lopez et al. 2023) and the specific relationships of these blooms with seagrass change is unclear, although the expectation is that seagrass growth may be limited by the degradation of the light environment with algal growth. These blooms are exacerbated by the hydrologic conditions in OTB that contribute to relatively longer water residence times (Phlips et al. 2006; Lopez et al. 2021). The effect of warming temperature and decreasing salinity in OTB will further complicate the understanding of how these blooms manifest and persist each year (e.g., Stelling et al. 2023), and ultimately contribute to changes in the light environment affecting seagrass resources in this bay segment.

Additional biotic factors could be influencing regional patterns in seagrass growth. In Tampa Bay and elsewhere, enhanced macroalgal production may also influence seagrass growth and recovery in Florida estuaries (L. M. Hall et al. 2022; Janicki Environmental, Inc. 2022; Brewton and Lapointe 2023; Scolaro et al. 2023). Attached macroalgae abundance has increased over time and has been observed to colonize locations where seagrass was formerly present in Tampa Bay (Beck 2020b). Competitive differences between seagrasses and macroalgae are poorly understood in these systems (but see Bell and Hall 1997; Brewton and Lapointe 2023), in addition to insufficient macroalgae data in Tampa Bay that cannot clearly describe seasonal growth and distribution patterns and nutrient cycling. Discrete pollutant loading events in Tampa Bay have been documented to promote both phytoplankton and macroalgae growth (Beck et al. 2022; Scolaro et al. 2023; Tomasko 2023). The role that evolving nutrient loading and changing climatic conditions may have on Tampa Bay’s primary producers – particularly algal and seagrass growth and interactions in recent years – is less understood. Finally, additional research has focused on how diseases and pathogens can influence seagrass growth patterns in Florida (Robblee et al. 1991; Van Bogaert et al. 2018; Duffin et al. 2021). For example, the parasitic slime mold *Labryinthula* spp. that causes seagrass wasting disease has been known to infect *Thalassia testudinium* in Tampa Bay (Blakesley et al. 2001), although it is unclear if these infections have had large-scale, population-level effects. Existing research has primarily focused on describing spatial patterns, past die-off events, or immunology of these pathogens (Robblee et al. 1991; Duffin et al. 2021). More research should be directed towards the influence of climate stressors on seagrass pathogen vulnerability.

Lastly, our result showing that salinity has decreased in Tampa Bay is generally contrary to expectations for coastal systems consistent with sea-level rise projections (Costa et al. 2023; Alarcon et al. 2024). Salinity changes with sea-level rise have caused numerous alterations of subtidal and nearshore habitats (Brinson et al. 1995; White and Kaplan 2017). In southwest Florida, the most common ecological example is the expansion of mangroves upland as porewater salinity and water levels have gradually increased over the past few decades (Borchert et al. 2018). Alteration of salinity regimes for surface and groundwater resources are also well documented. In Florida Bay, for example, widespread decline of *Thalassia testudinium* has been partially attributed to elevated salinity levels beyond the optimal range for the species (Margaret O. Hall et al. 2016). Sea level rise is further altering salinity dynamics in the region. Dessu et al. (2018) noted that sea level rise is expected to have the largest effect on salinity changes during periods of low freshwater outflow from the Florida Everglades, emphasizing that measured salinity represents the relative contributions of oceanic and freshwater surface waters. In Tampa Bay, the long-term trends of decreasing salinity, especially in the upper bay segments, suggest that the hydrologic load into the system has had a greater influence on salinity regimes than the effects of sea-level rise. This hypothesis is supported by our assessment of precipitation patterns over time, where the long-term increase is inversely correlated with the decrease in salinity.

### 4.1 Conclusions

This study provided a detailed assessment of long-term water temperature and salinity changes in Tampa Bay supported by datasets from three long-term monitoring programs of different length and sampling design. An evaluation of each dataset showed a clear pattern of increasing temperature and decreasing salinity mirrored by long-term changes in air temperature and precipitation, suggesting that Tampa Bay has become hotter and fresher with the trends likely continuing in the future. Simple regression models provided weak, but partially-supporting evidence, that these changes can be linked to recent seagrass losses since 2016. Our models suggested that rising temperatures and decreasing salinities are additively affecting seagrasses, rather than multiplicatively, as evidenced by lack of significant interactions of these stressors. Future analyses may show more significant associations between physical habitat conditions and seagrass change as the trends are very likely to continue to push seagrasses further outside of their tolerance ranges. These analyses should be supported by additional data collection efforts, particularly high-resolution continuous monitoring data that provide a more precise assessment of diurnal stress across multiple time-scales.

Natural resource managers should consider how these climate-related stressors may alter the effectiveness of intervention activities aimed at protecting ecological resources in Tampa Bay. Management actions that have historically been effective may have inadequate capacity to maintain ecosystem status due to changing resilience of ecological resources affected by climate change. For example, nitrogen load reductions have been effective at restoring seagrass in Tampa Bay, primarily due to wastewater load allocations being constrained to the historical nutrient assimilative capacity of Tampa Bay (Greening and Janicki 2006; Greening et al. 2014). As Tampa Bay becomes hotter and fresher, similar load allocations may no longer be effectively assimilated and algal and seagrass ecology dynamics may shift. Strategies that mimic or restore pre-development hydrology or that further reduce allowable load inputs from regulated entities (e.g., additional stormwater controls, hydrological modifications) may be needed to confer additional resilience and adaptive capacity for seagrass in Tampa Bay. These considerations are especially critical for upper parts of Tampa Bay where a majority of seagrass loss has occurred and where temperature and salinity trends have been most pronounced. Reversal of recent trends may be more likely to occur if aggressive actions and controls are pursued sooner rather than later, given the challenges of restoring degraded estuarine ecosystems due to hysteresis.

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## Figures

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| Figure 1: Map of Tampa Bay and the three datasets used for trend analysis, including (a) bay segments, 2022 seagrass coverage (green), and transect starting points (black), (b) Environmental Protection Commission (EPC) long-term monitoring sites, (c) Fisheries Independent Monitoring (FIM) random sampling for seine hauls, and (d) OTB portion of Pinellas County Department of Environmental Management (PDEM) random sampling. Date ranges for each dataset are shown in the title. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. |

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| Figure 2: Seagrass changes over time in Tampa Bay for (a) areal coverage 1988 - 2022 from mapping and (b) frequency occurrence of major species 1998 - 2022 from annual transect monitoring. Changes are shown for major bay segments. Red lines in (a) show approximate capacity of seagrass coverage based on the baywide target of 40,000 acres. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. |

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| Figure 3: Conceptual stressor diagram demonstrating a two-dimensional niche space for temperature and salinity. Tampa Bay is trending towards the bottom right. |

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| Figure 4: Long-term air temperature, precipitation (Jun-Aug), hydrologic load, Standard Precipitation Index (SPI), water temperature, and salinity trends from 1975 to 2022. The color shades for water temperature and salinity indicate sampling location and values shown are the averages (95% confidence interval) across all Environmental Protection Commission (EPC) stations in each bay segment and sampling months for each year. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. |

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| Figure 5: Trends from 1975 to 2022 for bottom water temperature and salinity measurements at long-term monitoring stations in Tampa Bay. Results for seasonal Kendall tests by station are shown in (a) with color and shape corresponding to the estimated annual slope as change per year (yr). Summarized seasonal trends by month are shown as (b) the percent of stations in each bay segment with significant increasing (temperature) or decreasing (salinity) trends. Bay segment outlines are shown in (a); OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. |

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| Figure 6: Example of mixed effects models for the estimated number of days per year that temperature (red) or salinity (blue) were above or below thresholds of 30 C or 25 psu, respectively, from the EPC data. The bottom row (black) shows the number of days when both temperature was above and salinity was below the thresholds. The models included station as a random effect for each bay segment, with grey lines indicating individual station trends, grey points as actual number of days, and thicker lines indicating the overall model fit. Slopes for significant models are shown in the bottom left of each facet. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. |

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| Figure 7: Predicted results from generalized linear models evaluating seagrass changes versus temperature or salinity predictors for the (a) EPC and (b) FIM datasets. Results are shown only for OTB, although the shape of the relationships do not change between bay segments. The predictors for (a) were the number of days when temperature was above the threshold and the number of days when salinity was below the threshold. The predictors for (b) were measured temperature and salinity at the bottom of the water column. Time periods were seagrass recovery prior to 2016 and seagrass decline after 2016. Shaded areas are 95% confidence intervals. Points are observed data that include aggregated effects of bay segment included in the models. |

## Tables

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| Table 1: Bottom temperature trends (C) by bay segments and datasets. Start year describes the range of the trend test to the present year (2022). The starting value is the estimated temperature at the start year and the end value is the estimated temperature at 2022. Total change is the difference between the two. Datasets evaluated were from the Environmental Protection Commission of Hillsborough County (EPC), Fisheries Independent Monitoring (FIM), and Pinellas County Department of Environmental Management (PDEM). Note that PDEM includes data only for the western portion of Old Tampa Bay from 2004 to present and EPC is the only dataset beginning prior to 1996. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. \*\* p < 0.005, \* p < 0.05   | Start year | Bay segment | Dataset | Change / year | Start value | End value | Total change | | --- | --- | --- | --- | --- | --- | --- | | 1976 | OTB | EPC | 0.03\*\* | 23.3 | 24.7 | 1.4 | |  | HB | EPC | 0.04\*\* | 23.2 | 25.2 | 2.0 | |  | MTB | EPC | 0.04\*\* | 23.3 | 24.9 | 1.6 | |  | LTB | EPC | 0.03\*\* | 23.3 | 24.8 | 1.5 | | 1996 | OTB | EPC | 0.04\* | 23.6 | 24.8 | 1.2 | |  |  | FIM | 0.05\* | 23.5 | 24.7 | 1.2 | |  | HB | EPC | 0.06\*\* | 23.8 | 25.3 | 1.5 | |  |  | FIM | 0.04 | 24.1 | 25.0 | 0.9 | |  | MTB | EPC | 0.04\*\* | 23.8 | 24.8 | 1.0 | |  |  | FIM | 0.02 | 24.0 | 24.7 | 0.7 | |  | LTB | EPC | 0.03\* | 23.9 | 24.8 | 0.9 | |  |  | FIM | 0.02 | 24.0 | 24.6 | 0.6 | | 2004 | OTB | EPC | 0.06\* | 23.8 | 25.0 | 1.2 | |  |  | FIM | 0.07\* | 23.6 | 24.9 | 1.3 | |  |  | PDEM | 0.05 | 24.4 | 25.2 | 0.8 | |  | HB | EPC | 0.09\*\* | 23.9 | 25.5 | 1.6 | |  |  | FIM | 0.1\* | 23.7 | 25.4 | 1.7 | |  | MTB | EPC | 0.07\*\* | 23.8 | 25.0 | 1.2 | |  |  | FIM | 0.07 | 23.8 | 25.0 | 1.2 | |  | LTB | EPC | 0.06\* | 23.8 | 25.0 | 1.2 | |  |  | FIM | 0.05 | 23.9 | 24.8 | 0.9 | |

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| Table 2: Bottom salinity trends (ppt) by bay segments and datasets. Start year describes the range of the trend test to the present year (2022). The starting value is the estimated salinity at the start year and the end value is the estimated salinity at 2022. Total change is the difference between the two. Datasets evaluated were from the Environmental Protection Commission of Hillsborough County (EPC), Fisheries Independent Monitoring (FIM), and Pinellas County Department of Environmental Management (PDEM). Note that PDEM includes data only for the western portion of Old Tampa Bay from 2004 to present and EPC is the only dataset beginning prior to 1996. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay. \*\* p < 0.005, \* p < 0.05   | Start year | Bay segment | Dataset | Change / year | Start value | End value | Total change | | --- | --- | --- | --- | --- | --- | --- | | 1976 | OTB | EPC | -0.06\* | 25.8 | 23.1 | -2.7 | |  | HB | EPC | -0.02 | 25.6 | 24.6 | -1.0 | |  | MTB | EPC | -0.03 | 28.2 | 26.6 | -1.6 | |  | LTB | EPC | -0.04\*\* | 33.4 | 31.3 | -2.1 | | 1996 | OTB | EPC | -0.08 | 24.9 | 22.8 | -2.1 | |  |  | FIM | -0.06 | 24.1 | 22.6 | -1.5 | |  | HB | EPC | -0.08 | 26.1 | 23.9 | -2.2 | |  |  | FIM | 0 | 24.0 | 24.0 | 0.0 | |  | MTB | EPC | -0.07 | 28.0 | 26.3 | -1.7 | |  |  | FIM | -0.03 | 26.6 | 25.8 | -0.8 | |  | LTB | EPC | -0.04 | 32.5 | 31.4 | -1.1 | |  |  | FIM | 0.01 | 31.6 | 32.0 | 0.4 | | 2004 | OTB | EPC | -0.2\* | 25.5 | 22.0 | -3.5 | |  |  | FIM | -0.15 | 24.7 | 21.9 | -2.8 | |  |  | PDEM | -0.19 | 24.3 | 20.9 | -3.4 | |  | HB | EPC | -0.19\* | 26.5 | 23.1 | -3.4 | |  |  | FIM | -0.08 | 24.8 | 23.4 | -1.4 | |  | MTB | EPC | -0.17\* | 28.6 | 25.6 | -3.0 | |  |  | FIM | -0.11 | 27.2 | 25.2 | -2.0 | |  | LTB | EPC | -0.12\* | 33.0 | 30.9 | -2.1 | |  |  | FIM | -0.05 | 32.5 | 31.5 | -1.0 | |

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| Table 3: Summary of mixed-effects models evaluating increases in the number of days each year from 1975 to 2022 when temperature was above 30 C, salinity was below 25 ppt, or both temperature and salinity were above/below the thresholds. The start and end columns show the estimated number of days at the beginning and end of the period of record when temperature or salinity were above or below the thresholds. Values are the estimated mean number of days (plus standard error) from 1975 and 2022. \*\* p < 0.005, \* p < 0.05. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay, LTB: Lower Tampa Bay.   | Bay Segment | Threshold | Slope | Start | End | | --- | --- | --- | --- | --- | | OTB | Temperature > 30 | 1.04\*\* | 8 (3.3) | 56 (3.3) | |  | Salinity < 25 | 1.96\*\* | 128 (13.2) | 219 (13.2) | |  | Both | 0.81\*\* | 0 (2.8) | 37 (2.7) | | HB | Temperature > 30 | 1.01\*\* | 8 (4.9) | 55 (4.8) | |  | Salinity < 25 | 0.86\* | 131 (12.5) | 171 (11.8) | |  | Both | 0.8\*\* | -2 (2.8) | 35 (2.7) | | MTB | Temperature > 30 | 1.06\*\* | 9 (3.1) | 57 (3.1) | |  | Salinity < 25 | 0.67\*\* | 51 (11) | 82 (11) | |  | Both | 0.37\*\* | -1 (1.7) | 16 (1.7) | | LTB | Temperature > 30 | 0.92\*\* | 21 (3.5) | 63 (3.5) | |  | Salinity < 25 | -0.06 | 4 (1.3) | 1 (1.3) | |  | Both | 0 | 0 (0) | 0 (0) | |

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| Table 4: Summary of the most parsimonious Generalized Linear Models (GLMs) developed to evaluate the effects of temperature and salinity variables on seagrass change between time periods. Models were developed for different datasets described in the model column. The significant intercept term for each model is not shown and described factor conditions not explicitly shown by the remaining terms (e.g., OTB and pre-2016). The model term estimates include the standard error in parentheses. Note that the “Temp” and “Sal” terms for the EPC models describe metrics that measure the number of days when temperature was above or salinity was below a threshold value, whereas the terms in all other models describe observed temperature or salinity (see text for description). \*\* p < 0.005, \* p < 0.05, p < 0.1. EPC: Environmental Protection Commission, FIM: Fisheries Independent Monitoring, PDEM: Pinellas County Department of Environmental Management. OTB: Old Tampa Bay, HB: Hillsborough Bay, MTB: Middle Tampa Bay.   | Model | Term | Estimate | t-statistic | | --- | --- | --- | --- | | EPC 1 | Sal | 0.00069 (0.00037) | 1.8 | |  | Temp | 0.0035 (0.0013) | 2.6\* | |  | Time\_post | 0.48 (0.28) | 1.7 | |  | Baysegment\_HB | -0.39 (0.042) | -9.3\*\* | |  | Baysegment\_MTB | -0.12 (0.047) | -2.6\* | |  | Sal:Temp | -1.3e-05 (7.5e-06) | -1.7 | |  | Sal:Time\_post | -0.0027 (0.0015) | -1.8 | |  | Temp:Time\_post | -0.0056 (0.0052) | -1.1 | |  | Sal:Temp:Time\_post | 3.6e-05 (2.6e-05) | 1.4 | | EPC 2 | Both | 0.0028 (0.00082) | 3.4\*\* | |  | Time\_post | 0.059 (0.039) | 1.5 | |  | Baysegment\_HB | -0.38 (0.04) | -9.4\*\* | |  | Baysegment\_MTB | -0.062 (0.042) | -1.5 | | FIM | Sal | 0.043 (0.22) | 0.2 | |  | Temp | 0.052 (0.42) | 0.12 | |  | Time\_post | 52 ( 32) | 1.6 | |  | Baysegment\_MTB | 33 (2.5) | 13\*\* | |  | Baysegment\_OTB | 28 (2.2) | 13\*\* | |  | Sal:Time\_post | 0.93 (0.5) | 1.8 | |  | Temp:Time\_post | -2.4 (1.1) | -2.2\* | | PDEM | Time\_post | -0.45 (0.24) | -1.8 | |

## References

Alarcon, V. J., A. C. Linhoss, C. R. Kelble, P. F. Mickle, A. Fine, and E. Montes. 2024. Potential challenges for the restoration of Biscayne Bay (Florida, USA) in the face of climate change effects revealed with predictive models. *Ocean & Coastal Management* 247: 106929. <https://doi.org/10.1016/j.ocecoaman.2023.106929>.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>.

Beck, M. W. 2020a. tbep-tech/wq-dash: v1.0 (version v1.0). Zenodo. <https://doi.org/10.5281/zenodo.3648664>.

Beck, M. W. 2020b. tbep-tech/seagrasstransect-dash: v1.0 (version v1.0). Zenodo. <https://doi.org/10.5281/zenodo.4319936>.

Beck, M. W., A. Altieri, C. Angelini, M. C. Burke, J. Chen, D. W. Chin, J. Gardiner, et al. 2022. Initial estuarine response to inorganic nutrient inputs from a legacy mining facility adjacent to Tampa Bay, Florida. *Marine Pollution Bulletin* 178: 113598. <https://doi.org/10.1016/j.marpolbul.2022.113598>.

Beck, M. W., D. E. Robison, G. E. Raulerson, M. C. Burke, J. Saarinen, C. Sciarrino, E. T. Sherwood, and D. A. Tomasko. 2023. Addressing climate change and development pressures in an urban estuary through habitat restoration planning. *Frontiers in Ecology and Evolution* 11: 1070266. <https://doi.org/10.3389/fevo.2023.1070266>.

Beck, M. W., M. Schrandt, M. Wessel, E. T. Sherwood, G. E. Raulerson, A. Prasad, and B. Best. 2021. tbeptools: An R package for synthesizing estuarine data for environmental research. *Journal of Open Source Software* 6: 3485. <https://doi.org/10.21105/joss.03485>.

Beck, M. W., E. T. Sherwood, J. R. Henkel, K. Dorans, K. Ireland, and P. Varela. 2019. Assessment of the cumulative effects of restoration activities on water quality in Tampa Bay, Florida. *Estuaries and Coasts* 42: 1774–1791. <https://doi.org/10.1007/s12237-019-00619-w>.

Beguería, S., and S. M. Vicente-Serrano. 2023. [SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index](https://CRAN.R-project.org/package=SPEI) (version R package version 1.8.1).

Beguería, S., S. M. Vicente-Serrano, F. Reig, and B. Latorre. 2013. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology* 34: 3001–3023. <https://doi.org/10.1002/joc.3887>.

Bell, S., and M. Hall. 1997. Drift macroalgal abundance in seagrass beds: investigating large-scale associations with physical and biotic attributes. *Marine Ecology Progress Series* 147: 277–283. <https://doi.org/10.3354/meps147277>.

Blakesley, B., P. Hall, D. Berns, J. Hyniova, M. Merello, and R. Conroy. 2001. [*Survey of the distribution of the marine slime mold Labyrinthula sp. in the seagrass Thalassia testudinum in the Tampa Bay area, fall 1999-fall 2000*](https://drive.google.com/file/d/1tUkGW7TRAJ_skWj-UemDVIJnUAsy0ITf/view?usp=drivesdk). 01-01. St. Petersburg, Florida: Tampa Bay Estuary Program.

Boesch, D. F., R. B. Brinsfield, and R. E. Magnien. 2001. Chesapeake bay eutrophication: Scientific understanding, ecosystem restoration, and challenges for agriculture. *Journal of Environmental Quality* 30: 303–320. <https://doi.org/10.2134/jeq2001.302303x>.

Borchert, S. M., M. J. Osland, N. M. Enwright, and K. T. Griffith. 2018. Coastal wetland adaptation to sea level rise: Quantifying potential for landward migration and coastal squeeze. *Journal of Applied Ecology* 55: 2876–2887. <https://doi.org/10.1111/1365-2664.13169>.

Brewton, R. A., and B. E. Lapointe. 2023. The green macroalga *Caulerpa prolifera* replaces seagrass in a nitrogen enriched, phosphorus limited, urbanized estuary. *Ecological Indicators* 156: 111035. <https://doi.org/10.1016/j.ecolind.2023.111035>.

Brinson, M. M., R. R. Christian, and L. K. Blum. 1995. Multiple states in the sea-level induced transition from terrestrial forest to estuary. *Estuaries* 18: 648–659. <https://doi.org/10.2307/1352383>.

Burkholder, J. M., D. A. Tomasko, and B. W. Touchette. 2007. Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology* 350: 46–72. <https://doi.org/10.1016/j.jembe.2007.06.024>.

Chamberlain, S., and D. Hocking. 2023. [rnoaa: NOAA weather data from R](https://CRAN.R-project.org/package=rnoaa) (version R package version 1.4.0).

Costa, Y., I. Martins, G. C. de Carvalho, and F. Barros. 2023. Trends of sea-level rise effects on estuaries and estimates of future saline intrusion. *Ocean & Coastal Management* 236: 106490. <https://doi.org/10.1016/j.ocecoaman.2023.106490>.

Dessu, S. B., R. M. Price, T. G. Troxler, and J. S. Kominoski. 2018. Effects of sea-level rise and freshwater management on long-term water levels and water quality in the Florida Coastal Everglades. *Journal of Environmental Management* 211: 164–176. <https://doi.org/10.1016/j.jenvman.2018.01.025>.

Duarte, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112. <https://doi.org/10.1080/00785236.1995.10422039>.

Duarte, C. M., W. C. Dennison, R. J. W. Orth, and T. J. B. Carruthers. 2008. The charisma of coastal ecosystems: Addressing the imbalance. *Estuaries and Coasts* 31: 233–238. <https://doi.org/10.1007/s12237-008-9038-7>.

Duffin, P., D. L. Martin, B. T. Furman, and C. Ross. 2021. Spatial patterns of *Thalassia testudinum* immune status and *Labyrinthula* spp. load implicate environmental quality and history as modulators of defense strategies and wasting disease in Florida Bay, United States. *Frontiers in Plant Science* 12: 612947. <https://doi.org/10.3389/fpls.2021.612947>.

Dunic, J. C., C. J. Brown, R. M. Connolly, M. P. Turschwell, and I. M. Côté. 2021. Long-term declines and recovery of meadow area across the world’s seagrass bioregions. *Global Change Biology* 27: 4096–4109. <https://doi.org/10.1111/gcb.15684>.

Dunic, J. C., and I. M. Côté. 2023. Management thresholds shift under the influence of multiple stressors: Eelgrass meadows as a case study. *Conservation Letters* 16: e12938. <https://doi.org/10.1111/conl.12938>.

Fourqurean, J. W., C. M. Duarte, H. Kennedy, N. Marbà, M. Holmer, M. A. Mateo, E. T. Apostolaki, et al. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5: 505–509. <https://doi.org/10.1038/ngeo1477>.

Garrett, M., J. Wolny, E. Truby, C. Heil, and C. Kovach. 2011. Harmful algal bloom species and phosphate-processing effluent: Field and laboratory studies. *Marine Pollution Bulletin* 62: 596–601. <https://doi.org/10.1016/j.marpolbul.2010.11.017>.

Greening, H. S., and A. Janicki. 2006. Toward reversal of eutrophic conditions in a subtropical estuary: Water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. *Environmental Management* 38: 163–178. <https://doi.org/10.1007/s00267-005-0079-4>.

Greening, H. S., A. Janicki, E. T. Sherwood, R. Pribble, and J. O. R. Johansson. 2014. Ecosystem responses to long-term nutrient management in an urban estuary: Tampa Bay, Florida, USA. *Estuarine, Coastal and Shelf Science* 151: A1–A16. <https://doi.org/10.1016/j.ecss.2014.10.003>.

Hall, L. M., L. J. Morris, R. H. Chamberlain, M. D. Hanisak, R. W. Virnstein, R. Paperno, B. Riegl, L. R. Ellis, A. Simpson, and C. A. Jacoby. 2022. Spatiotemporal patterns in the biomass of drift macroalgae in the Indian River Lagoon, Florida, United States. *Frontiers in Marine Science* 9: 767440. <https://doi.org/10.3389/fmars.2022.767440>.

Hall, Margaret O., M. J. Durako, J. W. Fourqurean, and J. C. Zieman. 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22: 445. <https://doi.org/10.2307/1353210>.

Hall, Margaret O., B. T. Furman, M. Merello, and M. J. Durako. 2016. Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: Initial observations. *Marine Ecology Progress Series* 560: 243–249. <https://doi.org/10.3354/meps11923>.

Han, Q., and D. Liu. 2014. Macroalgae blooms and their effects on seagrass ecosystems. *Journal of Ocean University of China* 13: 791–798. <https://doi.org/10.1007/s11802-014-2471-2>.

Hensel, M. J. S., C. J. Patrick, R. J. Orth, D. J. Wilcox, W. C. Dennison, C. Gurbisz, M. P. Hannam, et al. 2023. Rise of *Ruppia* in Chesapeake Bay: Climate change-driven turnover of foundation species creates new threats and management opportunities. *Proceedings of the National Academy of Sciences* 120. <https://doi.org/10.1073/pnas.2220678120>.

Hirsch, R. M., J. R. Slack, and R. A. Smith. 1982. Techniques of trend analysis for monthly water quality data. *Water Resources Research* 18: 107–121. <https://doi.org/10.1029/wr018i001p00107>.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427. <https://doi.org/10.1101/sqb.1957.022.01.039>.

Janicki, A. J., and D. L. Wade. 1996. [*Estimating critical nitrogen loads for the Tampa Bay Estuary: An empirically based approach to setting management targets*](https://drive.google.com/file/d/1kZkvuprvsMyN9nPS5PHYvXHyo1KQxKTr/view?usp=drivesdk). 06-96. St. Petersburg, Florida: Tampa Bay Estuary Program.

Janicki Environmental, Inc. 2022. [*Identifying potential drivers of change in seagrass and algal community composition in SWFL aquatic preserves*](https://sarasota.wateratlas.usf.edu/upload/documents/Final_AP_Seagrass_Report_040422.pdf). Charlotte Harbor; Estero Bay Aquatic Preserves.

Janicki Environmental, Inc. 2023. [*Estimates of total nitrogen, total phosphorus, total suspended solids, and biological oxygen demand loadings to Tampa Bay, Florida: 2017-2021*](https://drive.google.com/file/d/1KARuSC5fGx05MuT1wiOQFWNXysBokkQl/view?usp=share_link). 06-23. St. Petersburg, Florida: Tampa Bay Estuary Program.

Johansson, J. O. R. 2016. [*Seagrass transect monitoring in Tampa Bay: A summary of findings from 1997 through 2015*](https://drive.google.com/file/d/1Z_8L9sYQWSl1hon1tP1Y8zBo7MHQK9zC/view?usp=drivesdk). 08-16. St. Petersburg, Florida: Tampa Bay Estuary Program.

Johansson, J. O. R., and Janicki Environmental, Inc. 2015. [*Long-term underwater light climate variation and submerged seagrass trends in Tampa Bay, Florida: With a discussion of phytoplankton and CDOM interactions*](https://drive.google.com/file/d/19bNEs2qy6z0hXa1IE7OtbFTjqk1LarFN/view?usp=drivesdk). 06-15. St. Petersburg, Florida: Tampa Bay Estuary Program.

Lefcheck, J. S., R. J. Orth, W. C. Dennison, D. J. Wilcox, R. R. Murphy, J. Keisman, C. Gurbisz, et al. 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proceedings of the National Academy of Sciences* 115: 3658–3662. <https://doi.org/10.1073/pnas.1715798115>.

Lefcheck, J. S., D. J. Wilcox, R. R. Murphy, S. R. Marion, and R. J. Orth. 2017. Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Global Change Biology* 23: 3474–3483. <https://doi.org/10.1111/gcb.13623>.

Lewis III, R. R., M. Durako, M. Moffler, and R. Phillips. 1985. [Seagrass meadows of Tampa Bay - a review](https://drive.google.com/file/d/1sNp3FpjdeOjATZ9nDRRAiXEOqQen9W_p/view?usp=sharing). In *Proceedings, Tampa Bay Area Scientific Information Symposium, May 1982*, ed. S. F. Treat, J. L. Simon, R. R. Lewis III, and R. L. Whitman Jr., 210–246. Tampa, Florida: Bellweather Press.

Lirman, D., and W. P. Cropper. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries* 26: 131–141. <https://doi.org/10.1007/bf02691700>.

Lizcano-Sandoval, L., C. Anastasiou, E. Montes, G. E. Raulerson, E. T. Sherwood, and F. E. Muller-Karger. 2022. Seagrass distribution, areal cover, and changes (1990-2021) in coastal waters off West-Central Florida, USA. *Estuarine, Coastal and Shelf Science* 279: 108134. <https://doi.org/10.1016/j.ecss.2022.108134>.

Lopez, C. B., S. Shankar, S. G. Kaminski, M. Garrett, and K. A. Hubbard. 2021. [*Linking Pyrodinium bahamense physiology and behavior to population growth and loss in nature and implications for management*](https://drive.google.com/file/d/1iXX_JZP5fLS3ORIkFb7WwNYv8HjpHyKw/view?usp=sharing). 07a-21. St. Petersburg, Florida: Tampa Bay Estuary Program.

Lopez, C. B., S. Shankar, S. G. Kaminski, and K. A. Hubbard. 2023. *Pyrodinium bahamense* bloom dynamics in Old Tampa Bay, FL, with a focus on Feather Sound. *Florida Scientist* 86: 62–71.

Luther, M. E., and S. D. Meyers. 2022. [*Designing a genetic algorithm for the selection of causeway cut-throughs in Old Tampa Bay: Planning and prototyping*](https://drive.google.com/file/d/1-1Jq9vly5EvVwEp698brlBucXjSMDbNn/view?usp=sharing). 08-22. St. Petersburg, Florida: Tampa Bay Estuary Program.

Madeira, D., L. Narciso, H. N. Cabral, and C. Vinagre. 2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea Research* 70: 32–41. <https://doi.org/10.1016/j.seares.2012.03.002>.

Maxwell, P. S., J. S. Eklöf, M. M. van Katwijk, K. R. O’Brien, M. de la Torre-Castro, C. Boström, T. J. Bouma, et al. 2016. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems - a review. *Biological Reviews* 92: 1521–1538. <https://doi.org/10.1111/brv.12294>.

McMillan, C., and F. N. Moseley. 1967. Salinity Tolerances of Five Marine Spermatophytes of Redfish Bay, Texas. *Ecology* 48: 503–506. <https://doi.org/10.2307/1932688>.

Millard, S. P. 2013. [*EnvStats: An R package for environmental statistics*](https://www.springer.com). New York: Springer.

Moreno-Marín, F., F. G. Brun, and M. F. Pedersen. 2018. Additive response to multiple environmental stressors in the seagrass *Zostera marina* L. *Limnology and Oceanography* 63: 1528–1544. <https://doi.org/10.1002/lno.10789>.

Morrison, G., E. T. Sherwood, R. Boler, and J. Barron. 2006. Variations in water clarity and chlorophylla in Tampa Bay, Florida, in response to annual rainfall, 19852004. *Estuaries and Coasts* 29: 926–931. <https://doi.org/10.1007/bf02798652>.

Nickerson, A. K., R. H. Weisberg, L. Zheng, and Y. Liu. 2023. Sea surface temperature trends for Tampa Bay, West Florida Shelf and the deep Gulf of Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography* 211: 105321. <https://doi.org/10.1016/j.dsr2.2023.105321>.

Oliver, E. C. J., M. G. Donat, M. T. Burrows, P. J. Moore, D. A. Smale, L. V. Alexander, J. A. Benthuysen, et al. 2018. Longer and more frequent marine heatwaves over the past century. *Nature Communications* 9. <https://doi.org/10.1038/s41467-018-03732-9>.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, et al. 2006. A global crisis for seagrass ecosystems. *BioScience* 56: 987–996. <https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2>.

Orth, R. J., W. C. Dennison, J. S. Lefcheck, C. Gurbisz, M. Hannam, J. Keisman, J. B. Landry, et al. 2017. Submersed aquatic vegetation in Chesapeake Bay: Sentinel species in a changing world. *BioScience* 67: 698–712. <https://doi.org/10.1093/biosci/bix058>.

Orth, R. J., and K. L. Heck. 2023. The dynamics of seagrass ecosystems: History, past accomplishments, and future prospects. *Estuaries and Coasts* 46: 1653–1676. <https://doi.org/10.1007/s12237-023-01252-4>.

Orth, R. J., J. S. Lefcheck, K. S. McGlathery, L. Aoki, M. W. Luckenbach, K. A. Moore, M. P. J. Oreska, R. Snyder, D. J. Wilcox, and B. Lusk. 2020. Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. *Science Advances* 6: 1–9. <https://doi.org/10.1126/sciadv.abc6434>.

Osland, M. J., N. M. Enwright, R. H. Day, C. A. Gabler, C. L. Stagg, and J. B. Grace. 2015. Beyond just sea-level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology* 22: 1–11. <https://doi.org/10.1111/gcb.13084>.

Phillips, R. C. 1960. *Observations on the ecology and distribution of the florida seagrasses*. 44. Florida State Board of Conservation, Marine Laboratory.

Phlips, J., S. Badylak, E. Bledsoe, and M. Cichra. 2006. Factors affecting the distribution of *Pyrodinium bahamense var. bahamense* in coastal waters of Florida. *Marine Ecology Progress Series* 322: 99–115. <https://doi.org/10.3354/meps322099>.

Rasheed, M., and R. Unsworth. 2011. Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. *Marine Ecology Progress Series* 422: 93–103. <https://doi.org/10.3354/meps08925>.

Robblee, M. B., T. Barber, P. Carlson Jr, M. Durako, J. W. Fourqurean, L. Muehlstein, D. Porter, L. Yarbro, R. Zieman, and J. C. Zieman. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71: 297–299.

Robison, D., T. Ries, J. Saarinen, D. A. Tomasko, and C. Sciarrino. 2020. [*Tampa Bay Estuary Program: 2020 Habitat Master Plan Update*](https://drive.google.com/file/d/1Hp0l_qtbxp1JxKJoGatdyuANSzQrpL0I/view?usp=drivesdk). Technical report. Tampa Bay Estuary Program, St. Petersburg, Florida.

Roca, G., T. Alcoverro, D. Krause-Jensen, T. J. S. Balsby, M. M. van Katwijk, N. Marbà, R. Santos, et al. 2016. Response of seagrass indicators to shifts in environmental stressors: A global review and management synthesis. *Ecological Indicators* 63: 310–323. <https://doi.org/10.1016/j.ecolind.2015.12.007>.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. *Akaike information criterion statistics*. Dordrecht, The Netherlands: D. Reidel: Taylor & Francis.

Schmidt, N., and M. E. Luther. 2002. ENSO impacts on salinity in Tampa Bay, Florida. *Estuaries* 25: 976–984. <https://doi.org/10.1007/bf02691345>.

Schrandt, M. N., T. C. MacDonald, E. T. Sherwood, and M. W. Beck. 2021. A multimetric nekton index for monitoring, managing and communicating ecosystem health status in an urbanized Gulf of Mexico estuary. *Ecological Indicators* 123: 107310. <https://doi.org/10.1016/j.ecolind.2020.107310>.

Scolaro, S., M. W. Beck, M. C. Burke, G. E. Raulerson, and E. T. Sherwood. 2023. Piney Point, seagrass, and macroalgae: Impact assessment and a case for enhanced macroalgae monitoring. *Florida Scientist* 86: 339–345.

Sherwood, E. T., and H. S. Greening. 2013. Potential impacts and management implications of climate change on Tampa Bay estuary critical coastal habitats. *Environmental Management* 53: 401–415. <https://doi.org/10.1007/s00267-013-0179-5>.

Sherwood, E. T., H. S. Greening, L. Garcia, K. Kaufman, T. Janicki, R. Pribble, B. Cunningham, et al. 2015. [*Development of an integrated ecosystem model to determine effectiveness of potential watershed management projects on improving Old Tampa Bay*](https://drive.google.com/file/d/1BCviGfLykVX-p1tA3b0306deP3pKMagr/view?usp=drivesdk). 10-15. St. Petersburg, Florida: Tampa Bay Estuary Program.

Sherwood, E. T., H. S. Greening, A. J. Janicki, and D. J. Karlen. 2016. Tampa Bay estuary: Monitoring long-term recovery through regional partnerships. *Regional Studies in Marine Science* 4: 1–11. <https://doi.org/10.1016/j.rsma.2015.05.005>.

Sherwood, E. T., H. S. Greening, J. O. R. Johansson, K. Kaufman, and G. E. Raulerson. 2017. Tampa Bay (Florida, USA): Documenting seagrass recovery since the 1980’s and reviewing the benefits. *Southeastern Geographer* 57: 294–319. <https://doi.org/10.1353/sgo.2017.0026>.

Shi, J., and C. Hu. In review. Response of South Florida estuaries to the 2023 heatwave. *Estuaries and Coasts*. <https://doi.org/10.21203/rs.3.rs-3528678/v1>.

Statham, P. J. 2012. Nutrients in estuaries - An overview and the potential impacts of climate change. *Science of The Total Environment* 434: 213–227. <https://doi.org/10.1016/j.scitotenv.2011.09.088>.

Stelling, B., E. Phlips, S. Badylak, L. Landauer, M. Tate, and A. West-Valle. 2023. Seasonality of phytoplankton biomass and composition on the Cape Canaveral shelf of Florida: Role of shifts in climate and coastal watershed influences. *Frontiers in Ecology and Evolution* 11: 1134069. <https://doi.org/10.3389/fevo.2023.1134069>.

Tango, P. J., and R. A. Batiuk. 2016. Chesapeake Bay recovery and factors affecting trends: Long-term monitoring, indicators, and insights. *Regional Studies in Marine Science* 4: 12–20. <https://doi.org/10.1016/j.rsma.2015.11.010>.

Todd, A., H. Walsh, and J. Neville. 2023. [*2023 economic valuation of Tampa Bay*](https://drive.google.com/file/d/15zetRgrFKkWah9KAY1in7q0so8ywHzkA/view?usp=drive_link). 09-23. St. Petersburg, Florida: Tampa Bay Estuary Program.

Tomasko, D. A. 2023. Ecological impacts to Sarasota Bay from Piney Point discharges - examining the evidence. *Florida Scientist* 86: 301–313.

Tomasko, D. A., M. Alderson, R. Burnes, J. Hecker, N. Iadevaia, J. Leverone, G. Raulerson, and E. Sherwood. 2020. The effects of Hurricane Irma on seagrass meadows in previously eutrophic estuaries in Southwest Florida (USA). *Marine Pollution Bulletin* 156: 111247. <https://doi.org/10.1016/j.marpolbul.2020.111247>.

Usup, G., D. M. Kulis, and D. M. Anderson. 1994. Growth and toxin production of the toxic dinoflagellate in laboratory cultures. *Natural Toxins* 2: 254–262. <https://doi.org/10.1002/nt.2620020503>.

Van Bogaert, N., K. Rosario, B. T. Furman, M. O. Hall, A. M. Greco, and M. Breitbart. 2018. Discovery of a novel potexvirus in the seagrass *Thalassia testudinum* from Tampa Bay, Florida. *Limnology and Oceanography Letters* 4: 1–8. <https://doi.org/10.1002/lol2.10098>.

Vandermeer, J. H. 1972. Niche theory. *Annual Review of Ecology and Systematics* 3: 107–132. <https://doi.org/10.1146/annurev.es.03.110172.000543>.

Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. New York: Springer. <https://doi.org/10.1007/978-0-387-21706-2>.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377–12381. <https://doi.org/10.1073/pnas.0905620106>.

Webster, C. L., K. L. Kilminster, M. Sánchez Alarcón, K. Bennett, S. Strydom, S. McNamara, P. S. Lavery, and K. M. McMahon. 2021. Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries. *Journal of Ecology* 109: 3260–3279. <https://doi.org/10.1111/1365-2745.13648>.

Weisberg, R. H., and L. Zheng. 2006. Circulation of Tampa Bay driven by buoyancy, tides, and winds, as simulated using a finite volume coastal ocean model. *Journal of Geophysical Research: Oceans* 111. <https://doi.org/10.1029/2005jc003067>.

White, E., and D. Kaplan. 2017. Restore or retreat? Saltwater intrusion and water management in coastal wetlands. *Ecosystem Health and Sustainability* 3: e01258. <https://doi.org/10.1002/ehs2.1258>.

Wood, S. N. 2017. *Generalized Additive Models: An introduction with R*. 2nd ed. Chapman; Hall/CRC.

Zhang, M., H. Li, L. Zhang, and J. Liu. 2023. Heat stress, especially when coupled with high light, accelerates the decline of tropical seagrass (*Enhalus acoroides*) meadows. *Marine Pollution Bulletin* 192: 115043. <https://doi.org/10.1016/j.marpolbul.2023.115043>.

Zieman, J. C. 1975. Seasonal variation of turtle grass, *Thalassia testudinum König*, with reference to temperature and salinity effects. *Aquatic Botany* 1: 107–123. <https://doi.org/10.1016/0304-3770(75)90016-9>.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. New York: Springer. <https://doi.org/10.1007/978-0-387-87458-6>.