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Dark waters: Evaluating seagrass community response to optical water quality and freshwater discharges in a highly managed subtropical estuary

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ABSTRACT

Seagrass communities are vitally important ecosystems that support and foster organisms across trophic levels. Understanding the drivers of seagrass distribution and extent in estuary systems is valuable for conservation and restoration efforts. A critical driver of seagrass distribution is how light moves through the water column (i.e. light attenuation) and the availability of light to reach the estuary bottom. Light attenuation combined with the depth of seagrass colonization is used to estimate the percent surface irradiance and is an indicator of seagrass light requirements The objective of this study was to evaluate optical water quality parameters within the Caloosahatchee River Estuary (CRE) relative to changes in freshwater discharge conditions. During the study period, freshwater discharge significantly increased resulting in an increase of annual stressful and damaging discharge events to marine seagrass species. Concurrent with changes in freshwater discharge conditions, changes to optical water quality parameters including color, chlorophyll-*a*, total suspended solids, and light attenuation were detected along the estuary. Using photo-interpreted seagrass coverage data combined with bathymetric data, the depth of colonization was estimated for three survey years (2008, 2014, and 2020). This information combined with a spatial and temporal light attenuation generalized additive model percent surface irradiance (%SI) was estimated. Over the study period, %SI significantly increased across the lower CRE indicating an improvement in light attenuation. The current freshwater management plan has increased stressful and damaging discharge events, however recent changes in operations has minimized these damaging events which could be linked to the precipitous increase in %SI across the lower CRE. Seagrass density data collected from transects within the estuary suggest that prolonged stress and damaging ($>5.13\ hm^3 d^{-1}$) has significantly reduce species density. Future water management strategies are expected to reduce the frequency and volume of discharges to the CRE, effectively reducing stress and damaging freshwater discharge event.

Seagrasses are critically important communities that shape aquatic habitats for a variety of estuarine species. Unfortunately, seagrass ecosystems have been in a state of global decline since the early 20th century (Dunic et al., 2021). Primarily seagrass losses have been linked to anthropogenic deterioration of water quality indicated by increased nutrient pollution and other parameters that affect how light travels through the water column (Beck et al., 2018; Choice et al., 2014; Duarte, 1995; Krause et al., 2022; Turschwell et al., 2021). Several factors contribute to the survival and growth of seagrasses including salinity, temperatures, and subsurface irradiance. However, light is an important limiting factor affecting the health and extent of seagrass communities simply due to the fact that it drives photosynthesis (Hemminga and Duarte, 2000).

Seagrass coverage typically declines with water depth due to light attenuation and declines more rapidly in productive estuaries where light attenuation is relatively high (Duarte, 1995). As depth increases, light limitation to seagrass communities increases affecting where seagrass can grow (Beck et al., 2018). Empirical relationships between water column nutrients, light attenuation, and components that make up light attenuation and depth of colonization have been developed to characterize light regimes and other water quality requirements for healthy seagrass habitat (Chen and Doering, 2016; Choice et al., 2014; Dixon and Leverone, 1995; Dixon and Wessel, 2016; Duarte, 1995; McPherson and Miller, 1994; Tomasko et al., 2001).

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Generally, the spatial distribution of seagrass within a given estuary can be reduced down to two factors, water depth and light availability (Hall et al., 1999). Therefore, the depth of colonization is controlled by the light requirements of seagrass and average light attenuation (Beck et al., 2018). Operationally seagrass light requirements are defined as the average percentage of incident light present at the depth of colonization (Dennison et al., 1993). Published estimates of seagrass light requirements are highly variable and are species-specific due to the physiological adaptations of each species. The percent of light at the maximum depth limit in the literature range from less than 5% to greater than 30% (Choice et al., 2014; Dennison et al., 1993; Dixon and Leverone, 1995; Duarte, 1991; Michael Kemp et al., 2004; Tomasko and Hall, 1999). For management purposes in south Florida estuaries, a light requirement of ~20% is typically used (US EPA, 2012).

Estuaries rely on a balance of freshwater from watershed runoff, stream/river flow, groundwater and other sources and marine wate from tidal transport up the estuary (Buzzelli et al., 2014; Sklar and Browder, 1998; Tibby et al., 2022). Changes to hydrologic flows can affect sediment, nutrient, and dissolved organic matter transport, water depth, salinity regimes, and turbidity conditions within the coastal environment thereby potentially affecting light attenuation (Chen and Doering, 2016; Lee et al., 2006; Milbrandt et al., 2016; Moncada et al., 2021). Moreover, altered freshwater discharges to estuarine environments can substantively affect the composition, distribution, abundance, and status benethic communities (Buzzelli et al., 2015; Herbert et al., 2011; Santos and Lirman, 2012; Volety et al., 2009). In the Caloosahatchee river estuary (CRE) freshwater discharges are largely driven by upstream water management (Julian and Osborne, 2018; Tarabih and Arias, 2021) which in turn affect colored dissolved organic matter (CDOM) concentrations, a major component of light attenuation in the Caloosahatchee (Chen et al., 2015; Doering and Chamberlain, 1999).

The objective of this study was to evaluate changes in light attenuation spatially in a color-dominated estuary and the role of changes to freshwater inputs, either from a management perspective or climate-driven changes on ecosystem function. The concentration of CDOM strongly affects the optical properties of estuarine water and is generally inversely related to salinity in estuarine systems (Bowers and Brett, 2008; Branco and Kremer, 2005; Chen et al., 2015). Therefore changes to freshwater inputs to estuarine systems can affect the balance and mixing of CDOM and other optical characteristics that affect light attenuation. We hypothesize that changes in freshwater inputs will change light attenuation characteristics throughout the estuary and thereby affecting seagrass depth of colonization and spatial distributions as well as seagrass density within the estuary.

1. Methods

1.1. Study area

The Caloosahatchee River and estuary are located on the lower west coast of Florida, USA (Fig. 1). The historic Caloosahatchee River was originally a shallow, meandering river with its headwaters located approximately 100 km inland at Lake Hicpochee and tidal influenced approximately 70 km upstream from the Gulf of Mexico. To

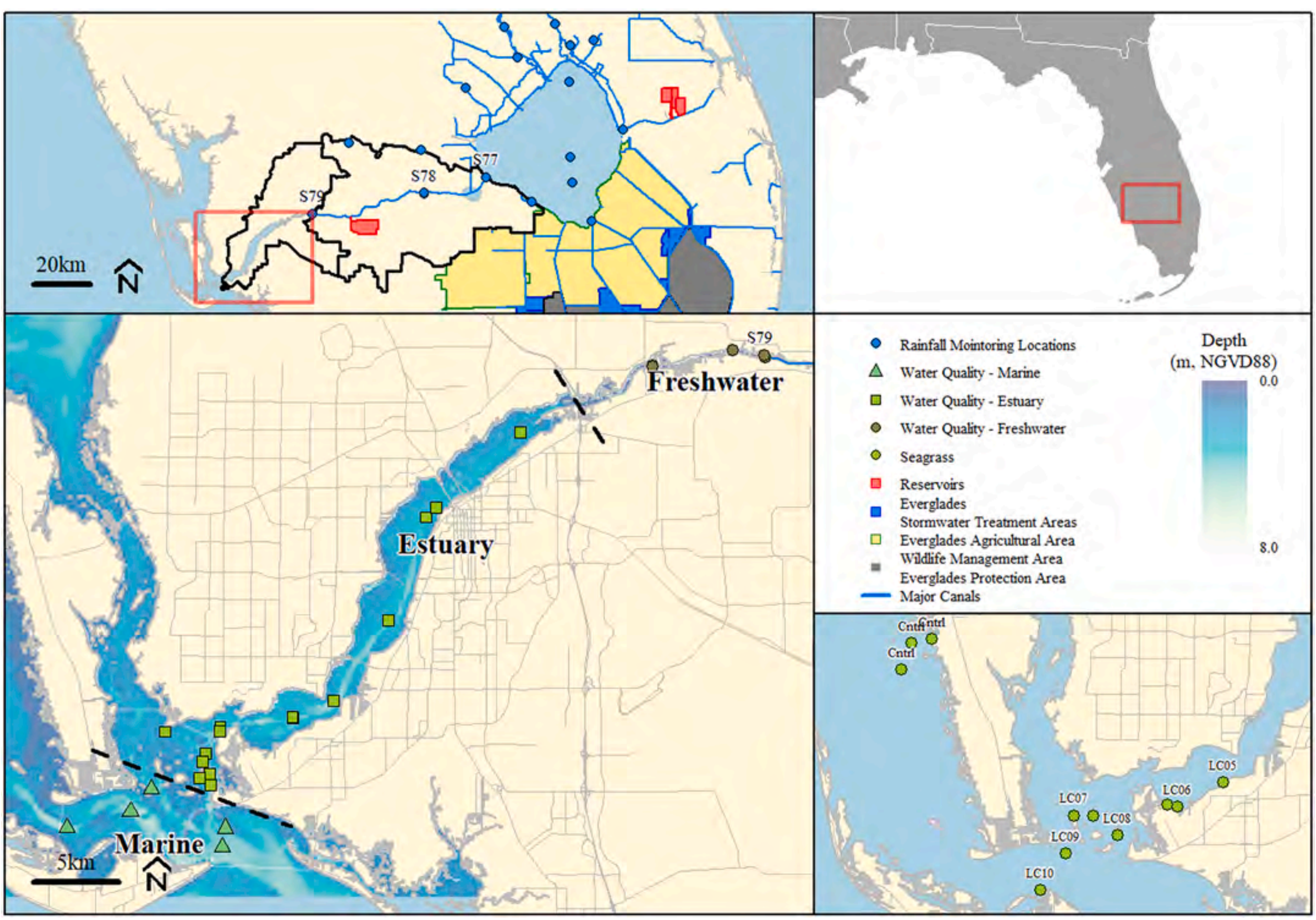

Fig. 1. Rainfall, discharge, water quality and seagrass monitoring locations within the C-43 basin Caloosahatchee River Estuary (CRE) and Lake Okeechobee relative to key landscape features.

accommodate navigation, flood control, and land reclamation needs the river was straightened and extended eastward and connected to Lake Okeechobee in the late 1800 s essentially converting the river to a canal, resulting in the C-43 canal designation. In the early 1900 s, three lock-and-dam structures were constructed to control flow and stage elevation along the river. Of the three lock-and-dam structures installed, the final downstream structure identified as the S-79 (Franklin Lock and Dam) regulates discharge from the canal to the estuary (Barnes, 2005; Doering and Chamberlain, 1999; Julian and Osborne, 2018). The estuary portion of the Caloosahatchee River (hereafter Caloosahatchee River Estuary or CRE) extends approximately 48 km from the S-79 to San Carlos Bay, where it empties into the Gulf of Mexico and Pine Island Sound (Fig. 1).

1.2. Data sources

Water quality and hydrologic data were retrieved from the South Florida Water Management District (SFWMD) online database (DBHYDRO; http://www.sfwmd.gov/dbhydro) and Lee County Environmental Laboratory (http://leegis.leegov.com/surfwater/) for sites within the CRE for the period of record May 2008 to May 2020 (Water Year (WY) 2009 – 2020). The period of record was limited by available data. Water quality parameters used in this study include salinity, chlorophyll-*a*, turbidity, color, and diffuse light attenuation coefficient (K_0). In addition to water quality parameters, daily discharge volume was retrieved for S-79 and S-77 from May 1979 to May 2020 (WY1979 – 2020). Regional average rainfall was estimated from monitoring locations across the Caloosahatchee watershed consistent with Julian and Osborne (2018). Water quality data were screened based on laboratory qualifier codes, consistent with FDEP's quality assurance rule (Florida Administrative Code, 2008). Any datum associated with a fatal qualifier indicating a potential data quality problem was removed from the analysis. Additional considerations in the handling of analytical data were the accuracy and sensitivity of the laboratory method used. For purposes of data analysis and summary statistics, data reported as less than the method detection limit (MDL) were assigned one-half the MDL. The optical water quality dataset used in this study is available via Julian (2023).

Geospatial data describing seagrass coverage and bathymetry were retrieved from the SFWMD geospatial open data portal (https://geo-sfwmd.hub.arcgis.com/). Seagrass coverage data were retrieved for the CRE for survey years 2008, 2014, and 2021. The coverage maps were produced by photo-interpreting aerial images to categorize seagrass as absent, discontinuous, or continuous. For this study, we aggregated the data into two categories, present (discontinuous and continuous) and absent.

Seagrass monitoring locations were established within the lower portion of the CRE along with three control locations outside of the CRE (Fig. 1). The sites located within the CRE include three sites in the upper portion of the lower estuary (LC05, LC06, and LC06A) where only the lower salinity-tolerant *Halodule wrightii* has been documented (Harris et al., 1983; McNulty et al., 1972), three sites in the mid portion of the lower estuary (LC07, LC07A, and LC08) and two sites in the lower part of the lower estuary. The mid and lower estuary sites have greater influence from the Gulf of Mexico tidal exchange and support multiple seagrass species including *Halodule wrightii*, *Thalassia testudinum*, and *Syringodium filiforme*. Control sites (Cntrl01, Cntrl02, and Cntrl03) were established outside of the zone of greatest impact from freshwater flows and exhibited sediment and seagrass community characteristics covering the range of conditions found at locations within the CRE. For purposes of the seagrass analysis locations will be labeled as lower, mid, upper, and control.

Seagrass monitoring occurred between June 2013 and September 2020. Sites were surveyed twice annually during the wet season before typical large freshwater releases from the S-79 structure and after one month of mean discharges above 6.85 hm^3d^{-1} (2800 cfs). In years when mean month discharges did not exceed 6.85 hm^3d^{-1}, sites were surveyed during the period which historically had the greatest runoff (August-September). At each survey location, two 100-meter transects were established, one parallel and one perpendicular to the shore. The perpendicular transect began at the nearest point to shore with at least 10% seagrass coverage. The parallel transect was located with its center point crossing the center point of the perpendicular transect. Along each transect one random sample was taken from each of five distance ranges: 1–20 m, 21–40 m, 41–60 m, 61–80 m, 81–100 m. Sampling included enumerating seagrass shoot density, canopy height, and percent cover for each seagrass species (Duarte and Kirkman, 2001).

1.3. Data analysis

To characterize and evaluate freshwater discharge to the estuary, annual discharge volumes were summarised for S-77, S-79, and C-43 basin. C-43 basin discharge was estimated as the difference between S-79 and S-77. Annual discharge trend analysis for the period of WY2009 - 2020 was performed using Kendall's τ correlation analysis (*'cor.test'* function). Changepoint detection in annual discharge volumes for S-77, S-79, and C-43 basin was performed using the '*CUSUM.test*' function in the CPAT R-package to test for changes relative to the mean. If a change point was detected, annual discharge volumes were compared between periods using the Kruskal-Wallis rank-sum test. Segmented regression was applied to long term (WY1979 –2020) cumulative annual flow volume from the S79 and cumulative annual average rainfall across the watershed to determine changes in the flow-rainfall relationship related to freshwater inputs into the estuary using the '*segmented*' function in the segmented R-package (Vito and Muggeo, 2003).

To evaluate the ecological effect of freshwater discharges to the CRE, the REstoration COordination & VERification (RECOVER) Northern Estuaries Salinity Envelope Performance Measure (RECOVER, 2020) was applied to the observed S-79 discharge time series between May 1978 and April 2020. As identified by RECOVER (2020), the potential physiological and ecology discharge thresholds of stress and damaging events were identified for the CRE. For purposes of this study, stress (5.14 – 6.36 hm^3d^{-1}; originally reported as 2100–2600 ft^3sec^{-1}) and damaging (>6.36 hm^3d^{-1}; originally reported as >2600 ft^3sec^{-1}) were aggregated to indicate unfavorable physiological and ecology conditions for benthic communities. The performance measure uses 14-day moving average discharges to count discharge events in the stress and damaging discharge categories. The count of stress and damaging events were tallied for each water year and Kendall's τ correlation analysis was used to evaluate the trend of events between water years 2008 and 2020.

Diffuse light attenuation coefficient (K_0) was calculate from vertical profiles of photosynthetically active radiation (PAR) generally collected at depth intervals of 0.25 – 0.50 m with a LI-COR, LI-193 spherical quantum sensor and a LI-1400 data logger (Chen et al., 2015; Chen and Doering, 2016; Doering and Chamberlain, 1999). Estimates of light attenuation can be affected by the solar elevation angle at the time and latitudinal location of K_0 therefore adjustments were made for the effects of solar elevation angle. The adjusted light attenuation coefficient, $K_{t,\ (adj)}$ was calculated using equations consistent with prior studies (Frankovich et al., 2017; McPherson and Miller, 1994; Miller and McPherson, 1995) taking into account the angular fraction of the year, julian date, latitude, solar hour angle, solar declination, and solar elevation.

Water quality monitoring locations were grouped into three regions based on long-term salinity values consisting of freshwater, estuary, and marine (Fig. 1) consistent with Julian and Osborne (2018). Chlorophyll-a, turbidity, color, and adjusted light attenuation ($K_{t,\ (adj)}$) were compared between regions and discharge periods using Dunn's test of multiple comparisons (dunn.test R-package; Dinno, 2015). Saptio-temporal modeling of $K_{t,\ (adj)}$ was conducted using Generalized Additive Model (GAM; mcgv R-package; Wood, 2017) across the study area. The purpose of the sptaio-temporal light attenuation GAM was two-fold, first to evaluate spatial and temporal trends of K_t and predict K_t across the lower estuary to evaluate spatial changes in surface irradiance. The GAM method examines the significance of both linear trends and higher-order trends using spline functions on model terms. The model was constructed using cubic regression spline applied to day-of-year (DOY), thin plate spline was applied to year (CY) and Duchon spline applied to longitude (Long) and latitude (Lat). Due to variability over the year cubic regression spline was selected, thin plate spline was selected to account for the long-term trend, and Duchon spline was selected for location as it is a constrained spline that is not affected by the boundary of the spline. In addition to individual splines, tensor interaction terms for CY, longitude, and latitude; DOY, longitude, and latitude; and DOY and CY were specified to account for spatial and temporal autocorrelation. Together, the GAM is represented by Eq. 1 where y_t is log-transformed K_t, α is the model intercept *s()* is a smooth spline function and *ti()* is a tensor product interaction.

$$E(y_t) = \alpha + s(DOY) + s(CY) + s(Long, Lat) + ti(DOY, CY) + ti(Long, Lat, DOY) + it(Long, Lat, CY) \quad (1)$$

Seagrass depth of colonization (Z_c) was estimated using methods identified by Beck et al. (2018) by overlaying seagrass coverage maps and bathymetry data to generate a point shapefile with attributes of location, depth, and seagrass presence/absence. Depth of colonization at particular locations was computed using observations found within a 1000 m buffer in a 400 m grid. At each sampled location, a logistic function was fitted to the extracted depth points using non-linear regression, quantifying the decrease in seagrass cover with respect to depth. Based on the linear curve of each depth curve, the median depth of colonization ($Z_{c,\ med}$) was estimated as consistent with Beck et al. (2018). The analysis was repeated for observation within a particular search radius of grid nodes spanning the study area, generating a map of depth of colonization (Fig S1). Seagrass depth of colonization was compared between years using the Kruskal-Wallis rank sum test and a post hoc Dunn's test of multiple comparisons (*"dunn.test"* function in the "dunn.test" R-package; Dinno, 2015).

Seagrass light requirements were estimated as the average fraction of surface irradiance reaching the median depth of colonization($Z_{c,\ med}$). Light attenuation ($K_{d,pred}$) was predicted from the space and time GAM (Eq. 1) on the same grid as the depth of colonizationMonthly $K_{d,pred}$ values were predicted between May and September (growing season) for the years of $Z_{c,\ med}$ (2008, 2014 and 2020). The percentage of surface irradiance (%SI) at the median depth of colonization was computed using Eq. 2 for each month and averaged for the survey year. The growing season mean percentage of surface irradiance was compared between regions using the Kruskal-Wallis rank sum test and a post hoc Dunn's test of multiple comparisons.

$$\%SI = \exp\left(-K_{d,pred} \times Z_{c,med}\right) \times 100 \quad (2)$$

To examine the effect of disturbance level freshwater discharges on seagrass communities in the CRE, Kruskal-Wallis rank sum test was used to compare semi-annually measured seagrass densities across estuary regions during disturbance events (i.e. stress and damaging flow events) versus non-event periods. To further evaluate the effect of freshwater discharges on seagrass communities, comparison of early season (June and/or July) seagrass density estimates were compared to stress and damaging flow events in two ways. For the purposes of this analysis, the number of days where freshwater discharges were within the stress and damaging flow envelope (i.e. 14-day moving average > 5.13 hm^3d^{-1}) during the year prior (365-day moving window) to the seagrass surveys were tabulated. The analysis focused on the impact duration of stress and damaging events by comparing seagrass density to the number of days within the stress and damaging flow envelope using Spearman's rank correlation for each seagrass species and estuary region. To evaluate longer-term impact of freshwater releases on seagrass density, comparison of seagrass density for grouped sites between years which had greater than 120 days of stress and damaging flow events relative to those with less than 120 days of stress and damaging flow events. The 120 day threshold was identified as a changepoint in stress and damaging events observed during the seagrass monitoring period and determined using the "*cpt.mean*" function of the "changepoint" R-package (Killick and Eckley, 2014). Due to the relatively low occurrence of *Syringodium filiforme* at transect locations all analyses focus on *Halodule wrightii* and *Thalassia testudinum*.

Unless otherwise noted, all statistical operations were performed using the base stats R-package. All statistical operations were performed with R© (Ver 4.0.4, R Foundation for Statistical Computing, Vienna, Austria). The critical level of significance was set to α = 0.05.

2. Results

2.1. Discharge conditions

Annual freshwater discharge volumes (i.e. S-79) ranged from 0.11 to 3.20 km^3 WY^{-1} during the period of record with a significantly increasing trend (τ = 0.49; ρ-value <0.05). A significant change point was detected in the S-79 annual discharge volume time-series after WY2013 (A = 1.82; ρ-value <0.01; Fig. 2 and S2) with annual discharge volumes being significantly different between periods (2008 – 2012 and 2013 – 2020; $\chi^2 = 5.90$; df =1; ρ-value <0.05; Fig S3). Annual discharge volume from Lake Okeechobee (i.e. S-77) ranged from 0.05 to 1.63 km^3 WY^{-1}, and the percent of water from the Lake that made it to the estuary ranged from < 1% to ~97% during the period of record with the remaining volume being from the upstream watershed (C-43). Annual discharge volume from Lake Okeechobee during the period of record significantly increased (τ = 0.46; ρ-value <0.05). Similar to S-79, a change point was detected in the S-77 annual discharge volume time-series after WY2013 (A=1.90; ρ-value <0.01; Fig. 2 and S2) with annual discharge volumes being significantly different between periods ($\chi^2 = 5.90$; df =1; ρ-value <0.05; Fig S3). Annual discharge volume from the upstream watershed (i.e. C-43 Basin) ranged from 0.11 to 1.66 km^3 WY^{-1} during the period of record with no significant change in trend (τ = 0.36; ρ-value =0.10). Additionally, no statistically significant change point was detected in the C-43 basin annual discharge volume time-series (A=1.31; ρ-value =0.06).

During the beginning of this study period (2008 – 2012), rainfall was below the historic average and the regulation schedule used to dictate upstream water management was updated (Graham et al., 2016). After 2012, regional rainfall exceeded the period of record average, and water management upstream increased discharges to the Estuary from Lake Okeechobee (Fig. 2). Both the change point analysis (Fig S2) and the long-term break-point analysis of the rainfall-runoff relationship (Fig. 2) indicate changes in freshwater discharge conditions to the CRE which could have implications on salinity, water quality, and optical characteristics of the estuary.

In addition to changes in absolute discharge volumes to the CRE, the frequency of stress and damaging discharges from the watershed and Lake Okeechobee significantly increased between 2008 and 2020 (τ = 0.43; ρ-value <0.05; Fig S4). Moreover, this trend is consistent even after removing the uncharacteristically low count years of 2008 (drought) and 2020 (operational deviation; USACE, 2020) with a significant increase in stress and damaging event counts (τ = 0.57; ρ-value <0.05) since 2009.

2.2. Light attenuation

Using the equations to correct for variations in solar elevation angle, adjusted values ($K_{t,(adj)}$) were lower than uncorrected estimates (K_0). Uncorrected light attenuation values were < 1 – 43% greater than the adjusted values ($K_{t,(adj)}$)(Fig S5). Estimates of $K_{t,(adj)}$ calculated from 1054 measurements of light attenuation ranged from 0.10 to 5.57 m^{-1} across the Caloosahatchee Estuary and San Carlos Bay (Table 1).

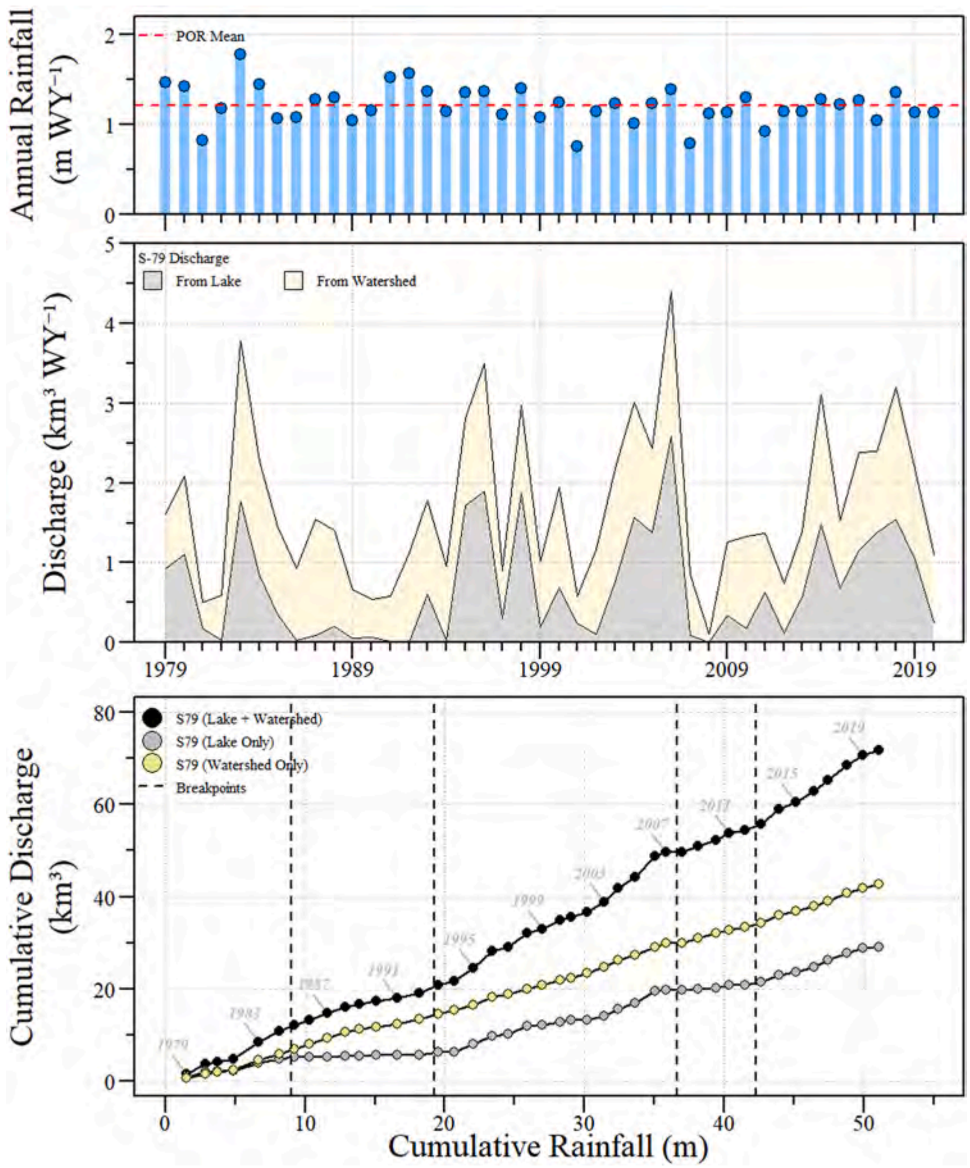

Fig. 2. Annual regional rainfall (top), annual discharge into the Caloosahatchee River Estuary with water identified (i.e. Lake Okeechobee and Watershed; middle), and double mass curve comparing cumulative rainfall and discharge since water year 1979. Significant breakpoints in the double-mass curve as identified by segmented regression are identifed with vertical dash lines.

Adjusted light attenuation varied across space and time (Fig. 3) with all parameters being significantly different from zero except for the interaction term of day-of-year, longitude, and latitude (Table 2). The spatial and temporal GAM model resulted in 73.5% of the deviance explained (equivalent to R^2) in the observed data (Table 2). By inspecting the effects plots from the fitted model, $K_{t,(adj)}$ is greater in the upper part of the estuary (Fig. 3) where color is greatest (Fig. 4), and during the later part of the year (June [Day ~150] to November [Day ~334]; Fig. 3). Additionally, $K_{t,(adj)}$ exhibits more variable during the early part of the calendar year (January - ~ March), which corresponds to the late dry season. Throughout the study period, interannual variability in $K_{t,(adj)}$ was somewhat variable with large changes associated with major disturbance events such as drought (2007/2008 and 2014/2015) and high discharge years (2013–2014), and Hurricane Irma with effects lasting from 2017 to 2018 (Fig. 2 and 3).

2.3. Optical water quality

Water quality parameters specific to light attenuation characteristics varied along the CRE (Table 1). All water quality parameters were significantly different between periods and regions. However, pairwise comparisons revealed that some parameters differed by region but not by period throughout the CRE ($K_{t,(adj)}$) or within specific regions of the CRE (Fig. 4). Generally, color, chlorophyll-*a*, and $K_{t,(adj)}$ were greatest in the freshwater portion of the CRE and gradually declined with distance downstream (Fig. 4). Meanwhile, TSS was lowest in the freshwater segment and greatest in the marine region of the CRE (Fig. 4). Color was significantly different between regions and discharge periods (χ^2 = 888.3, df=5, ρ-value<0.01) with generally high discharge periods having significantly greater color along the CRE (Fig. 4). Chlorophyll-*a* was not significantly different across all regions except for the estuary region (χ^2 = 261.2, df=5, ρ-value<0.01) where chlorophyll-*a* concentrations were typically greater during the low discharge period (Fig. 4).

Table 1
Summary statistics of optical water quality parameters across the Caloosahatchee River Estuary.

Variable	Region	Mean	Median	Standard Deviation	Minimum	Maximum	N
Chl-a (μg L^{-1})	Marine	3.85	2.80	5.35	0.25	71.23	569
	Estuary	4.70	2.80	6.40	0.25	119.00	1592
	Freshwater	11.42	6.00	17.91	0.25	265.00	733
Color (PCU)	Marine	16.33	9.17	20.34	0.50	134.00	392
	Estuary	53.10	36.00	49.90	0.50	285.00	1549
	Freshwater	91.92	73.00	53.88	17.90	278.00	740
TSS (mg L^{-1})	Marine	16.62	14.80	11.49	0.70	73.30	309
	Estuary	7.62	5.45	7.12	0.30	53.60	1527
	Freshwater	3.45	2.45	2.96	0.30	31.80	738
Turbidity (NTU)	Marine	3.02	2.40	2.48	0.10	25.20	594
	Estuary	2.62	2.16	1.89	0.10	21.60	1596
	Freshwater	3.05	2.40	2.89	0.05	47.31	745
Secchi Depth (m)	Marine	1.60	1.50	0.66	0.30	4.70	577
	Estuary	1.28	1.20	0.56	0.20	3.40	1491
	Freshwater	0.95	0.90	0.37	0.20	2.90	610
K_0 (m^{-1})	Marine	0.92	0.81	0.51	0.10	3.67	232
	Estuary	1.49	1.22	0.89	0.17	6.21	638
	Freshwater	2.26	2.01	1.01	0.33	6.31	184
$K_{t,(adj)}$ (m^{-1})	Marine	0.83	0.73	0.46	0.10	3.14	232
	Estuary	1.27	1.05	0.78	0.14	5.07	638
	Freshwater	2.00	1.74	0.92	0.29	5.57	184

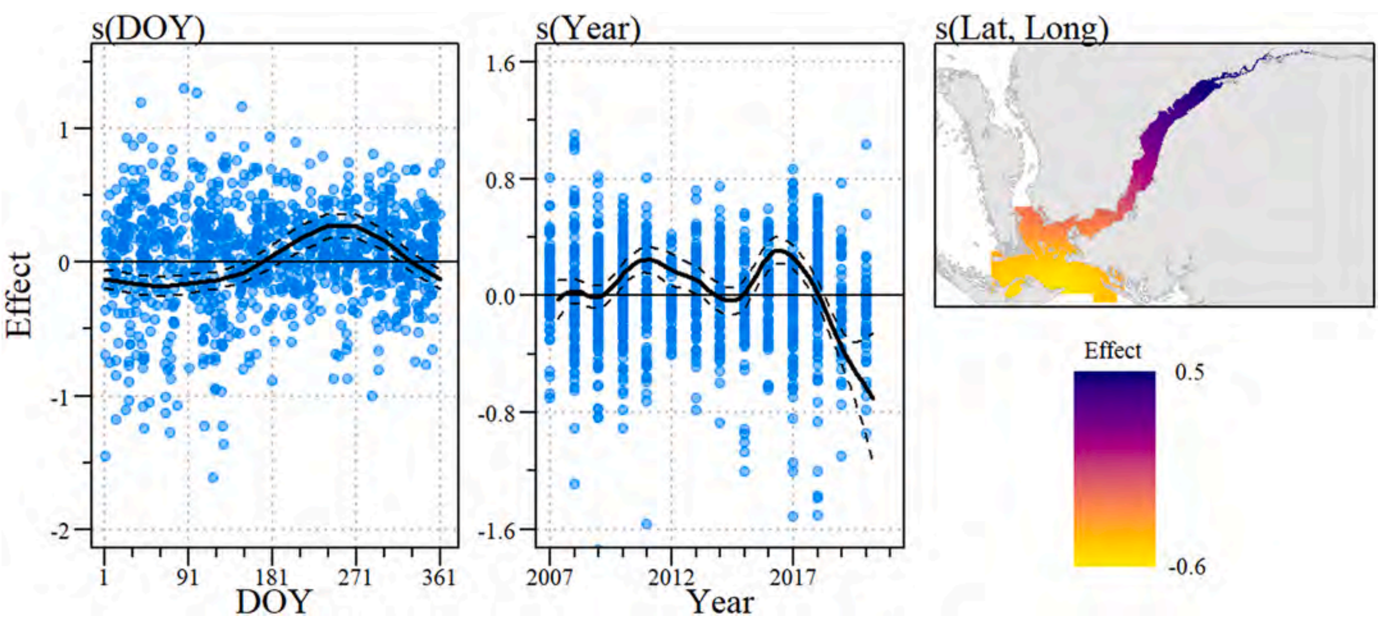

Fig. 3. Light attenuation effects plots of the spatio-temporal generalized additive model with the day-of-year (DOY), year, and spatial (Lat, Long) effects. Interaction terms and DOY x Year effect plots are not shown.

Total suspended solid was significantly different between regions and discharge periods (χ^2 = 660.8, df=5, ρ-value<0.01) with some variability differences in discharge period between regions. Turbidity was significantly different between regions but only discharge periods for the freshwater and marine regions (χ^2 = 56.2, df=5, ρ-value<0.01, Fig. 4). Light attenuation was significantly different between regions (χ^2 =258.0, df=5, ρ-value<0.01) but not discharge periods (Fig. 4).

Estimates of colonization depth ($Z_{c,\ med}$) ranged from 0.56 to 3.30 m across the study area and survey years (Fig. 5). Overall, $Z_{c,\ med}$ did not significantly differ between years (χ^2 = 3.38, df=2, ρ-value=0.18) however, pairwise differences were detected with 2008 being significantly different from 2014 (z-value =−1.68, ρ-value <0.05; Fig. 5) and both 2008 and 2014 being similar to 2020 (z-value =−1.51, ρ-value=0.07 and z-value =0.13, ρ-value=0.44, respectively; Fig. 5). Growing season mean %SI values ranged from 7.8% to 78.9% across the study area and survey years. Growing season mean %SI was significantly different between survey years (χ^2 = 1713, df=2, ρ-value<0.01) with a significant increase in values from 2008 to 2020 (Fig. 5). This significant increase in %SI correspond with reduction in $K_{t,(adj)}$ (Fig. 3 and S6).

2.4. Seagrass survey

Within the CRE, *Halodule* density was observed between 0 and 21,400 shoots m^{-2} while *Thalassia* density was observed between 0 and 1380 shoots m^{-2} during the course of the field survey period (Table 3). *Halodule* was observed throughout the study area at the seagrass monitoring location while *Thalassia* was present along the estuary except for the upper estuary locations. *Halodule* density values were significantly greater in non-disturbance events (14-day mean discharge <5.13 $hm^3\ d^{-1}$) in the upper portion of the estuary (Fig. 6 and Table 3). Meanwhile in other portions of the estuary (i.e. mid, lower and control) *Halodule* densities were not significantly different between disturbance

Table 2
Light attenuation space and time Generalized Additive Model results for the Caloosahatchee River Estuary.

Component	Term	Estimate	Std Error	t-value	ρ-value
A. parametric coefficients	(Intercept)	0.087	0.074	1.177	0.24
Component	**Term**	**edf**	**Ref. df**	**F-value**	**ρ-value**
B. smooth terms	s(DOY)	5.239	78.000	0.683	< 0.01
	s(CY)	9.331	10.448	9.504	< 0.01
	s(Lat,Long)	7.172	19.000	45.705	< 0.01
	ti(CY,DOY)	85.129	355.000	1.327	< 0.01
	ti(DOY,Long, Lat)	5.613	189.000	0.046	0.05
	ti(CY,Long, Lat)	14.358	187.000	0.148	< 0.01

Adjusted R-squared: 0.698, Deviance explained 0.735
fREML: 511.873, Scale est: 0.116, N: 1054

and non-disturbance events (Fig. 6 and Table 3). Meanwhile, *Thalassia* density values were significantly different greater in non-disturbance events in the lower estuary with mid and control having no significant differences between events (Fig. 6 and Table 3).

Halodule density values was negatively correlated with the annual cumulative days where 14-day moving average discharges were greater than 5.13 $hm^3\ d^{-1}$ (stress and damaging events; $r = -0.60$; $\rho < 0.01$) in the upper estuary. Meanwhile, *Halodule* density values were not correlated with annual cumulative days of stress and damaging events in the mid ($r = 0.05$; $\rho = 0.83$), lower ($r = 0.001$; $\rho = 1.00$), and control ($r = 0.27$; $\rho = 0.30$) locations. *Thalassia* density values was negatively correlated with annual cumulative days of stress and damaging events in the mid region ($r = -0.46$; $\rho < 0.05$) of the estuary and no correlation at low ($r = -0.09$; $\rho = 0.73$) and control ($r = -0.02$; $\rho = 0.92$) locations. *Halodule* density in the upper estuary was significantly greater during years where stress and damaging events were less than 120 days, meanwhile no significant differences were apparent at mid, low and control locations (Fig. 7 and Table 4). Similarly, *Thalassia* density values were significantly greater in the mid estuary during years where stress and damaging events were less than 120 days while no significant differences were observed at low and control locations (Fig. 7 and Table 4).

3. Discussion

3.1. Hydrologic conditions

Over the past century the water courses of south Florida have changed dramatically due to land reclamation and drainage efforts in the later 19th and early 20th century and the construction and operation of the Central and Southern Florida (C&SF) project in the mid 20th century for flood protection, water supply and navigation (Sun et al., 2016). In the more recent history as observed by the rainfall and discharge period of record, discharge conditions to the CRE has been highly variable influenced by both climatic conditions (i.e. rainfall-runoff) and upstream water management (Fig. 2). Consistent with Julian and Osborne (2018), the cumulative annual discharge of S-79 accounting for the combined C-43 watershed and Lake Okeechobee regulatory releases exhibited identical breaks relative to cumulative rainfall across the C-43 watershed (Fig. 2). As discussed by Julian and Osborne (2018), these breakpoints correspond with changes in Lake Okeechobee water management. Build on the analysis of Julian and Osborne (2018), the components of the cumulative total discharge at S-79 were separated demonstrating that both watershed and lake discharge contribute unequally to the total discharge. Generally, the cumulative discharge from the watershed climbs almost linearly per unit rainfall, meanwhile changes in the cumulative discharge from the Lake are consistent with the changes in the cumulative discharge curve (Fig. 2).

Management of water levels and associated discharges from Lake Okeechobee has evolved over time through various different regulation schedules, each resulted in different freshwater delivery regimes to the CRE (Julian and Osborne, 2018; Julian and Welch, 2022; Tarabih and Arias, 2021). Since the late 1970 s, there have been four regulation schedules. The last three regulation schedules allowed for deeper conditions in Lake Okeechobee and therefore higher discharges to downstream areas (Julian and Welch, 2022). These high water levels and associated discharges resulted in unintended impacts to lake and estuary ecology (Doering and Chamberlain, 1999; Havens and Steinman, 2015; Vearil, 2008). During the most recent regulation schedule (Lake Okeechobee Regulation Schedule of 2008 or LORS08) water levels in the Lake were kept lower than prior schedules (Julian and Welch, 2022) but highly impactful discharges to the estuaries remained with an increased in total volume and stress and damaging events occurring for nearly the past decade circa 2020 (Fig. 2 and S4). However, operational deviations associated with Lake Okeechobee in the form of operational flexibility were adapted (USACE, 2020), allowing reduced stressful and damaging discharge events to the CRE (Fig S4).

Freshwater flows to the CRE is a combination of sources that interact with dynamics processes like climate and water management rules. The dynamic processes are overlaid with the intended goals of water management including flood protection, water supply, navigation and the ecology of the system. As such the management of Lake Okeechobee and regulatory discharges to downstream systems including the CRE can be decoupled resulting in unintended impacts as seen in prior water management schemes. However, an updated regulation schedule is being developed, called the Lake Okeechobee System Operating Manual (LOSOM) that will manage water to improve conditions for the downstream estuaries (Julian and Reidenbach, Submitted).

3.2. Light attenuation

Absorption and scatter by water its self in addition to dissolved and suspended material control the quantity and quality of light in the water column. The quality and quantity in-turn affects aquatic photosynthetic organisms (Kirk, 1994; McPherson and Miller, 1994). Water column constituents such as CDOM is typically measured as color, suspended sediments are quantified as turbidity or total suspended solids and phytoplankton or algae measured as chlorophyll-*a*. The relative contribution of these constituents to the total light attenuation varies from region to region and season to season (Chen et al., 2015; Dixon and Wessel, 2016; Ganju et al., 2020, 2014; Kelble et al., 2005; Kostoglidis et al., 2005; Lund-Hansen, 2004; McPherson and Miller, 1994; Xu et al., 2005). For instance, in Århus Bay at the transition between the North and Baltic seas, light attenuation is predominately controlled by suspended material (i.e. turbidity) and phytoplankton (chlorophyll-*a*) with CDOM contributing < 20% to the light attenuation (Lund-Hansen, 2004). While drivers of light attenuation in the back-bay estuaries of coastal New Jersey varies spatially with contributions to light attenuation being influenced by physical, hydrodynamic and biogeochemical characteristics (Ganju et al., 2014). In the microtidal estuary of the Swan River in southwestern Australia CDOM accounts for the majority of the variation in light attenuation (Kostoglidis et al., 2005). Each system is unique in how light attenuation is modulated. While these systems are all located in different places and have different boundary conditions they in part represent the variety of drivers in light attenuation seen across many estuarine systems.

In southwest Florida, regulators of light attenuation varies spatially along the length of the CRE, driven by a combination of freshwater and CDOM contributions, salinity balance, mixing behaviors of fresh and marine waters and suspended material (Chen and Doering, 2016). As such light attenuation significantly varies along the CRE (Fig. 3 and Table 2). In the lower CRE light attenuation is predominately regulated

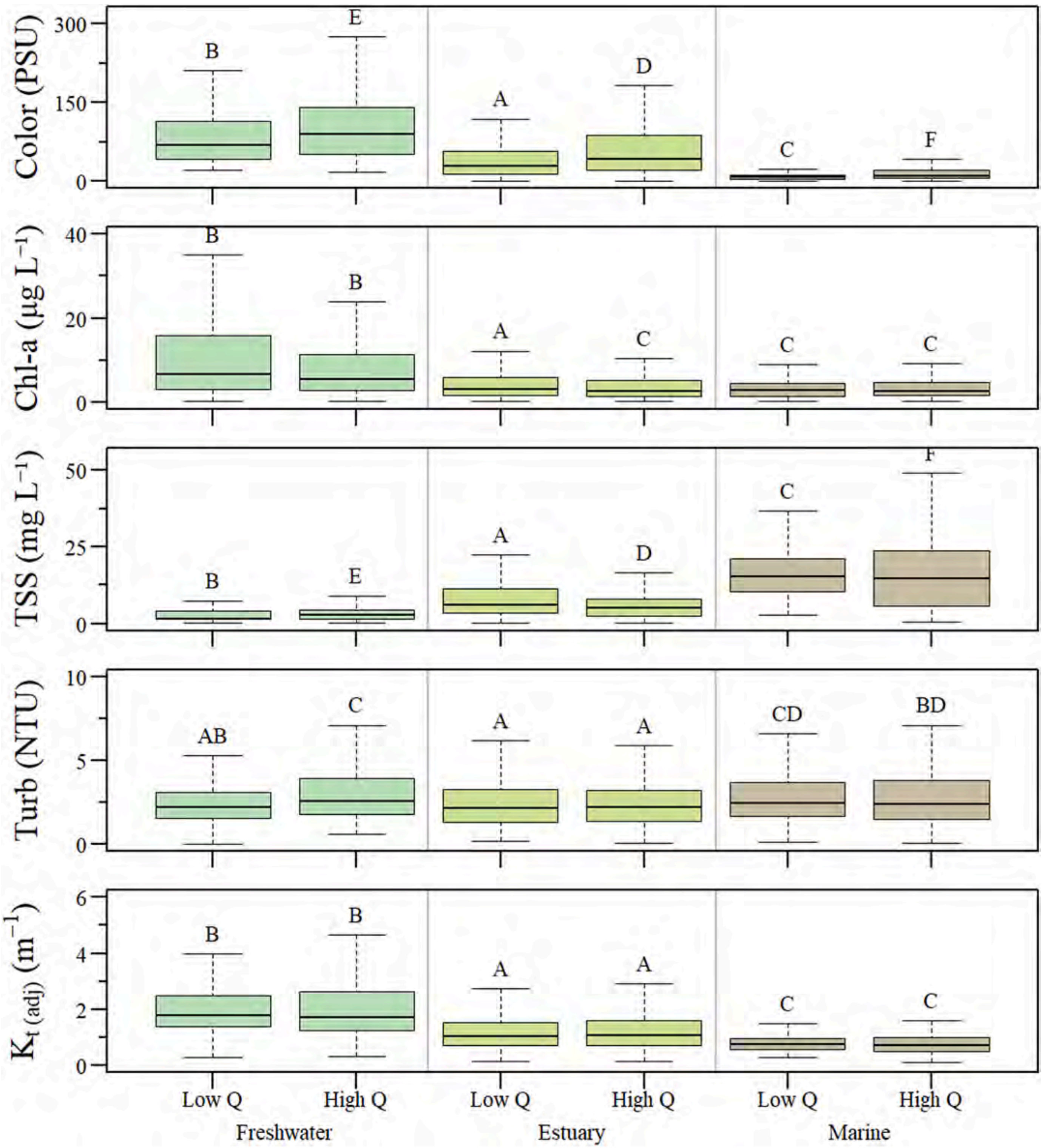

Fig. 4. Comparison of optical water quality parameters along the Caloosahatchee river estuary and flow regimes. Loh and High discharge categories were identified based on breakpoint analysis of discharge time series. The letters above boxplots indicate pairwise comparisons between alternatives using Dunn's test of multiple comparisons.

by turbidity while the upper estuary is regulated largely by CDOM as determined by partitioning the components that make up the total light attenuation (Chen et al., 2015). The relative values of the individual components of light attenuation vary significantly across the estuary (Fig. 4) consistent with results presented by Chen et al. (2015). However, freshwater discharges also affect the relative concentration and potentially their contributions to the total light attenuation along the estuary (Fig. 4) consistent with results presented by Milbrandt et al. (2016). Milbrandt et al. (2016) determined that the individual components of light attenuation were significantly higher, thereby decreasing light attenuation, during periods of lower salinity due to increased freshwater inputs in the lower CRE. The combined effect of decreased

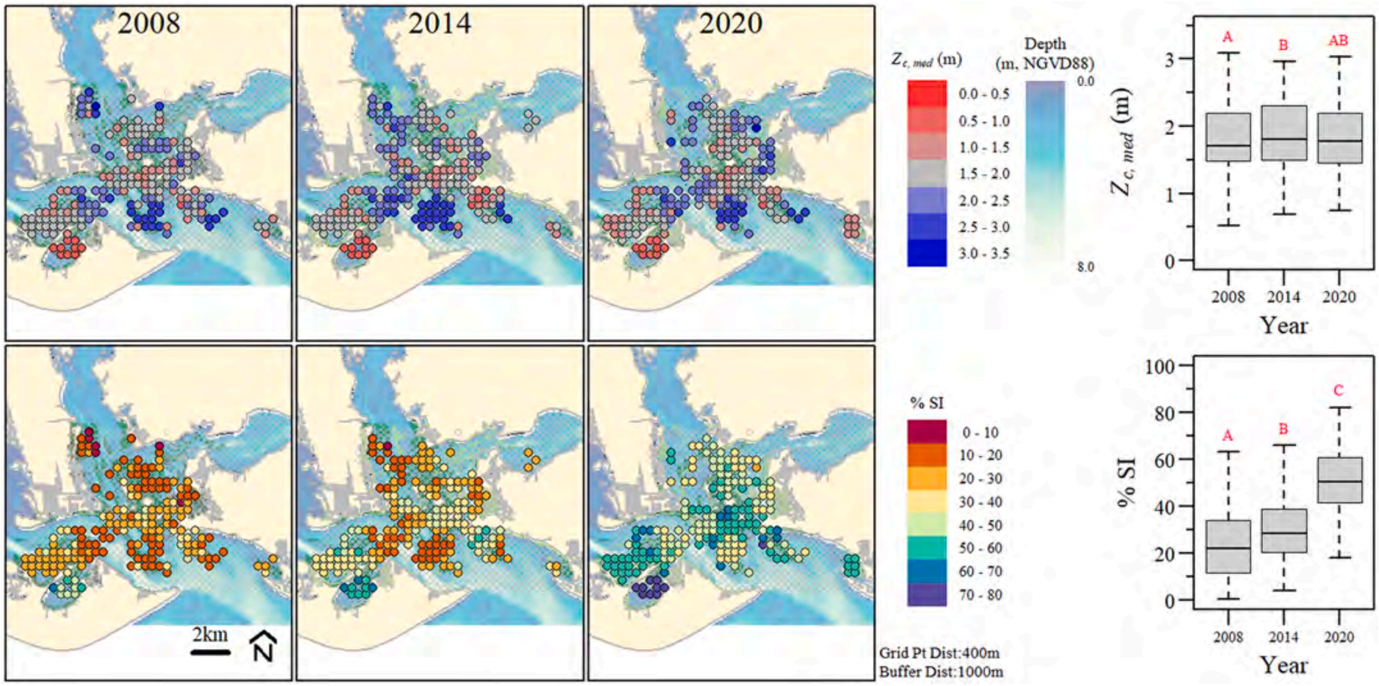

Fig. 5. Depth of seagrass colonization (Z_c; Top) with a comparison of Z_c values across survey years. Percent surface irradiance (% SI; Bottom) with a comparison of % SI across survey years. The letters above boxplots indicate pairwise comparisons between alternatives using Dunn's test of multiple comparisons.

Table 3
Mean, standard deviation and Kruskal-Wallis rank sum test results comparing seagrass density between disturbance and non-disturbance events by seagrass species and estuary region.

		14 Day Discharge < 5.13 hm^3d^{-1}		14 Day Discharge > 5.13 hm^3d^{-1}		Kruskal-Wallis Statistics	
Seagrass Species	Region	Mean	Std Dev	Mean	Std Dev	χ^2	ρ-value
Halodule wrightii	Upper	415.4	443.6	196.3	787.2	24.4	*< 0.01*
	Mid	365.6	370.2	319.9	358.8	1.6	0.21
	Low	692.8	1968.0	427.5	1206.7	1.2	0.28
	Control	879.6	3117.9	645.4	1746.0	0.2	0.65
Thalassia testudinum	Upper	0.0	0.0	0.0	0.0	—	—
	Mid	163.8	180.6	115.9	133.7	1.4	0.23
	Low	334.1	253.7	239.5	157.6	7.2	*< 0.01*
	Control	298.7	249.9	275.6	258.5	1.1	0.30

light attenuation and depressed salinities can have sublethal effect to seagrass species thereby reducing seagrass density and coverage (Dennison et al., 1993; Milbrandt et al., 2016).

3.3. Changes to seagrass

Seagrass depth of colonization is an important measure of the status and conditions of seagrass communities in estuaries because it relates and integrates light attenuation and environmental conditions including water quality and quantity over time (Beck et al., 2018; Burkholder et al., 2007; Dennison et al., 1993). Because seagrasses are ecological significant, integrate conditions over time and serve as environmental indicators both seagrass coverage and depth of colonization have been used to define water quality management objective in estuarine systems (Chen and Doering, 2016; Corbett and Hale, 2006; Greening et al., 2014; Milbrandt et al., 2016). Estimates of light attenuation, seagrass depth of colonization and corresponding light requirements for all locations in the lower CRE indicate substantial variation spatially and across years (Figs. 3 and 5). While it is uncertain how periods of low salinity and low light (i.e. high freshwater discharge) influence within community dynamics such as species composition and density (Irlandi, 2006; Milbrandt et al., 2016), at a regional level the cumulative effect can be detected from the distribution of seagrass communities, depth of colonization and light requirements (Fig. 5).

Seagrass surveys performed in the CRE demonstrate that stress and damaging freshwater discharge events decrease seagrass density and constitute a community disturbance-level impact (Figs. 6 and 7). Density changes were found along a 15 km upstream to downstream gradient in the CRE (45–60 km below S79). These results are consistent with modeling predictions that freshwater releases above stress and damaging threshold over different time steps could have a detrimental affect seagrass communities (Doering and Chamberlain, 1999; Douglass et al., 2020; RECOVER, 2020). The decrease in seagrass density found in the early season surveys following a year which had over 120 days above a 14-day moving average of 5.14 hm^3 d^{-1} provides additional evidence of the unfavorable relationship between the occurrence, intensity and duration of freshwater releases and seagrass density in the CRE.

Seagrass communities in the CRE have many anthropogenic stressors and most are rooted in intense land development within the watersheds of the CRE. As more and more natural lands are converted to urban landscapes, the scale and timing of freshwater additions to the CRE are altered and the estuary trends towards greater eutrophication due to increased nutrient loadings. Dissolved organic matter associated with increased freshwater runoff leads to darker water which decreases light

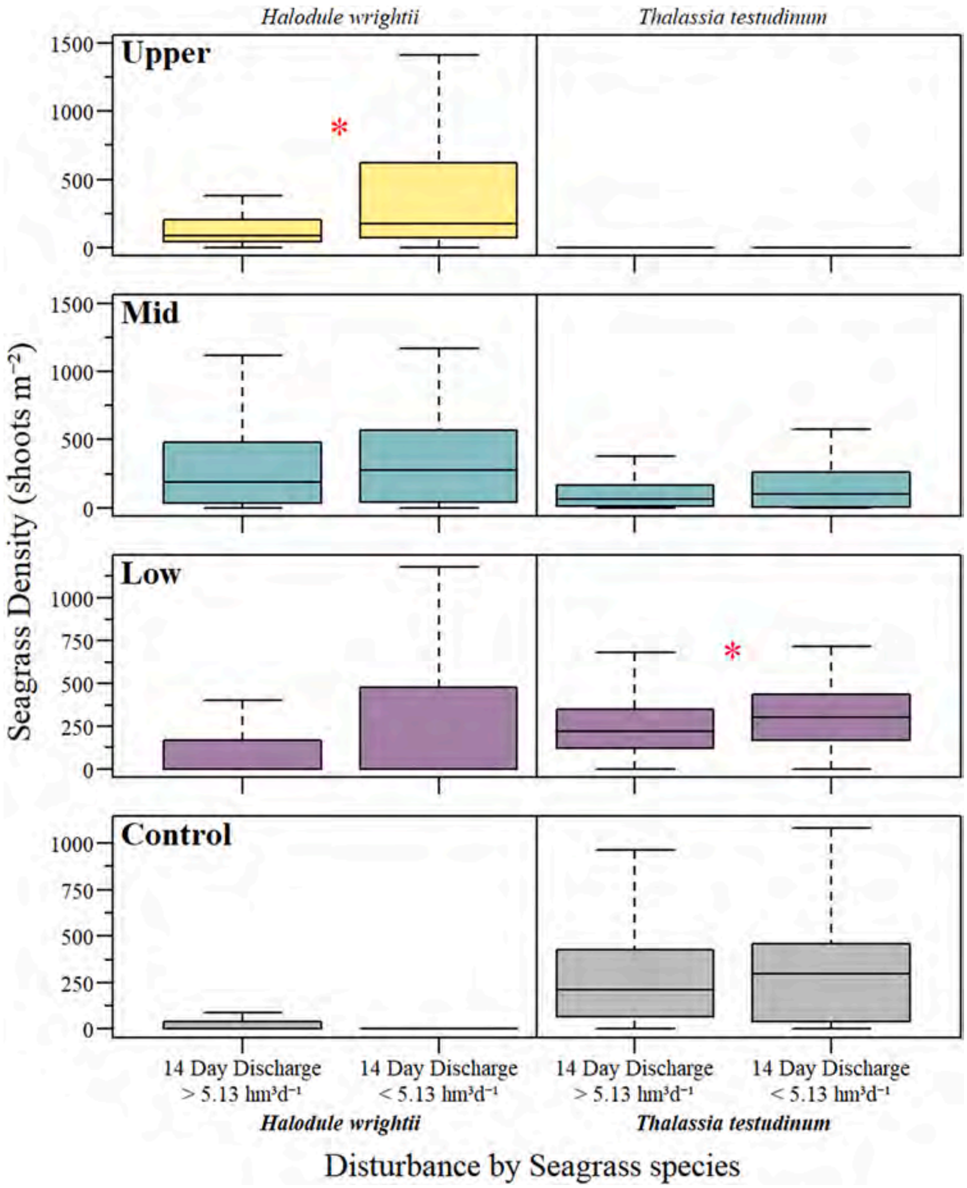

Fig. 6. Boxplots comparing *Halodule wrightii* (left) and *Thalassia testudinum* (right) density between disturbance (14-day moving average discharge > 5.13 hm^{-3} d^{-1}) and non-disturbance (14-day moving average discharge < 5.13 hm^{-3} d^{-1}) events by estuary region. Red astriks between boxplots indicate a significant difference between disturbance categories.

penetration and increases water temperature. Photodegradation through exposure to UV is thought to be the largest contributor to decreased CDOM (Coble, 2007). The more rapid discharge of stormwater runoff associated with an urbanizing landscape leads to less time for water to be photodegraded (Eckard et al., 2017; Oh et al., 2013; Schafer et al., 2020; Singh et al., 2014). Climate change, its associated temperature rise and potential storm intensification will likely have significant impact in the shallow depths colonized by seagrass in the CRE.

Light attenuation is a major controlling factor in the productivity and depth distribution of seagrass across the Charlotte Harbor, CRE and San Carlos Bay region (Chen and Doering, 2016; Corbett and Hale, 2006; Dixon and Kirkpatrick, 1999; McPherson et al., 1990). In this region, the resource-based water quality target is 25% surface irradiance which dictate the critical depth of seagrass (Corbett and Hale, 2006). Changes in light attenuation has a direct effect on this critical depth (Fig S7). In the lower CRE, Chen et al. (2015) determined that the mixing behavior of CDOM between high DOM freshwater flow and low DOM marine waters has the potential to influence light attenuation by up to 30%. Moreover, high freshwater discharge events has the potential to significantly increase CDOM/color concentration in the lower CRE (Fig. 4; Milbrandt et al., 2016) driven by elevated freshwater discharges and more importantly increases in stressful and damaging discharges (Fig S4). Salinity is also an important factor as it relates to seagrass growing conditions (Douglass et al., 2020; Milbrandt et al., 2016; Montague and Ley, 1993; Tomasko and Hall, 1999; Torquemada et al., 2005). The modeling suggests that higher discharges change light attenuation and salinities for seagrass regions. The field data show negative effects on *Halodule* and *Thalassa* but the effects are occurring in different regions for the two species. The negative effects are caused by a combination of light requirements and salinity tolerances for each species (Fig. 5).

4. Conclusions

The combined effect of water management (i.e. freshwater discharges to the CRE) and climate can significantly influence estuary

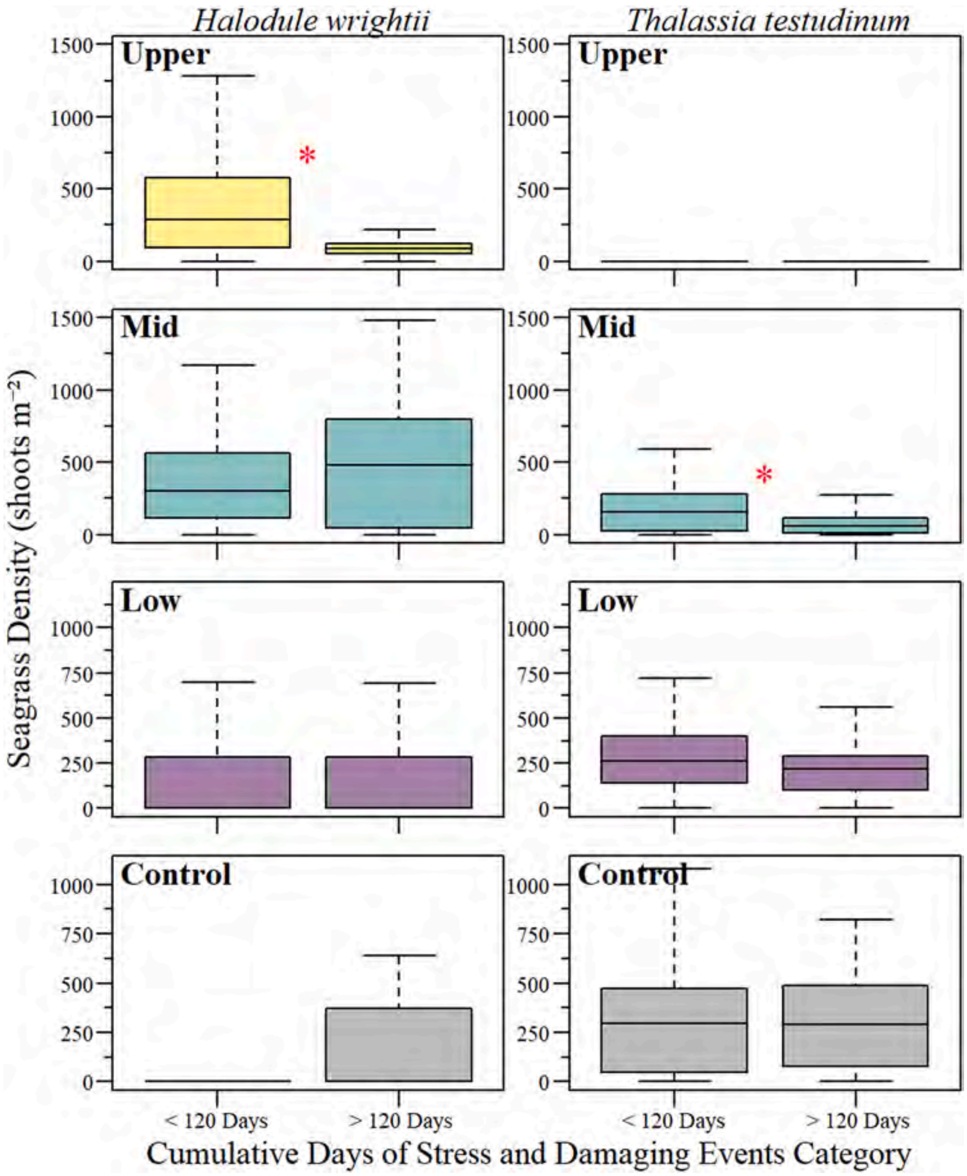

Fig. 7. Boxplots comparing *Halodule wrightii* (left) and *Thalassia testudinum* (right) density between annual cumulative days of stress and damaging events (14-day moving average discharge > 5.13 hm^{-3} d^{-1}) by estuary region. Red astriks between boxplots indicate a significant difference between disturbance categories.

Table 4
Mean, standard deviation and Kruskal-Wallis rank sum test results comparing seagrass density between annual cumulative days of stress and damaging events (14-day moving average discharge > 5.13 hm^{-3} d^{-1}) events by seagrass species and estuary region.

		> 120 Days Stress and Damaging Events		< 120 Days Stress and Damaging Events		Kruskal-Wallis Statistics	
Seagrass Species	Region	Mean	Std Dev	Mean	Std Dev	χ^2	ρ-value
Halodule wrightii	Upper	99.1	80.0	385.5	372.6	35.8	*< 0.01*
	Mid	490.3	446.6	388.9	368.3	1.1	0.29
	Low	471.6	1177.4	602.8	1709.4	0.3	0.58
	Control	686.6	1713.0	758.0	2616.0	0.8	0.36
Thalassia testudinum	Upper	0.0	0.0	0.0	0.0	—	—
	Mid	86.8	112.0	181.4	176.2	12.2	*< 0.01*
	Low	233.4	171.5	303.6	225.2	3.7	0.05
	Control	306.0	247.6	309.7	272.7	0.0	0.85

function by altering freshwater balance for the better (supplemental water during dry season/drought) or worst (prolong high volume discharges altering salinity and color/CDOM) regimes affecting benthic communities. Climate and water management are inherently intertwine where a set of management criteria driven by upstream water balances, weather dynamics trigger operational rule developed to manage and mitigate water deliveries. The current freshwater water management regime has resulted in an increase in stressful and damaging discharge events and higher light attenuation across the study area, especially during the 2008–2018 period. However, operational flexibility post 2018 has reduced stressful and damaging events and thereby improving light attenuation and %SI (i.e. seagrass light requirements) in the lower estuary. While the affect of the current water management regime in the lower estuary has historically not been sustainable there is a glimmer of hope in what was learned during the operational deviation (2018 – current), the potential of future water management process (i.e. LOSOM) and ongoing restoration efforts to manage water more sustainably thereby building a more resistant and resilient ecosystem.

Ethics approval and consent to participate

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CRediT authorship contribution statement

Thompson Mark: Writing – review & editing, Writing – original draft, Data curation. **Paul Julian II**: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Milbrandt Eric C.:** Writing – review & editing, Writing – original draft, Data curation.

Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

Data Availability

Optical water quality data and metadata are available in the Environmental Data Initiative data repository (https://doi.org/10.6073/pasta/b7d005b197c02f9258e35c8682b9ed6d). Rainfall and hydrologic data can be retrieved from the South Florida Water Management District online environmental database (https://www.sfwmd.gov/science-data/dbhydro). All other data are available upon request.

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Consent for publication

Not Applicable.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2023.103302.

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