



Submerged Vegetation Responses to Climate Variation and Altered Hydrology in a Subtropical Estuary: Interpreting 33 Years of Change

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Abstract

Links between hydrologic modifications, flow and salinity regimes, and submerged aquatic vegetation (SAV) species composition and abundance were assessed with an empirical analysis of 33 years of monitoring data collected at nine sites in Florida's Caloosahatchee River Estuary (CRE). Freshwater inflows to the estuary (30-day means) were often outside the previously recommended envelope of 12.74 to 79.29 m³ s⁻¹. Discharges from Lake Okeechobee through a synthetic hydrologic link were responsible for 43% of the above-envelope flows, but reduced the incidence of below-envelope flows by 30%. A salinity model and salinity stress indices developed for each SAV species indicated that the observed flows generated variable salinity conditions likely to harm both seagrasses and freshwater SAV in the estuary. Regression modeling of SAV abundance generally confirmed the flow and salinity responses expected for each species: *Halodule wrightii* and *Thalassia testudinum* in the lower estuary were both harmed by high-flow, low-salinity conditions, while *Vallisneria americana* in the upper estuary was decimated by low-flow, high-salinity conditions. There was a species-specific effect of the seasonal timing of high flows—*T. testudinum* was more negatively correlated with high flows in the dry season; *H. wrightii* in the wet season. The regression analyses also highlighted strong, year-to-year autocorrelations in SAV abundance, indicating reduced resilience after severe losses, particularly for *V. americana*. Large residual variation in some regression models suggested that factors other than salinity (e.g., optical water quality or grazing impacts) may also influence the system dynamics and should be incorporated in continuing research. This analysis suggests that use of artificial water management infrastructure to reduce extreme high and low flows to the Caloosahatchee and other estuaries could help maintain SAV health in light of intensifying climate variability and degraded watershed flow regulation capacity.

Keywords Hydrologic alteration · Seagrass · *Vallisneria* · Restoration · Salinity suitability · HSI model

Introduction

Submerged aquatic vegetation (SAV), which includes both seagrasses and freshwater aquatic plants, forms productive and species-rich habitats throughout the world (Hemminga and Duarte 2000). SAV contributes to human well-being by

stabilizing sediments, improving water quality, and enhancing fisheries resources (Worm et al. 2006). SAV abundance, however, has declined dramatically worldwide (Orth et al. 2006; Waycott et al. 2009). Effects of human activities on physico-chemical conditions have been implicated in most of these declines (Short and Wyllie-Echeverria 1996). For example, physical alteration of coastal and estuarine hydrology may result in salinity regimes that exceed SAV species' physiological tolerances (Short and Wyllie-Echeverria 1996; Doering and Chamberlain 2000; Doering et al. 2001). In south Florida, changing hydrography due to alteration of the greater Everglades watershed has been identified as a particularly serious threat to SAV (Light and Dineen 1994; Fourqurean and Robblee 1999; Barnes 2005; Frankovitch et al. 2011; Buzzelli et al. 2015).

This threat is evident in southwest Florida's Caloosahatchee River and Estuary (CRE), which has been dramatically altered via changes in its local watershed and

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changes in the interconnected water management region of central and southern Florida (Central and Southern Florida Flood Control District 1954). In addition to deforestation and drainage of much of the CRE watershed for urban and agricultural development, the Caloosahatchee River itself has

been artificially connected to Lake Okeechobee (Fig. 1a) to allow cross-state vessel traffic and freshwater releases for regulating water levels in the Lake. The Caloosahatchee River has also been straightened and deepened, and three water control structures (S-77, S-78, and S-79) have been added to



Fig. 1 **a** Watersheds and water control structures of the Caloosahatchee River and Estuary. **b** South Florida Water Management District SAV monitoring sites in the estuary

improve conveyance (Antonini et al. 2002). The most downstream structure (S-79) also serves as a salinity barrier (Flaig and Capece 1998), which separates the freshwater river from the estuary that terminates 42 km further downstream (Fig. 1b). The “tamed” Caloosahatchee River is now referred to as the C-43 canal, and its local watershed as the C-43 basin (Fig. 1a).

As might be expected for a watershed with extensive drainage features, freshwater inflow to the CRE has become more variable and drives corresponding fluctuations in salinity (Hopkinson and Vallino 1995; Doering et al. 2001). These fluctuations cause mortality of freshwater organisms (e.g., tape-grass, *Vallisneria americana*) at the head of the estuary (Kraemer et al. 1999; Doering et al. 2002) and marine organisms at its mouth (Chamberlain and Doering 1998a, b).

In recent decades, the effects of these changes on SAV and other natural resources in the CRE have become the focus of intense scientific scrutiny and management concern (Doering et al. 2002; Barnes 2005; Douglass 2014; Buzzelli et al. 2015). Restoration of SAV beds through water management infrastructure improvements is one of the explicit goals of the “Comprehensive Everglades Restoration Plan” (CERP), the largest environmental restoration program in history, as detailed in the plan’s project implementation report (USACE and SFWMD 2010). An enormous challenge in this unprecedented effort is reconciling the conflicting water flow, level, and salinity needs of the different organisms and biotopes of the Greater Everglades Ecosystem, e.g., maintaining salinity within the range of freshwater SAV versus seagrasses.

To guide the restoration and “reconciliation” effort in the CRE, Doering et al. (2002) proposed high and low freshwater inflow limits at S-79 (mean monthly values of $79.29 \text{ m}^3 \text{ s}^{-1}$ and $8.49 \text{ m}^3 \text{ s}^{-1}$, respectively). These limits were based on salinity tolerances of SAV determined in the laboratory and limited time series of monthly monitoring data (Feb 1986–May 1989; Nov 1994–Dec 1995). Within the bounds of this flow envelope (i.e., the range from low to high flow limits), appropriately low salinities preventing mortality of *Vallisneria americana* would be maintained in the upper estuary, and appropriately high salinities preventing mortality of *Halodule wrightii* would be maintained in the middle estuary (Doering et al. 2002). Subsequent analysis associated with restoration planning (USACE and SFWMD 2010) recommended a somewhat greater lower limit of $12.74 \text{ m}^3 \text{ s}^{-1}$, which we use in the analyses presented here.

In the years since the envelope was first proposed, monitoring of SAV in the Caloosahatchee has continued. Though the impact of flow on SAV has been assessed over brief time periods (Hoffacker 1994; Kraemer et al. 1999; Doering and Chamberlain 2000; Doering et al. 2001; Mazzotti et al. 2007a, b), the effectiveness of this flow envelope at maintaining the distribution and abundance of SAV along the estuarine salinity gradient has not been quantitatively evaluated. Evaluating its

efficacy with a long-term time series that includes data not used in its derivation is a necessary step in validating the flow envelope as a hydrologic target to guide restoration efforts. We assess the envelope’s efficacy using CRE freshwater flow, salinity, and SAV data from 1985 to 2017, a period including flows above, below, and within the $12.74\text{--}79.29 \text{ m}^3 \text{ s}^{-1}$ envelope. To do so, we develop species-specific salinity stress indices and a regression-based evaluation approach that is applicable to other systems where managers seek to use longitudinal datasets to interpret and forecast biotic responses to hydrologic alteration and climate change.

Methods

SAV Monitoring

The SAV monitoring effort in the CRE began in 1986 and ultimately included nine sites, numbered from the most river-influenced to the most marine (Fig. 1b). Not all sites were monitored in all years, and monitoring methodologies changed over time (Table 1), but the basic monitoring scheme was consistent. Each site was defined as an approximately 1-ha area, within which SAV characteristics were assessed monthly or bimonthly. Prior to 1998, 10–20 seagrass quadrats (0.1 m^2) were distributed randomly within each site (Table 1a). From 1998 to 2009, 20 quadrats (1.0 m^2) were randomly arranged along two 100-m transects intersecting to form a “+” shape. After 2009, the crossed transects were replaced by a polygon encompassing 30 quadrat locations designated with mapping software (ArcGIS). In 2012, the polygon for site 6 was moved slightly to avoid an oyster reef in the original location, and the new site was designated as Site 6.1 (Beth Orlando pers. comm). Also in 2012, the polygon for site 1 was removed, and reinstated in 2013 with broader boundaries and 9-m^2 quadrats at each point (Table 1a). This change was needed to enhance the power to detect increasingly rare *Vallisneria americana* in the upper estuary.

Over the period of record, several changes were made to the types of SAV data collected within each quadrat (Table 1b). Prior to 1998 the primary metric of SAV abundance was blades per square meter. From 1998 to 2007, shoots per square meter was also recorded. In 2008 and 2009, presence/absence of shoots was recorded within each $10 \times 10 \text{ cm}$ or $20 \times 20 \text{ cm}$ cell of the 1-m^2 quadrat. These “grid counts” ranged from 0 to 100 and 0 to 25, respectively. After 2009, only 0–25-grid counts were made. In 2012, a visual percent cover estimate for the whole 1-m^2 quadrat was added as a complement to the grid counts. This method was based on the Braun-Blanquet method commonly used in SAV abundance surveys (e.g., Fourqurean et al. 2001), but instead of collapsing percent cover estimates into ordinal ranks as in that method, percent cover estimates were left in raw form.

Table 1 Summary of SAV site locations, years sampled, and sampling scheme

		Year																															
(a)	Site #	Estuarine zone	Predominant SAV species	1986	1987	1988	1989	1994	1995	1996	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017			
	1	Upper									T	T	T	T	T	T	T	T	T	T	T	T	P	P	P	P	P	P	P	P			
	2		<i>V. americana</i> ,								T	T	T	T	T	T	T	T	T	T	T	T	P	P	P	P	P	P	P	P			
	3		<i>R. maritima</i>								T	T	T	T	T	T	T	T	T	T	T	T	P	P	P	P	P	P	P	P			
	4										T	T	T	T	T	T	T	T	T	T	T	T	P	P	P	P	P	P	P	P			
	5	Middle	<i>H. wrightii</i> ,	H	H	H	H																										
	6		<i>R. maritima</i>	H	H	H	H																										
	6.1																																
	7	Lower	<i>T</i>	H	H	H	H	H	H	H																							
	8		<i>testudinum</i> ,	H	H	H	H	H	H	H																							
	9		<i>H. wrightii</i>	H	H	H	H																										
Key: H = sampled haphazardly, T = sampled along transects, P = sampled within polygons, 9 = sampled using 3 × 3 m quadrat																																	
(b)			Year																														
	Principle types of SAV data collected		1986	1987	1988	1989	1994	1995	1996	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017				
	Blades*m ⁻²		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
	Shoots*m ⁻²																																
	Grid counts (0–100)																																
	Grid counts (0–25)																																
	Percent cover estimate																																
	Canopy height		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Key: X = data type was collected during this period																																	

For time series analyses, all SAV abundance measures were converted to percent cover, because it could be derived from the other data types. Conversions from blades per square meter to percent cover were developed for the pre-1998 data, from shoots per square meter to percent cover for 1998–2007, and from 0- to 25-grid count to percent cover for 2008–2011. There was no period of overlap of shoots per square meter and percent cover measurements in our dataset. Therefore, we developed the conversion factors for these using a large set of overlapping measurements from the St. John's River Water Management District (SJRWMD's) SAV monitoring in east Florida's Indian River Lagoon (IRL). The range of climate, water quality, and SAV conditions in the IRL approximates that of the CRE, and the quadrat monitoring methods used are similar in both systems. We regressed percent cover against shoots per square meter in the SJRWMD's 1994–2017 data, with the intercept set at 0, to generate simple conversions from shoots per square meter to percent cover. For *Thalassia testudinum*, we determined with $R^2 = 0.79$ that 1010 shoots m^{-2} was equivalent to 100% cover. For *Halodule wrightii* we determined with $R^2 = 0.76$ that 3060 shoots m^{-2} was equivalent to 100% cover. For *Ruppia maritima*, we determined with $R^2 = 0.65$ that 1580 shoots m^{-2} was equivalent to 50% cover; our *R. maritima* shoot densities never exceeded the 50% cover equivalent. We lacked the data to develop a conversion specific for *Vallisneria americana*, so we apply the *T. testudinum* conversion factor to morphologically similar *V. americana*. Where shoots per square meter in a quadrat exceeded the 100% cover equivalent, cover was entered as 100%. For the pre-1998 data, an additional step of converting blades per square meter to shoots per square meter was required. Linear regressions on the data from 2004 to 2007, a period in which both blades per square meter and shoots per square meter were recorded, were used to generate the formulae for these conversions: *H. wrightii* shoots = 0.3488 [*H. wrightii* blades] ($R^2 = 0.94$), *T. testudinum* shoots = 0.2942 [*T. testudinum* blades] ($R^2 = 0.93$). Conversion of 0–25 grid count to percent cover was based on linear regression analyses of the 2012–2013 SAV data in which grid count and visually estimated percent cover were recorded concurrently. Initial regressions were poor fits, but better fits were achieved by incorporating both canopy height (cm) and grid count into the following linear model: percent cover = $C \times$ (canopy height \times grid count), where C is the regression coefficient. For *H. wrightii*, $C = 0.0953$ ($R^2 = 0.60$), for *T. testudinum* $C = 0.1018$ ($R^2 = 0.58$), and for *Ruppia maritima* $C = 0.1161$ ($R^2 = 0.70$). The coefficient derived for *T. testudinum* was also applied to morphologically similar *V. americana*. While there is some residual variability in our percent cover conversion models at the single quadrat scale, estimates of mean percent cover, per site, per month, are insulated from this variability because each is an average of 20 to 30 individual quadrat estimates.

Hydrology and Salinity Data and Models

Freshwater flows through S-77, S-78, and S-79 on the Caloosahatchee River (C-43 canal) have been recorded continuously since the structures were built. Flows to the estuary at S-79 (Fig. 1) reflect the sum of freshwater inputs from Lake Okeechobee and the C-43 basin, minus losses such as evaporation and withdrawals for agricultural and municipal uses. C-43 basin runoff and Lake Okeechobee's contributions to the estuary were separated through water budget analyses on a daily time scale using flow data collected at S-77, S-78, and S-79 (K. Haunert pers. comm.). The estuary also receives freshwater from the "tidal basin" seaward of S-79 (Fig. 1a). Flows of five tributaries in the tidal basin were measured during 2008–2013, and these data were used to calibrate a hydrological model used to estimate daily freshwater inflow from the tidal basin into the estuary (Wan and Konyha 2015). All measured data were obtained from the SFWMD database.

To hindcast daily mean salinity at the nine SAV monitoring stations from 1985 to 2017, we relied on a salinity time series model developed for the estuary (Qiu and Wan 2013). The model consists of an autoregressive term representing system persistence and an exogenous term accounting for driving factors including freshwater inflow, rainfall, and tidal water surface elevation. An inverse distance weighting interpolation method, validated using the Caloosahatchee three-dimensional hydrodynamic model (Wan et al. 2013), was embedded into the salinity simulations. The model was calibrated against 6 years of measured daily salinities at seven locations across the estuary, yielding R^2 values ranging from 0.89 to 0.96.

Statistical Analyses

To facilitate our interpretation of the relationship between salinity variation and SAV abundance, we developed three salinity stress indices. The indices were designed to equate observed salinity levels with theoretical magnitudes of harm to SAV, based on published information on the biological responses of key SAV species to salinity variation. For *Vallisneria americana*, mesocosm experiments under replete light conditions determined that the rate of growth progressively declined as salinity increased, approaching zero at a salinity of 10 (SFWMD 2003). In addition, Doering et al. (2001) reported that significant loss of shoots occurred after 20 days of exposure to a salinity of 18 in mesocosms. This is consistent with Kraemer et al. (1999), who observed complete mortality of *V. americana* in the Caloosahatchee Estuary after 2 to 4 weeks when salinity increased from 15 to 22. The above results formed the foundation for the Salinity Suitability Index reported in Mazzotti et al. (2007b), whereby maximum stress leading to mortality was set at 18. We also considered these results when designing our own *Vallisneria* Stress Index

(VSI). Our VSI is a logistic curve that increases from near zero at salinities < 3 to near 1 at 18: $VSI = (1 + e^{-0.5[\text{Salinity} - 10]})^{-1}$. The VSI was applied at upper estuary SAV sites 1–4 using site-specific daily mean salinities.

Similarly, we developed a *Halodule wrightii* stress index ($HSI = 1 - (1 + e^{-0.4[\text{Salinity} - 12]})^{-1}$) and *Thalassia testudinum* stress index ($TSI = 1 - (1 + e^{-0.4[\text{Salinity} - 17]})^{-1}$) based on results of experimental and monitoring studies reviewed in Mazzotti et al. (2007a). These indices reflect the fact that both these seagrasses grow well in marine salinities and poorly at very low salinities, but that *H. wrightii* tolerates low salinities better than *T. testudinum* (Zieman and Zieman 1989; Lirman and Cropper 2003). We recognize that in addition to physiological stress, ecological competition between *H. wrightii* and *T. testudinum* plays an important role in determining the optimal “salinity climates” for each. For example, a moderate decrease in salinity or increase in salinity variability may harm *T. testudinum* but indirectly benefit *H. wrightii* via competitive release, resulting in a shift in species composition rather than an overall loss of seagrass (Fourqurean et al. 2003; Herbert et al. 2011). These community dynamics are considered when we interpret our monitoring and modeling results.

Though we had SAV abundance data at the monthly or bimonthly scale, seasonal variation in SAV abundance was high, and the timing and frequency of sample dates varied somewhat from year to year. We dealt with this in two steps. First, we used linear interpolation between sample dates to estimate SAV percent cover for each day of the record. Second, we used these measured and interpolated daily values to calculate mean May–October SAV abundance for each site and year, which we used as our primary response variable in statistical analyses. May–October spans the peak seasonal abundance of SAV in this region (Herzka and Dunton 1997). The linear interpolation step was deemed necessary to reduce the potential bias of sample dates occurring just inside or outside the May–October period.

Comparisons between SAV percent cover, flow, and salinity metrics were made using a multiple linear regression framework. As with the SAV data, the abiotic data used as predictors in regression models were also integrated over multi-month periods. Some predictor metrics were integrated over the 12-month period leading up to and including the May–October SAV response period. Others were integrated over the wet season of the focal year (May–October), or the preceding dry season (November–April). Flow and salinity metrics included (1) the number of days in the period that 30-day mean flow through the S-79 lock and dam exceeded $79.29 \text{ m}^3 \text{ s}^{-1}$, (2) the number of days that 30-day mean flow was below $12.74 \text{ m}^3 \text{ s}^{-1}$, and (3) the mean or maximum VSI, HSI, or TSI values for the focal SAV site, as appropriate to the SAV species at that site. Regressions were performed at the scale of estuarine region, aggregating the data from all sites within the region; sites 1–4 for the upper estuary, sites 5 and 6

for the middle estuary, and sites 7–9 for the lower estuary. The SAV species evaluated were *Vallisneria americana* and *Ruppia maritima* in the upper estuary, *Halodule wrightii* in the middle and lower estuary, and *Thalassia testudinum* in the lower estuary. Five to eight linear regression models were tested for each SAV species in each region (Table 2). In addition to the regressions specific to estuarine region, we ran models for total SAV in the estuary; the sum of SAV cover at sites 2, 4, 5, 6, 7, and 8, which were the most regularly monitored sites. Predictors in these total SAV models included the annual standard deviation of 30-day mean flow via S-79, as well as seasonally averaged flow metrics for S-79 and Lake Okeechobee inputs. All models included the previous year’s May–October SAV percent cover as a predictor to account for likely autocorrelation of year-to-year abundance in these perennial plants. The regression models used were a subset of all possible variable combinations; we only tested for correlations that could be interpreted in light of our hypotheses about the system (Burnham and Anderson 2002). The predictors included in each model are indicated by the presence of their standardized regression coefficients in Table 2. Each model also estimated a constant term, not shown. Adjusted- R^2 values were calculated for all models, and the relative likelihood of models was compared using Akaike’s information criterion (AIC) and weighted model probability (ω_i) (Burnham and Anderson 2002). We considered good models to be those that explained a sizeable portion of the variance in a response, and which were weighted favorably relative to the other models by ω_i , as in Douglass et al. (2010). Statistical analyses were performed using Microsoft Excel and IBM® SPSS® Statistics version 22.

Results

Freshwater Flow

From 1985 through 2017, 79% of freshwater flow to the Caloosahatchee Estuary was via the S-79 lock and dam structure, with the tidal basin watershed contributing the remaining 21% (Fig. 2). Flows through S-79 were predominantly derived from the C-43 basin, which contributed 49% of total flow to the estuary. Regulatory releases from Lake Okeechobee averaged 30% of total freshwater flow to the estuary, but this was extremely variable, with monthly average Lake Okeechobee contributions to freshwater input ranging from 0% to more than 80% (Fig. 2).

All sources of freshwater were seasonally variable, generally with higher flows in the May–October wet season than the November–April dry season. Interannual variability was pronounced, driven by hurricanes and tropical storms in 1995, 1999, 2003, 2004–2005, 2013, and 2017, and regional droughts in 1986, 1989, 2000–2001, 2007–2008, and 2012.

Table 2 Results of regression analyses of mean May to October SAV abundance vs. freshwater flow and salinity stress metrics in the Caloosahatchee Estuary. Model sets are aggregated by SAV response variable and estuarine region. Within each set, weighted model probability ω_j is calculated based on corrected Akaike's information criterion AICc. Models with $\omega_j > 0.13$ are in *italic type*. All models included the previous year's May–October SAV abundance as a predictor, and also estimated a constant term, not shown. The response variable for models a1–a6 is the sum of percent cover of all species of SAV at sites 2, 4, 5, 6, 7, and 8 for the years where SAV was monitored at all those sites. The response variables in the other model sets are species-specific. The predictor variables were mean, maximum, or standard deviation (SD) statistics calculated over the full year (Nov.–Oct.) including the SAV response period, or just the wet season (May–Oct.) or dry season

(Nov.–Apr.) of that year. “Days of above-envelope S-79 flow” is number of days in the Nov.–Oct. period that 30-day mean flow through the S-79 lock and dam exceeded $79.29 \text{ m}^3 \text{ s}^{-1}$. “Days of below-envelope S-79 flow” is the number of days that 30-day mean flow was below $12.74 \text{ m}^3 \text{ s}^{-1}$. The species-specific SAV stress indices, VSI, HSI, and TSI are the *Vallisneria* Stress Index, *Halodule* Stress Index, and *Thalassia* Stress Index, respectively (see “Methods”). Metrics of annual-mean freshwater flow from the various freshwater sources to the estuary (Lake Okechobee, C-43 Basin, Tidal Basin—see “Methods”) are predictors in some models. The predictors included in each model are indicated by the presence of standardized regression coefficients

Response variable	Predictor variable and standardized				Days of below-envelope S-79 Flow	SD of S-79 flows	Mean S-79 flow, Nov.–Oct.	Mean tidal basin flow, Nov.–Oct.
	Model number	Prior year May–Oct. cover May	Days of above-envelope S-79 flow	Days of below-envelope S-79 Flow				
Sum of mean May–Oct. SAV % cover at site 2 and sites 4–8	a1	<i>0.59</i>						
	a2	0.51	–0.27		0.05			
	a3	0.53				–0.16		
	a4	<i>0.51</i>					–0.29	
	a5	<i>0.60</i>						–0.26
	a6	0.54					–0.21	–0.15
May–Oct. <i>Ruppia maritima</i> % cover at sites 1–4	b1	<i>0.69</i>						
	b2	0.69		–0.11				
	b3	0.68			–0.06			
	b4	<i>0.65</i>		–0.21	–0.18			
	b5	0.69						
May–Oct. <i>Vallisneria americana</i> % cover at sites 1–4	c1	0.78						
	c2	0.78		0.17				
	c3	0.78						
	c4	<i>0.77</i>			–0.17			
	c5	0.77				–0.05		
	c6	<i>0.81</i>					–0.20	
	c7	<i>0.83</i>					–0.16	
	c8	0.84						–0.21
Response variable	Predictor variables and standardized							
	Model number	Prior year May–Oct. cover	Days of above-envelope S-79 flow	Days of below-envelope S-79 flow	Mean HSI or TSI: wet season	Mean HSI or TSI: dry season	Mean Lake O. flow, Nov.–Oct.	Mean tidal basin flow, Nov.–Oct.
	d1	0.51						
	d2	<i>0.47</i>		–0.31				
	d3	0.55			0.21			
	d4	0.53					–0.25	
	d5	0.44						
	d6	<i>0.50</i>						
	d7	0.54						
							–0.37	
							–0.23	

Table 2 (continued)

Response variable	Model assessment parameters				Residual sum of squares	Corrected AIC	Weighted model probability	Adjusted R ²
	Sample size	# of parameters	RSS	AIC _C				
May–Oct. <i>Halodule wrightii</i> % cover at Sites 7–9	d8	0.51						
	e1	0.53						
	e2	0.41						
	e3	0.51						
	e4	0.39						
	e5	0.53						
	e6	0.30						
	e7	0.48						
	e8	0.50						
	f1	0.42						
	f2	0.36						
	f3	0.49						
	f4	0.39						
f5	0.35							
f6	0.37							
f7	0.42							
f8	0.41							
Sum of mean May–Oct. SAV % cover at site 2 and sites 4–8								
May–Oct. <i>Ruppia maritima</i> % cover at sites 1–4	d8	0.51						
	e1	0.53						
	e2	0.41						
	e3	0.51						
	e4	0.39						
	e5	0.53						
	e6	0.30						
	e7	0.48						
	e8	0.50						
	f1	0.42						
	f2	0.36						
	f3	0.49						
	f4	0.39						
f5	0.35							
f6	0.37							
f7	0.42							
f8	0.41							
Sum of mean May–Oct. SAV % cover at sites 1–4								
May–Oct. <i>Vallisneria americana</i> % cover at sites 1–4	d8	0.51						
	e1	0.53						
	e2	0.41						
	e3	0.51						
	e4	0.39						
	e5	0.53						
	e6	0.30						
	e7	0.48						
	e8	0.50						
	f1	0.42						
	f2	0.36						
	f3	0.49						
	f4	0.39						
f5	0.35							
f6	0.37							
f7	0.42							
f8	0.41							
Sum of mean May–Oct. SAV % cover at sites 1–4								

Table 2 (continued)

Response variable	Mode 1 assessment parameters		Residual sum of squares RSS	Corrected AIC AICc	Weighted model ω_i	Adjusted R^2
	Sample size n	# of parameters K				
May–Oct. <i>Halodule wrightii</i> % cover at Sites 5 and 6	55	3	0.14	-322.9	0.39	0.64
	55	4	0.138	-320.5	0.12	0.64
	32	2	0.430	-133.5	0.06	0.23
	32	3	0.376	-135.3	0.14	0.30
	32	3	0.406	-132.9	0.04	0.25
	32	3	0.378	-135.2	0.13	0.30
	32	3	0.396	133.7	0.06	0.27
	32	3	0.351	-137.5	0.43	0.35
	32	3	0.400	-133.4	0.05	0.26
	32	3	0.390	-134.2	0.08	0.28
May–Oct. <i>Halodule wrightii</i> % cover at Sites 7–9	34	2	0.923	-118.2	0.11	0.26
	34	3	0.878	-117.5	0.08	0.27
	34	3	0.909	-116.3	0.04	0.25
	34	3	0.828	-119.5	0.21	0.31
	34	3	0.923	-115.8	0.03	0.24
	34	3	0.795	-120.9	0.42	0.34
	34	3	0.880	-117.4	0.07	0.27
	34	3	0.918	-116.0	0.04	0.24
	35	2	0.713	-131.9	0.09	0.15
	35	3	0.675	-131.4	0.07	0.17
May–Oct. <i>Thalassia testudinum</i> % cover at sites 7–9	35	3	0.673	-131.5	0.07	0.17
	35	3	0.702	-130.0	0.04	0.14
	35	3	0.600	-135.5	0.55	0.26
	35	3	0.678	-131.3	0.06	0.17
	35	3	0.686	-130.9	0.05	0.16
	35	3	0.679	-131.2	0.06	0.17

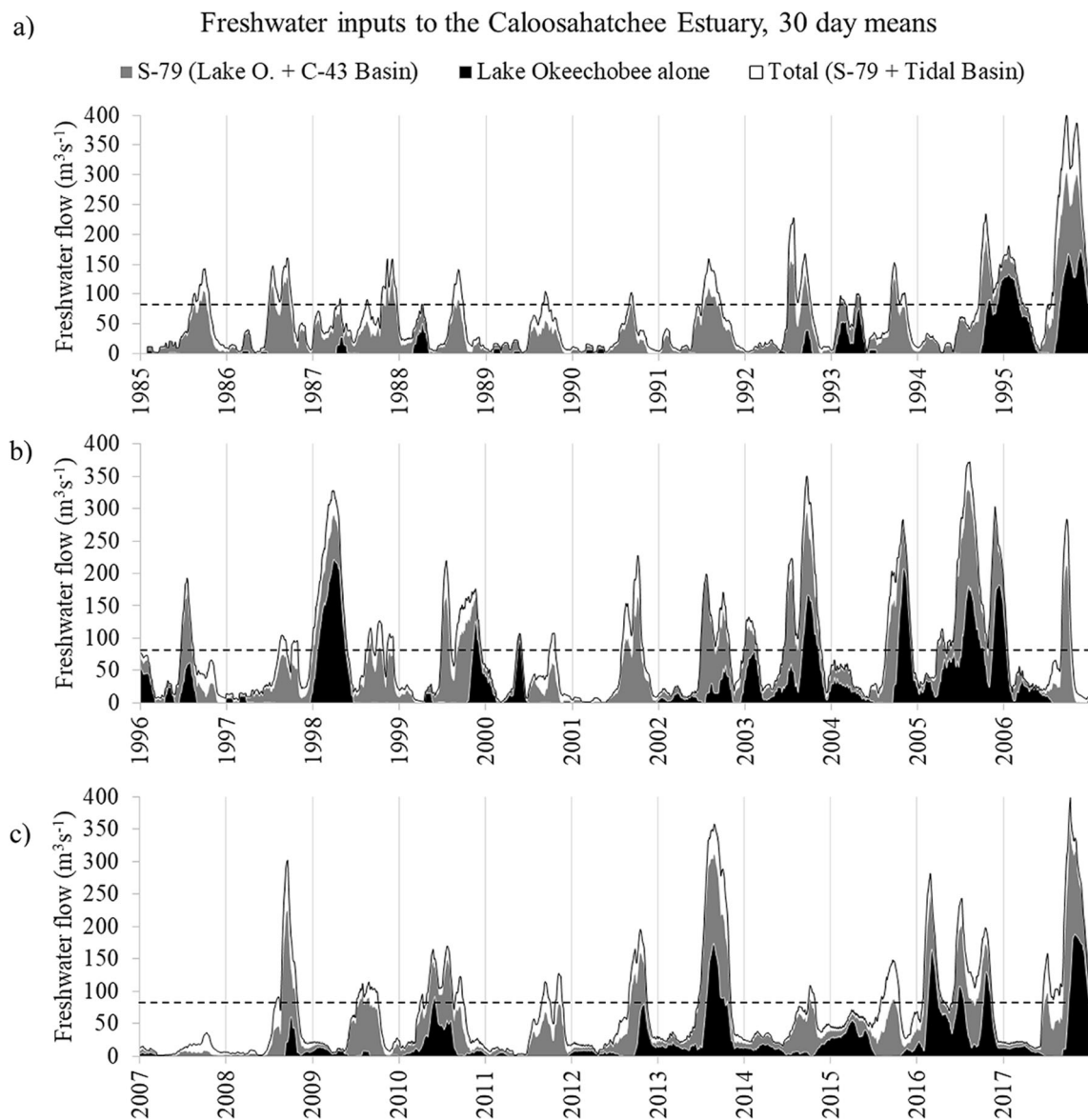


Fig. 2 Monthly mean freshwater inputs to the Caloosahatchee Estuary for the periods from 1985 to 1996 (**a**), 1996–2007 (**b**), and 2007–2017 (**c**). Total freshwater input (thin black line) is the sum of measured flows through the S-79 structure and modeled inputs from the tidal basin.

S-79 inputs are a combination of discharges from Lake Okeechobee (black shading), and runoff from the C-43 basin (gray shading). Plots overlay one another; they are not stacked. Horizontal dashed lines in each panel indicate $79.29 \text{ m}^3 \text{ s}^{-1}$ target maximum flow for S-79

Exceptions to the typical seasonal pattern of flow occurred in 1998 and 2016: strong El Niño years in which flows were very high in the dry season and surpassed those of the wet season. The most variable components of flow were those from Lake Okeechobee and via S-79, reflecting management actions that alternated between releasing water for flood control and withholding water for agricultural usage (Fig. 2). Monthly mean S-79 flows were often outside the flow envelope (Fig. 3). For example, in high precipitation year 2005, monthly mean S-79 flow exceeded $79.29 \text{ m}^3 \text{ s}^{-1}$ for more than 250 days of the year (Fig. 3a). Likewise, in drought year 2007, monthly mean S-79 flow was below $12.74 \text{ m}^3 \text{ s}^{-1}$ for over 350 days (Fig. 3b). The number of

days of outside-envelope S-79 flow was strongly affected by regulatory releases from Lake Okeechobee. Flow from S-79 would have exceeded the upper limit 43% less often if not for lake discharges. For example, in 1998, S-79 overages were almost entirely due to input from Lake Okeechobee, illustrating how managed flows can exacerbate the effects of climate variation (e.g., that year's El Niño) in this system (Fig. 3a). Though regulatory releases from Lake Okeechobee often pushed flows above the target maximum, lake inputs helped meet the target minimum flow 30% of the time that C-43 basin flow alone was insufficient (Fig. 3b), illustrating the potential for managed flows to maintain environmental stability.

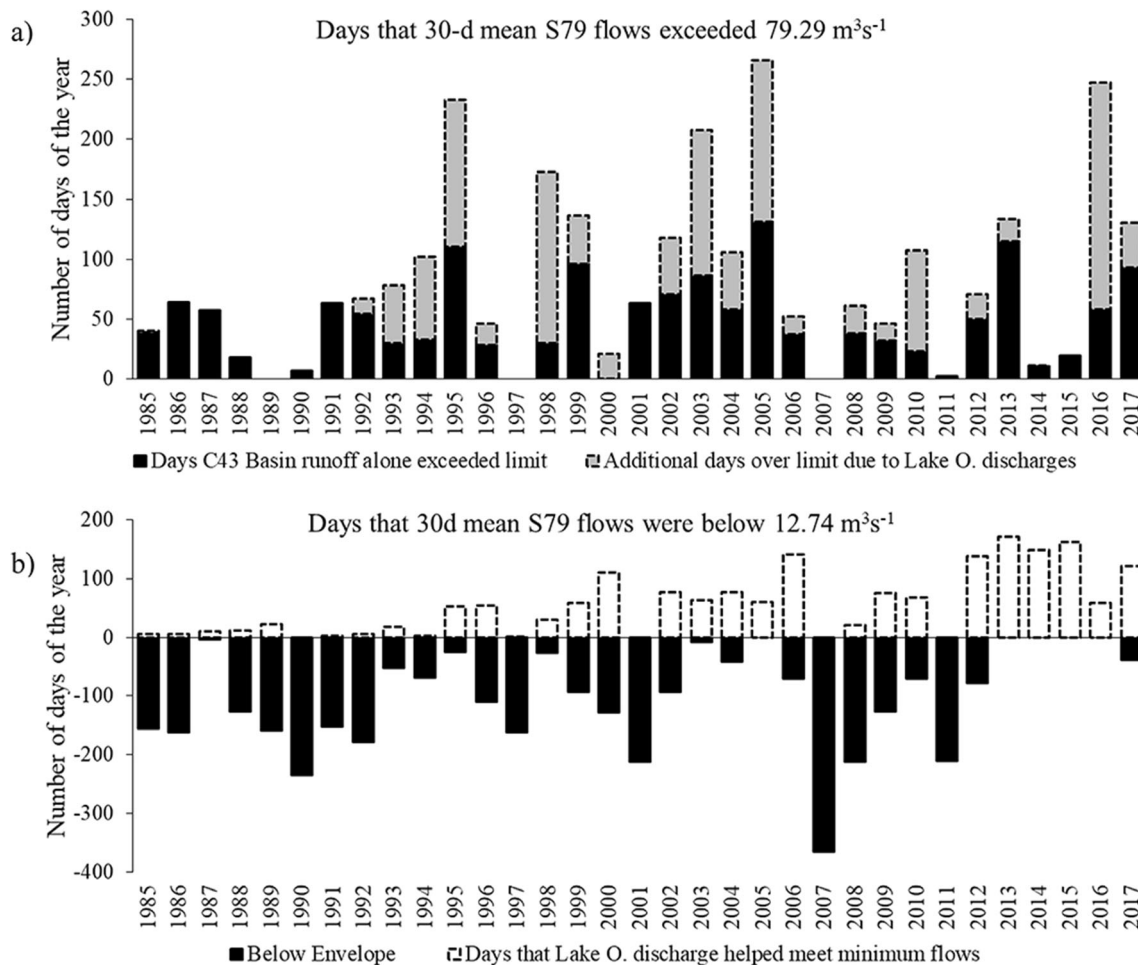


Fig. 3 Annual metrics of freshwater flow through the S-79 lock and dam at the head of the Caloosahatchee Estuary. **a** The total height of columns indicates the number of days each year that 30-day mean S-79 flows exceeded the recommended upper limit of 79.29 m³ s⁻¹. The black portion of columns indicates the number of days that water inputs from the C-43 basin alone would have exceeded 79.29 m³ s⁻¹, and the gray portion of columns indicates the days of excess S-79 flow that occurred

only because of additional inputs from Lake Okeechobee. **b** The magnitude of the black columns indicates the number of days each year that 30-day mean S-79 flows fell below the recommended lower limit of 12.74 m³ s⁻¹. The magnitude of the white columns indicates the number of days that water releases from Lake Okeechobee were responsible for keeping 30-day mean S-79 flows above the lower limit

Salinity Regimes Modeled salinity data for the 1985–2017 period indicated that upper estuary sites 1–4 had median salinities < 10, but often experienced salinities > 20 (Fig. 4). Middle estuary sites 5 and 6 had median salinities of 18 and 22, respectively, but had the most variable salinities in the study region, spanning marine to nearly freshwater conditions, with broad interquartile ranges. Lower estuary sites 7 and 8 had median salinities > 27, and remained above 23 for 75% of the time, but occasionally experienced salinities < 5 (Fig. 4). Site 9, with a median salinity of 34 and a minimum of 22, had consistently higher and more stable salinity than the other sites.

Salinity Stress Indices

Variability in the Vallisneria Stress Index (VSI) was high at upper estuary sites 1–4, ranging from benign levels associated

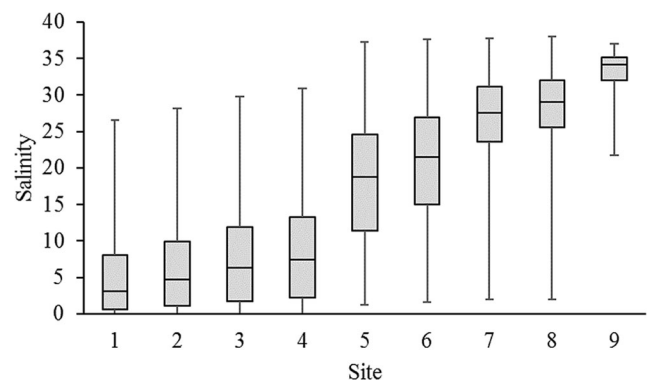


Fig. 4 Distribution of salinity values at Caloosahatchee Estuary SAV monitoring sites, based on 12,053 daily means for each site calculated for the period from 1985 to 2017. Boxes depict median and middle quartiles of the values, and whiskers depict minimum and maximum values. Daily mean salinity data were estimated with a salinity model (Qiu and Wan 2013)

with freshwater conditions to maximal levels associated with salinities > 18. The greatest VSI values occurred in 2001 and 2007–2008, when two persistent droughts created water shortages across south Florida (Fig. 2). During both periods, freshwater SAV die-offs were observed in the upper estuary (Fig. 5a). However, the period from 1993 to 1999 is notable

for relatively low VSI values, and coincides with reports of extensive *Vallisneria americana* in the upper estuary (Hoffacker 1994).

Stresses on seagrasses from low salinity, represented by the *Halodule* Stress Index (HSI) and *Thalassia* Stress Index (TSI), were seasonally high in the middle estuary and periodically

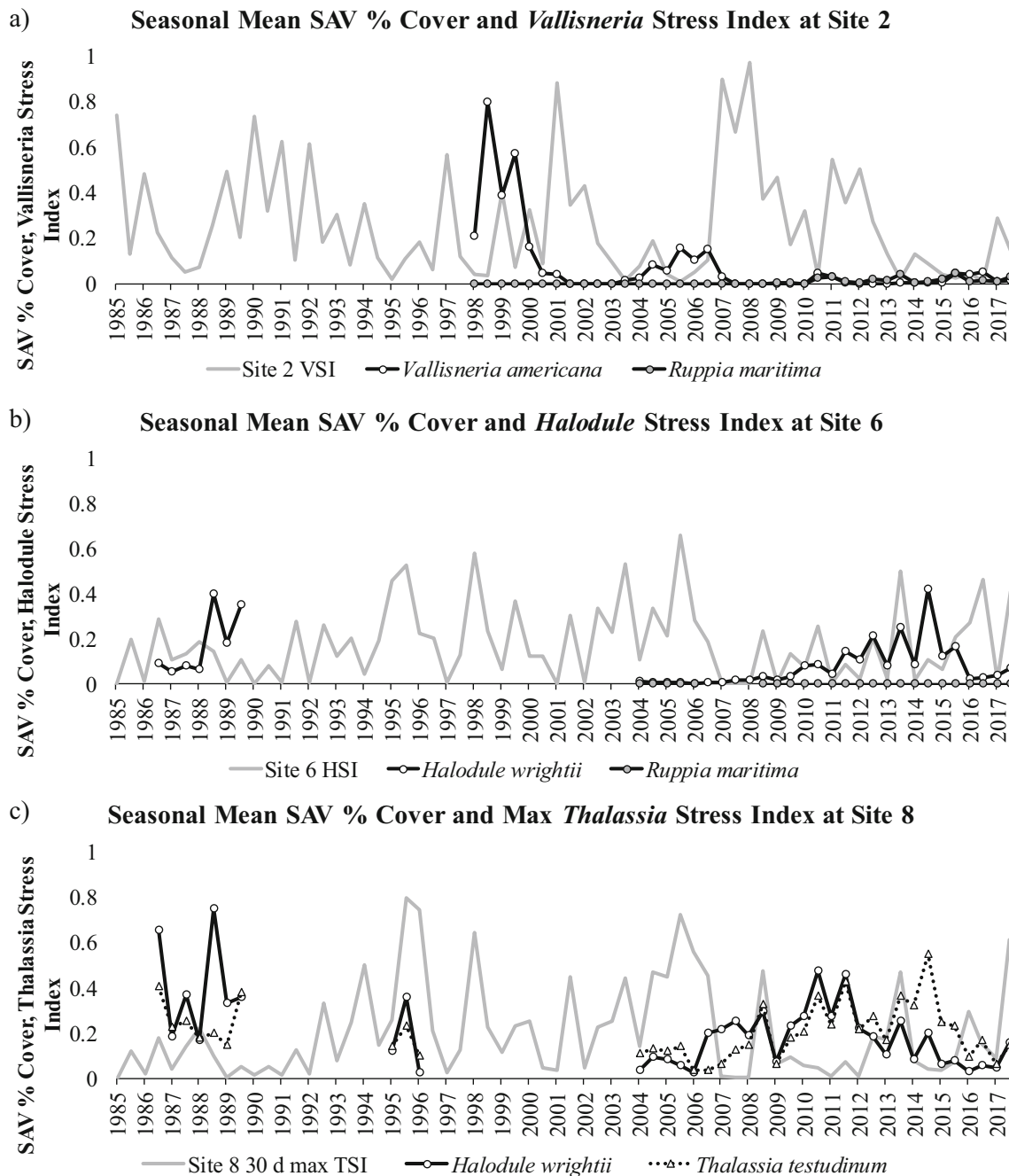


Fig. 5 Time series of wet season (May–Oct.) and dry season (Nov.–Apr.) mean submerged aquatic vegetation (SAV) percent cover by site and year, overlain on species-specific salinity stress index values (VSI: *Vallisneria* Stress Index, HSI: *Halodule* Stress Index, TSI: *Thalassia* Stress Index) from the same time periods. Breaks in the SAV time series indicate years in which no data was collected; not years of zero SAV abundance. **a** Time series for site 2, representative of the upper estuary region, with

Vallisneria americana, *Ruppia maritima*, and mean VSI. **b** Time series for site 6, representative of the middle estuary region, with *Halodule wrightii*, *Ruppia maritima*, and mean HSI. **c** Time series for site 8, representative of the lower estuary region, with *Halodule wrightii*, *Thalassia testudinum*, and the maximum 30-day mean value of TSI for each season

high in the lower estuary (Fig. 5b, c). However, interannual variation was pronounced. For example, in the 2005 wet season the HSI for site 6 was > 0.5 , indicating mean salinities < 12 , whereas in 2007 the HSI for site 6 was near 0, indicating consistently high salinity. At site 8, seasonal mean HSI and TSI values were generally low, but 30-day mean TSI values could exceed 0.5, indicating salinities < 17 (Figs. 2 and 5c).

SAV Abundance Trends in Relation to Salinity

Vallisneria americana was abundant in the upper CRE when monitoring began there in 1998 (Fig. 5a), but it was decimated by low flow, high salinity events in 1999, 2000, and 2001, especially downstream at sites 3 and 4. Though salinities were relatively benign between 2002 and 2006 (low VSI values), *V. americana* remained nearly absent until a partial recovery was notable by 2004 (Fig. 5a). In late 2006, *V. americana* was again decimated by a high salinity event. It remained absent in the CRE from 2007 to 2009, with a minimal reoccurrence in 2010 that was eliminated by high salinities in 2011. There was also a small resurgence of *V. americana* in 2015 and 2016 associated with a decrease in the VSI, but this was eliminated as salinity increased in 2017 (Fig. 5a).

In the late 1980s, a period of moderate freshwater stress at middle estuary sites 5 and 6, *Halodule wrightii* was present in low-moderate abundance (Fig. 5b). Though freshwater flows were relatively low in this period compared to subsequent years, they still exceeded the target maximum during some portion of each wet season, even without contributions from Lake Okeechobee (Fig. 3a). There was a hiatus in SAV monitoring in the middle estuary between 1989 and 2004. *Halodule wrightii* cover was low when monitoring resumed, amidst a high flow period augmented by lake releases between 2002 and 2006. *Halodule wrightii* began a modest resurgence in the high-salinity, drought period of 2007 (Figs. 2 and 5b). The recovery trend continued through 2014 at site 6, but abundance fell again with the high freshwater flows of 2016 (Fig. 5b).

At lower estuary sites 7–9, *Halodule wrightii* has co-occurred and likely competed with *Thalassia testudinum*, which makes the ups and downs in *H. wrightii* abundance harder to interpret (Fig. 5c). The lower estuary trends in *Thalassia testudinum* percent cover are similarly challenging to interpret, although a major decline after 2005 appears related to high freshwater flows associated with active hurricane seasons in 2004 and 2005 (Fig. 5c). After the 2005 low salinity event, *H. wrightii* recovered faster and replaced *T. testudinum* as the most abundant species at site 8 for 2006 and 2007. A decline in both species after 2014 was not clearly attributable to salinity stress, but may have been exacerbated by unusually low salinities in the dry season related to the 2016 El Niño.

SAV Regression Model Results

Regressions comparing May–October SAV percent cover to the previous year's SAV abundance and to freshwater flow or salinity stress indices explained between 15% and 64% of the variance among years in SAV percent cover (Table 2). The autoregressive term was important in most models, i.e., SAV abundance in a given year largely reflected SAV abundance the previous year. For whole-estuary SAV abundance, the most strongly weighted model in the set included only the autoregressive term (model a1, Table 2). However, the models including mean annual S-79 flow and mean annual Tidal Basin flow were also weighted highly, suggesting that increasing freshwater input to the system tended to reduce overall SAV cover (models a4 and a5, Table 2). The relatively low abundance of upper estuary SAV during the period of record likely made the whole-estuary SAV models less sensitive to factors influencing freshwater SAV. There may also be mechanisms at play by which extreme high freshwater flows are harmful to freshwater SAV as well as seagrasses (see Discussion).

Though *Ruppia maritima* was the least abundant SAV species in the CRE, and though it is euryhaline and should be resistant to direct effects of flow and salinity changes, we modeled it regardless, with the idea that it might be indirectly affected by flow due to water quality changes. Unsurprisingly, the *R. maritima* model based only on the autoregressive term was the most strongly weighted (model b1, Table 2). There was only a weak suggestion that above- and below-envelope freshwater flows might negatively impact *R. maritima* (model b5, Table 2).

For upper estuary *Vallisneria americana*, the model with strongest support (model c7, Table 2) was based on the 30-day maximum *Vallisneria* Stress Index (VSI) occurring in the dry season prior to the wet season in which *V. americana* abundance was evaluated. The other two best models were very similar: model c4 was based on mean dry season VSI, and model c6 was based on the 30-day maximum VSI from the entire year including the evaluation period (Table 2). In all models for *V. americana*, the signs of the regression coefficients suggested that high salinity associated with below-envelope S-79 flows harmed *V. americana*, while above-envelope S-79 flows were benign. It should be noted that the model including only the autoregressive term explained almost as much of the variation in *V. americana* as any of the other models, reflecting the importance of hysteresis in this system.

For middle estuary *Halodule wrightii*, coefficients of the leading models suggested that high flows and lower than average salinities harmed *H. wrightii* (Table 2). The best model was based on mean annual freshwater input from Lake Okeechobee, and explained 35% of the annual variance in *H. wrightii* abundance (model d6, Table 2). The second best model was based on the number of days of the year that 30-

day mean S-79 discharge exceeded $79.29 \text{ m}^3 \text{ s}^{-1}$ (model d2, Table 2). In all models, metrics of freshwater flow or low salinity stress had negative standardized regression coefficients, as expected.

For lower estuary *Halodule wrightii*, the best model was again based on Lake Okeechobee discharge, which negatively impacted *H. wrightii* abundance. The signs of all regression terms were as expected, but the effect of *Halodule* Stress Index (HSI) in the dry season was very weak. Interestingly, for lower estuary *Thalassia testudinum*, *Thalassia* Stress Index in the dry season was the best predictor (model f5, Table 2). This is consistent with the ecology of *H. wrightii* vs. *T. testudinum*, with the former being a faster-growing species responding more to conditions within the season of evaluation, and the latter being a slower-growing species whose present abundance is more reflective of prior stresses.

Discussion

Our results reveal a SAV ecosystem that is sensitive to natural and anthropogenic changes in flow and salinity, in which frequent, large deviations from established flow guidelines have had strong, negative impacts on SAV. However, these impacts vary widely by SAV species and estuarine region, highlighting the importance of integrating species-specific and spatially explicit monitoring and modeling efforts. One important result of our species-specific analysis is the observation that dominant, late-successional SAV species like *Thalassia testudinum* and *Vallisneria americana* exhibit strong year-to-year autocorrelation in abundance and reduced resilience after severe reductions in SAV cover. Such species appear particularly vulnerable to recidivism of salinity stresses, and would benefit from water management infrastructure projects that reduce extreme high and low flows. However, large residual variation in many of our models indicate that SAV abundance in this system cannot be fully predicted and managed by hydrologic/salinity drivers alone. Incorporation of other factors such as optical water quality and ecological mechanisms enforcing alternate states is needed to advance the understanding and conservation of SAV in the Caloosahatchee, as in other estuaries.

Ecohydrological Controls on SAV Distribution

Syntheses of long-term hydrologic, salinity, and SAV data often reveal complex interactions between climate, anthropogenic factors, and the biological responses of SAV habitats (e.g., Cambridge et al. 1986; Orth et al. 2010). Our synthesis for the CRE illustrates how these interactions can affect the decline, persistence, or recovery of SAV. The CRE has experienced extreme temporal variability in freshwater inflow and therefore salinity on daily, seasonal, and interannual scales

(Figs. 2 and 3). This is similar to other Florida estuaries and is largely reflective of south Florida's subtropical climate, featuring distinct wet and dry seasons along with episodic droughts and tropical storms (Obeysekera et al. 2007). However, the natural climatic variability is exacerbated by local watershed development and regional water management, especially the artificial connection with Lake Okeechobee, thus restricting the distribution and reducing the abundance of SAV in the estuary (Barnes 2005; Qiu and Wan 2013).

Existence of *Vallisneria americana* in the upper CRE has been ephemeral due to episodic high salinity events (e.g., 2000–2001, 2007–2008, and 2011–2012), which have reduced the plant to insignificant levels (Fig. 5a). Given the return period of a regional drought in south Florida, typically every 3–7 years in association with the El Niño–Southern Oscillation (Obeysekera et al. 2007), maintaining a permanent *V. americana* bed is extremely challenging. This is particularly true under future sea level rise conditions, which may increase salt intrusion into the upper estuary. Increasing development, drainage, and percentage of impervious surface in the watershed will worsen the problem by reducing rates of groundwater recharge in wet seasons and stream base-flow in dry periods (Shuster et al. 2005).

While high salinities have been devastating for *V. americana*, unusually low salinities have harmed seagrasses in the middle and lower estuary. The seagrass most vulnerable to low salinity stress is the sparse and seasonally transient *Halodule wrightii* in the middle estuary (Fig. 5b). Though annual median salinities in this region are near 20, the level suggested as minimally suitable for *H. wrightii* growth (Rudolph 1998), much lower salinities may prevail for extended periods, to the detriment of the seagrass (Fig. 4a). For example, *H. wrightii* was scarce between 2004 and 2006, when four hurricanes made landfall in south Florida, resulting in consecutive months of S-79 flows much greater than $79.29 \text{ m}^3 \text{ s}^{-1}$, and persistent low salinity. Similar periods of prolonged, excessive flow have occurred several times in the period of record, emphasizing seagrass' vulnerable status in the middle estuary (Fig. 2). This vulnerability has been exacerbated by basin expansion to include Lake Okeechobee's watershed and associated regulatory releases. Indeed, among the metrics of flow and salinity examined, annual Lake Okeechobee discharge was the single best predictor of *H. wrightii* abundance in both the middle and lower estuary (Table 2).

It might be supposed that the euryhaline SAV *Ruppia maritima* would prevail in variable-salinity regions where *H. wrightii* does poorly, but *R. maritima* never reached bed-forming densities in any portion of the estuary during our monitoring period. We are inclined towards the hypothesis that *R. maritima* is limited by factors other than salinity in this system—perhaps light limitation, and/or grazing by unknown herbivores. The grazing limitation hypothesis is supported by

reports that *R. maritima* can form dense beds in the CRE when sparse shoots are protected by grazer-exclusion fences (Bartleson 2010).

Typical salinity conditions in the lower CRE are suitable for *Thalassia testudinum* and *Halodule wrightii*, but both seagrasses decline in association with low salinity events (Table 2, Fig. 5c). The most severe low-salinity disturbances to lower estuary seagrasses were in late 2005 and early 2006, associated with high discharges related to hurricane activity (Wilma, October 2005) and the overwhelming of Lake Okeechobee's storage capacity that preceded the storm and necessitated regulatory releases. However, some declines in lower estuary SAV are not explained well by flow and salinity stress alone. For example, both *H. wrightii* and *T. testudinum* at lower estuary site 8 declined markedly from 2014 to 2015 despite relatively benign flow and salinity conditions in 2015 (Fig. 5c). A further decline in 2016 could be more clearly attributed to environmental stress; from large Lake Okeechobee releases in that year's wet, El Niño dry season (Figs. 2 and 5c).

SAV Disturbance and Recovery Dynamics

While the impact of altered hydrologic and salinity regimes on SAV is also reported in other estuaries in Florida (Indian River Lagoon; Buzzelli et al. 2012, Biscayne Bay; Lirman et al. 2014, Kings Bay; Frazer et al. 2006, Florida Bay; Montague and Ley 1993), and elsewhere (Chesapeake Bay; Shields et al. 2012, Laguna de Rocha, Uruguay; Rodriguez-Gallego et al. 2015), this study provides unique insight into the linkage between these drivers and long-term SAV dynamics (Table 2). Understanding the dynamics of SAV recovery is especially important in light of ongoing ecosystem restoration efforts (USACE and SFWMD 2010). The distinct response patterns of SAV recovery rate to antecedent stress index (Fig. 5) suggest different recovery mechanisms for *V. americana* in the upper estuary and seagrasses in the middle and lower estuary. Recovery of *V. americana* after dieback events is slow, requiring a minimum of 2 to 3 years of low salinity conditions (Fig. 5a). Factors contributing to this slow recovery may include grazing and the need for a seed source to re-establish in the area. Several restoration studies conducted in the upper Caloosahatchee Estuary have been unable to successfully establish transplanted colonies without protection (exclusion cages) from herbivores (Ceilley et al. 2003; Mote Marine Lab 2007; Bartleson 2010). Jarvis and Moore (2008) concluded that seed germination in a tributary to Chesapeake Bay was unlikely to contribute significantly to the spring emergence of plants following the winter die back, but may contribute to recovery after a large scale decline. The role of seeds in maintaining or reestablishing *V. americana* in the Caloosahatchee has not been well studied. However, in a 7-month, field restoration feasibility study in the upper Caloosahatchee

(beginning August 2002) Ceilley et al. (2003) found no evidence of recruitment from seeds in unplanted sediments. Assisted restoration (planting) of *V. americana* could hasten the recovery process as implemented in the Chesapeake Bay (Orth et al. 2010; Moore et al. 2010), but only if a suitable salinity regime for recovery is established by maintaining appropriate freshwater flows to the estuary (Kraemer et al. 1999; Doering et al. 2002; Bartleson 2010). Additionally, plantings may require protection from herbivory until such time as they can withstand grazing pressure (Hauxwell et al. 2004; Moore et al. 2010).

In contrast with *V. americana*, the seagrass *Halodule wrightii* begins to recover relatively quickly after major freshwater stress events, even in the stressful middle estuary. For example, significant *H. wrightii* recovery took place when flows from S-79 were below $79.29 \text{ m}^3 \text{ s}^{-1}$ for more than a year in 2007, following 4 years of damaging high flows (Fig. 5b). In the lower estuary, *H. wrightii* recovered even more quickly from disturbance (Fig. 5c), though *Thalassia testudinum* required about 3 years to return to dominance (Fig. 5c). Both *H. wrightii* and *T. testudinum* perform best in stable, marine salinities. However, *H. wrightii* tends to recover faster following disturbances and is more likely than *T. testudinum* to occur in environments with low and/or variable salinity (Lapointe et al. 1994; Lirman et al. 2014). It has been hypothesized previously that hydrologic changes resulting in increased freshwater delivery to estuaries in south Florida could shift the competitive balance between *T. testudinum* and *H. wrightii* in favor of the latter (Fourqurean et al. 2003; Barnes 2005; Mazzotti et al. 2007a; Herbert et al. 2011), and our current analysis supports this hypothesis for the CRE (Fig. 5c).

Although our proposed salinity stress indices and SAV antecedent conditions explained up to 64% of variation in SAV percent cover (Table 2), there are certainly other factors that influence the variability of SAV abundance in the CRE. In addition to causing wide fluctuations in salinity, high freshwater inflows may increase nutrient and colored dissolved organic matter loading, decrease light penetration, and further degrade SAV habitats (Buzzelli et al. 2014).

Outdoor mesocosm studies with *V. americana* indicate that light requirements for growth increase with increasing salinity and may be 50% higher at 5 psu than at 0 psu (French and Moore 2003). However, during a 1-year field study in the Caloosahatchee, plant growth parameters were generally higher at sites 2 and 4 (Fig. 1), where salinity and water clarity were higher, than at sites 1 and 3 (Fig. 1), where salinity and water clarity were lower (Bortone and Turpin 2000). For *V. americana* to thrive in systems like the Caloosahatchee with colored freshwater, an important balance between fresh and saltwater may be required, with enough saltwater to relieve light stress and enough freshwater to reduce salinity stress (Bortone and Turpin 2000). Considering the needs of

seagrasses in the lower estuary, as well, an optimal distribution of flows to the estuary might be one skewed towards the lower range of the 12.74–79.29 m³ s⁻¹ flow envelope. Indeed, the project implementation report for the C-43 West Basin Reservoir recommended a flow distribution whereby about 75% of the S-79 discharges range between 12.74 and 22.65 m³ s⁻¹, and 94% range between 12.74 and 42.47 m³ s⁻¹ (USACE and SFWMD 2010).

Poor water clarity related to excessive nutrient loading has been identified as a limiting factor for SAV growth in Tampa Bay (Beck et al. 2017) and Florida Bay (Lapointe et al. 1994), and potential adverse effects of nutrient loading in the CRE should be investigated more comprehensively. However, since light penetration in the CRE is largely controlled by CDOM rather than chlorophyll a, reducing the nutrient load through reduction of N or P concentrations in the incoming freshwater may not result in significant increases in biomass of seagrasses in the lower estuary (Buzzelli et al. 2014). In the St. Lucie Estuary, another managed system connected to Lake Okeechobee, an SAV growth model indicated that *Syringodium filiforme* was about four times more sensitive to changes in salinity than changes in light availability, indicating the primacy of water quantity effects (Buzzelli et al. 2012). Grazing by herbivores (e.g., manatees and turtles), and physical disturbance by boat wakes and hurricane-induced sediment scouring, may also impact seagrass meadows (van Tussenbroek et al. 2008), and could be important as a mechanisms slowing recovery of depleted meadows in the CRE (Bartleson 2010).

Ecosystem Restoration and Management Implications

The changes observed in SAV abundance in the CRE over a 33-year period indicate that all species in the estuary will respond positively to reduced temporal variation in salinity, which can be achieved when S-79 flows are mostly maintained within the recommended 12.74 to 79.29 m³ s⁻¹ envelope (Doering et al. 2002; USACE and SFWMD 2010). This range of flows also appears to be compatible with the needs of other habitat-forming species in this system, e.g., oysters (Barnes et al. 2007), as well as general benthic community health throughout the system (Palmer et al. 2015). Further, our analysis provides an important quantitative evaluation of the proposed flow envelope with additional results that validate its use in restoration planning and implementation.

Achieving the flow envelope targets will require a combination of restoration efforts, given the constraints of existing water management infrastructure, competing demands for water by urban and agricultural interests, and losses of the watershed's ability to naturally store and slowly release water (USACE and SFWMD 2010; Qiu and Wan 2013; Wan and Konyha 2015). Planned improvements in water management infrastructure should help meet the targets: The C-43 West

Basin Storage Reservoir to be constructed under CERP (USACE and SFWMD 2010), will capture and store fresh water during the wet season and release it during the dry season when flow to the estuary often falls below the envelope target.

In general, construction of reservoirs for human appropriation of water tends to reduce the supply of freshwater to downstream estuarine systems (Alber 2002; Montagna et al. 2013). To compensate, reservoir management rules often reserve or set aside a portion of the impounded water for environmental purposes, which can include freshwater discharge to downstream estuaries (see Montagna et al. 2013 for examples). The C-43 West Basin Reservoir is unusual, in that all the water in the reservoir has been set aside for the protection of fish and wildlife in the downstream estuary (SFWMD 2014). Modeling indicates that when this 170,000 ac-ft (2.1×10^8 m³) reservoir is operational, daily flows greater than 12.74 m³ s⁻¹ at S-79 can be supplied 90% of the time. Occurrence of daily flows greater than 79.29 m³ s⁻¹ at S-79 will be reduced by about 10% (Interagency Modeling Center 2007; USACE and SFWMD 2010). To fully dampen high discharges, especially those that include lake releases, up to 400,000 ac-ft (4.9×10^8 m³) of storage in the Caloosahatchee watershed could be required (Graham et al. 2015). High discharges will more likely be addressed by regional hydrological fixes that follow recommendations to send excess water in Lake Okeechobee south to the Everglades, via improved conveyance and additional storage facilities (Buzzelli et al. 2015; Graham et al. 2015). These restoration measures at both local and regional scales should be able to help achieve within-envelope flows at S-79, reduce temporal variation in salinity, and increase SAV coverage and density in all regions of the estuary.

Recommendations for Ecological Monitoring

There is a large body of literature on design, implementation, and modification of monitoring programs to detect environmental change and support environmental restoration (see National Academies of Science Engineering and Medicine 2017 and references therein). However, our experience of the challenges of analyzing this longitudinal dataset of SAV abundance in a managed system highlights five particularly important considerations for the design of similar studies: (1) Data on biological indicators should be monitored as consistently over the long term as abiotic environmental data. This is especially important for biological indicators like slow-growing seagrasses whose present abundance is highly dependent on antecedent conditions. (2) Standardized, fully quantitative methods should be employed for assessment of biological indicators, and the monitoring methods should not be changed without an adequate period of overlap to facilitate

conversion. For example, seagrass monitoring should include counts of shoots and measurements of blade length alongside less quantitative methods like percent cover estimates. (3) For a system in which particular management choices may have divergent impacts on different indicator species, e.g., seagrasses in the lower estuary versus freshwater SAV in the upper estuary, it is imperative that the indicators be monitored concurrently. Otherwise, the ability to weigh the overall system impacts of management decisions will be compromised. (4) Environmental variables hypothesized to influence the biological indicators of interest should be monitored at an ecologically relevant spatiotemporal scale and resolution, or integrative proxies for those environmental variables should be developed. For example, integrating light sensors could be maintained at SAV monitoring sites to provide relevant information on optical water quality. Also, the nutrient stoichiometry or C and N stable isotope ratios of SAV and algal tissue samples could be taken as integrative proxies for nutrient loading and the trophic state of the meadows (e.g., Johnson et al. 2006). (5) Finally, the reliance on annually or seasonally averaged abundance as the indicator of SAV health is a significant impediment to understanding and modeling the mechanisms leading to SAV growth or decline. Shorter-term field measurements of SAV health status, like shoot growth rates, photosynthetic efficiencies, and tissue nutrient stoichiometries, would be easier than annual mean abundances to relate to high resolution data on salinity, optical water quality, nutrient loading, etc. Of course, such short-term efforts should be repeated with appropriate spatiotemporal distribution and replication to incorporate the full range of relevant environmental conditions.

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Compliance with Ethical Standards

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References

- Alber, M. 2002. A conceptual model of estuarine freshwater inflow management. *Estuaries* 25: 1246–1261.
- Antonini, G.A., D.A. Fann, and P. Roat. 2002. *A historical geography of Southwest Florida waterways*. Vol. two. Placida Harbor to Marco Island: National Seagrass College Program.
- Barnes, T. 2005. Caloosahatchee Estuary conceptual ecological model. *Wetlands*. 25: 884–897.
- Barnes, T.K., A.K. Voley, K. Chartier, F.J. Mazzotti, and L. Pearlstein. 2007. A habitat suitability index model for the eastern oyster (*Crassostrea virginica*), a tool for restoration of the Caloosahatchee Estuary, Florida. *Journal of Shellfish Research* 26: 949–959.
- Bartleson, R. 2010. Feasibility of Widgeon Grass restoration in the Caloosahatchee Estuary using exclosures. Report to West Coast Inland Navigation District through Lee County, FL, USA.
- Bortone, S.A., and R.K. Turpin. 2000. Tape grass life history metrics associated with environmental variables in a controlled estuary. In *Seagrasses monitoring, ecology, physiology and management*. 318 pp, ed. S.A. Bortone, 65–79. Boca Raton: CRC Press.
- Beck, M.W., J.D. Hagy, and C. Le. 2017. Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization. *Estuaries and Coasts* 41: 592–601.
- Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd ed. Springer.
- Buzzelli, C., R. Robbins, P. Doering, Z. Chen, D. Sun, Y. Wan, B. Welch, and A. Schwarzschild. 2012. Monitoring and modeling of *Syringodium filiforme* (manatee grass) in Southern Indian River Lagoon. *Estuaries and Coasts* 35: 1401–1415.
- Buzzelli, C., P.H. Doering, Y. Wan, and D. Sun. 2014. Modeling ecosystem processes with variable freshwater inflow to the Caloosahatchee River Estuary, Southwest Florida. II. Nutrient loading, submarine light, and seagrasses. *Estuarine, Coastal and Shelf Science* 151: 272–284.
- Buzzelli, C., P. Gorman, P.H. Doering, Z. Chen, and Y. Wan. 2015. The application of oyster and seagrass models to evaluate alternative inflow scenarios related to Everglades restoration. *Ecological Modelling* 297: 154–170.
- Cambridge, M.L., A.W. Chiffings, C. Brittan, L. Moore, and A.J. McComb. 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquatic Botany* 24: 269–285.
- Ceiley, D.W., I. Bartozek, G. C. Buckner, M. J. Schuman. 2003. Tape grass (*Vallisneria americana*) restoration feasibility study. The Conservancy of Southwest Florida, Naples Florida. Final Report to the South Florida Water Management District. 11 pp.
- Central and Southern Florida Flood Control District. 1954. Central and Southern Florida Flood Control Project: Five years of progress 1949-1954. West Palm Beach. <https://www.amazon.com/Central-Southern-Florida-Control-Project/dp/1391494768>.
- Chamberlain, R.H., and P.H. Doering. 1998a. Freshwater inflow to the Caloosahatchee Estuary and the resource-based method for evaluation. In *Proceedings of the 1997 Charlotte Harbor Public Conference and Technical Symposium*. South Florida Water Management District and Charlotte Harbor National Estuary Program, Technical Report No. 98-02, ed. S.F. Treat, 81–90. Washington, D.C..
- Chamberlain, R.H., and P.H. Doering. 1998b. Preliminary estimate of optimum freshwater inflow to the Caloosahatchee Estuary: A resource-based approach. In *Proceedings of the 1997 Charlotte Harbor Public Conference and Technical Symposium*. South Florida Water Management District and Charlotte Harbor

- National Estuary Program, Technical Report No. 98–02, ed. S.F. Treat, 121–130. Washington, D.C..
- Doering, P.H., and R.H. Chamberlain. 2000. Experimental studies on the salinity tolerance of turtle grass, *Thalassia testudinum*. In *Seagrasses: Monitoring, ecology, physiology, and management*, ed. S.A. Bortone, 81–98. CRC Press LLC.
- Doering, P.H., R.H. Chamberlain, and J.M. McMunigal. 2001. Effects of simulated saltwater intrusion on the growth and survival of wild celery, *Vallisneria americana*, from the Caloosahatchee Estuary (South Florida). *Estuaries* 24: 894–903.
- Doering, P.H., R.H. Chamberlain, and D.E. Haunert. 2002. Using submerged aquatic vegetation to establish minimum and maximum freshwater inflows to the Caloosahatchee Estuary, Florida. *Estuaries* 25: 1343–1354.
- Douglass, J.G., K.E. France, J.P. Richardson, and J.E. Duffy. 2010. Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. *Limnology and Oceanography* 55: 1499–1520.
- Douglass, J.G. 2014. Caloosahatchee River Estuary submerged aquatic vegetation. In *Comprehensive everglades restoration plan, restoration coordination and verification, 2014 Systems Status Report*, ed. South Florida Water Management District, 279–291. West Palm Beach. https://evergladesrestoration.gov/ssr/2014/ssr_full_2014.pdf.
- Flaig, E.G., and J. Capece. 1998. Water use and runoff in the Caloosahatchee watershed. In *Proceedings of the Charlotte Harbor Public Conference and Technical Symposium; 1997 March 15–16, Punta Gorda, Florida. Charlotte Harbor National Estuary Program Technical Report No. 98–02*, ed. S.F. Treat, 73–80. West Palm Beach: South Florida Water Management District.
- Fourqurean, J.W., and M.B. Robblee. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22: 345–357.
- Fourqurean, J.W., A. Willsie, C.D. Rose, and L.M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in South Florida. *Marine Biology* 138: 341–354.
- Fourqurean, J.W., J.N. Boyer, M.J. Durako, L.N. Hefty, and B.J. Peterson. 2003. Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Applications* 13: 474–489.
- Frankovitch, T.A., D. Morrison, and J.W. Fourqurean. 2011. Benthic macrophyte distribution and abundance in estuarine mangrove lakes and estuaries: Relationships to environmental variables. *Estuaries and Coasts* 34: 20–31.
- Frazer, T.K., S.K. Notestein, C.A. Jacoby, C.J. Littles, S.R. Keller, and R.A. Swett. 2006. Effects of storm-induced salinity changes on submerged aquatic vegetation in Kings Bay, Florida. *Estuaries and Coasts* 29: 943–953.
- French, G.T., and K.A. Moore. 2003. Interactive effects of light and salinity stress on the growth, reproduction, and photosynthesis capabilities of *Vallisneria americana* (wild celery). *Estuaries* 26: 1255–1268.
- Graham, W.D., M.J. Angelo, T.K. Frazer, P.C. Frederick, K.E. Havens, and K.R. Reddy. 2015. *Options to reduce freshwater flows to the St. Lucie and Caloosahatchee estuaries and move more water from Lake Okeechobee to the Southern Everglades*. Gainesville: Independent technical review by University of Florida Water Institute 143 pp.
- Hauxwell, J., T.K. Frazer, and C.W. Osenberg. 2004. Grazing by manatees excludes both new and established wild celery transplants: Implications for restoration in Kings Bay, FL, USA. *Journal of Aquatic Plant Management* 42: 49–53.
- Hemminga, M. A., and C. M. Duarte. 2000. *Seagrass ecology*. New York: Cambridge University Press.
- Herbert, D.A., W.B. Perry, B.J. Cosby, and J.W. Fourqurean. 2011. Projected reorganization of Florida bay seagrass communities in response to the increased freshwater inflow of Everglades restoration. *Estuaries and Coasts* 34: 973–992.
- Herzka, S.Z., and K.H. Dunton. 1997. Seasonal photosynthetic patterns of the seagrass *Thalassia testudinum* in the western Gulf of Mexico. *Marine Ecology: Progress Series* 152: 103–117.
- Hoffacker, V. A. 1994. Caloosahatchee River submerged grass observation during 1993. W. Dexter Bender and Associates, Inc. Letter-report and map to Chip Meriam, South Florida Water Management District.
- Hopkinson, C.S., Jr., and J.H.J. Vallino. 1995. The relationships among man's activities in watersheds and estuaries: A model of runoff effects on patterns of estuarine community metabolism. *Estuaries* 18: 598–621.
- Interagency Modeling Center. 2007. Spreadsheet model and water budget analysis for C-43 Project Delivery Team. Technical Memorandum MSR 262. 58 pp. U.S. Army Corps of Engineers and South Florida Water Management District. West Palm Beach, Florida.
- Jarvis, J.C., and K.A. Moore. 2008. Influence of environmental factors on *Vallisneria americana* seed germination. *Aquatic Botany* 88: 283–294.
- Johnson, M.W., K.L. Heck Jr., and J.W. Fourqurean. 2006. Nutrient content of seagrasses and epiphytes in the northern Gulf of Mexico: Evidence of phosphorus and nitrogen limitation. *Aquatic Botany* 85: 103–111.
- Kraemer, G.P., R.H. Chamberlain, P.H. Doering, A.D. Steinman, and M.D. Hanisak. 1999. Physiological responses of *Vallisneria americana* transplants along a salinity gradient in the Caloosahatchee Estuary (SW Florida). *Estuaries* 22: 138–148.
- Lapointe, B.E., D.A. Tomasko, and W.R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54: 696–717.
- Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: A historical perspective. In *Everglades: The ecosystem and its restoration*, eds. SM Davis and JC Ogden. Delray Beach: St. Lucie Press.
- Lirman, D., and W.P. Cropper Jr. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries* 26: 131–141.
- Lirman, D., T. Thyberg, R. Santos, S. Schopmeyer, C. Drury, L. Collado-Vides, S. Bellmund, and J. Serafy. 2014. SAV communities of Western Biscayne Bay, Miami, Florida, USA: Human and natural drivers of seagrass and macroalgae abundance and distribution along a continuous shoreline. *Estuaries and Coasts* 37: 1243–1255.
- Mazzotti, F.J., L.G. Pearlstine, R. Chamberlain, T. Barnes, K. Chartier, and D. DeAngelis. 2007a. Stressor response models for the seagrasses, *Halodule wrightii* and *Thalassia testudinum*. In *JEM Technical Report. Final report to the South Florida Water Management District and the U.S. Geological Survey*. Fort Lauderdale: University of Florida, Fort Lauderdale Research and Education Center.
- Mazzotti, F.J., L.G. Pearlstine, R. Chamberlain, M.J. Hunt, T. Barnes, K. Chartier, and D. DeAngelis. 2007b. *Stressor response model for tapegrass (Vallisneria americana)*. University of Florida CIR 1524.
- Montagna, P.A., T. A. Palmer, and J. Beseres-Pollack. 2013. Hydrologic changes and estuarine dynamics. *Springer Briefs in Environmental Science*. <https://doi.org/10.1007/978-1-4614-5833-3>.
- Montague, C.L., and J.A. Ley. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries* 16: 703–716.
- Moore, K.A., E.C. Shields, and J.C. Jarvis. 2010. The role of habitat and herbivory on the restoration of tidal freshwater submerged aquatic vegetation populations. *Restoration Ecology* 18: 596–604.
- Mote Marine Laboratory. 2007. *Vallisneria americana restoration research in th Caloosahatchee River, Lee County, Florida*. Mote

- Marine Laboratory Technical Report No. 1230. 10 pp. Sarasota: Mote Marine Laboratory.
- National Academy of Sciences, Engineering and Medicine. 2017. *Effective monitoring to evaluate ecological restoration in the Gulf of Mexico*. Washington, DC: The National Academies Press.
- Orth, R.J., T.J.B. Carruthers, W.C. Dennison, et al. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56: 987–996.
- Orth, R.J., M.R. Williams, S.R. Marion, D.J. Wilcox, T.J.B. Carruthers, K.A. Moore, W.M. Kemp, W.C. Dennison, N.B. Rybicki, P. Bergstrom, and R.A. Batiuk. 2010. Long-term trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. *Estuaries and Coasts* 33: 1144–1163.
- Obeysekera, J., P. Trimble, C. Neidrauer, and L. Cadavid. 2007. Consideration of climate variability in water resources planning and operations — South Florida's experience. *World Environmental and Water Resources Congress* 2007: 1–11.
- Palmer, T.A., P.A. Montagna, R.H. Chamberlain, P.H. Doering, Y. Wan, K.M. Haurert, and D.J. Crean. 2015. Determining the effects of freshwater inflow on benthic macrofauna in the Caloosahatchee Estuary, Florida. *Integrated Environmental Assessment and Management* 12: 529–539.
- Qiu, C., and Y. Wan. 2013. Time series modeling and prediction of salinity in the Caloosahatchee River Estuary. *Water Resources Research* 49: 5804–5816.
- Rodriguez-Gallego, L., V. Sabaj, S. Masciadri, C. Kruk, R. Arocena, and D. Conde. 2015. Salinity as a major driver of submerged aquatic vegetation in coastal lagoons: A multi-year analysis in the subtropical Laguna de Rocha. *Estuaries and Coasts* 38: 451–465.
- Rudolph, H. D. 1998. Freshwater discharges to the Lake Worth Lagoon – Recommendations for maximum and minimum discharges to maintain optimum salinity ranges for the Lake Worth Lagoon's ecosystem. White Paper, Palm Beach County Department of Environmental Resources Management. West Palm Beach
- SFWMD (South Florida Water Management District). 2003. Technical documentation to support development of minimum flows and levels for the Caloosahatchee River and estuary, status update report. May 2003.
- SFWMD. 2014. Document to support a water reservation rule for the CERP Caloosahatchee River (C-43) West Basin Storage Reservoir. 63 pp. South Florida Water Management District. West Palm Beach Florida 57 pp.
- Shields, E.C., K.A. Moore, and D.B. Parrish. 2012. Influence of salinity and light availability on abundance and distribution of tidal freshwater and oligohaline submersed aquatic vegetation. *Estuaries and Coasts* 35: 515–526.
- Short, F.T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27.
- Shuster, W.D., J. Bonita, H. Thurston, E. Warnemuende, and D.R. Smith. 2005. Impacts of impervious surface on watershed hydrology: A review. *Urban Water Journal* 2: 263–275.
- USACE, and SFWMD. 2010. *Central and southern Florida project Caloosahatchee River (C-43) West Basin storage reservoir project, final integrated project implementation report and final environmental impact statement*. Jacksonville District and South Florida Water Management District: U.S. Army Corps of Engineers.
- van Tussenbroek, B., M.G.B. Santos, J.K. van Dijk, S.N.M. Alcaraz, and M.L.T. Calderon. 2008. Selective elimination of rooted plants from a tropical seagrass bed in a back reef lagoon: A hypothesis tested by Hurricane Wilma (2005). *Journal of Coastal Research* 24: 278–281.
- Wan, Y., C. Qiu, P. Doering, M. Ashton, D. Sun, and T. Coley. 2013. Modeling residence time with a three-dimensional hydrodynamic model: Linkage with chlorophyll *a* in a sub-tropical estuary. *Ecological Modelling* 268: 93–102.
- Wan, Y., and K. Konyha. 2015. A simple hydrologic model for rapid prediction of runoff from ungauged coastal catchments. *Journal of Hydrology* 528: 571–583.
- Waycott, B.M., C.M. Duarte, T.J.B. Carruthers, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106 (30): 12377–12381.
- Worm, E.B., N. Barbier, N. Beaumont, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790.
- Zieman, J.C. and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: A community profile. U.S. Fish and Wildlife Service Biological Report 85(7.25). 155 pp.