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BIOMASS AND PRODUCTIVITY OF *THALASSIA TESTUDINUM* IN ESTUARIES OF THE FLORIDA PANHANDLE

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ABSTRACT: *Thalassia testudinum* often dominates seagrass meadows of the Florida panhandle but few measurements of productivity, biomass, density, turnover or leaf area index in this region have been made. We targeted 5 estuaries located at similar latitudes, 30º ± 0.3ºN: Big Lagoon, Santa Rosa Sound, St. Andrew Bay, St. Joseph Bay, and St. George Sound. This study was one component of a collaborative partnership of state and local researchers examining factors preventing recovery in panhandle estuarine areas that had historically contained seagrass in the 1940s and 1950s. Measurements were made twice in 2016, once in June and then again in summer or fall, except in Santa Rosa Sound where measurements were made 3 times. In the estuaries sampled for the second time in July or August, aboveground productivity was greater than in June. St. Joseph Bay had the highest aboveground productivity (4.3 g/m^2/d) and 1—sided leaf area index (4.2) while St. George Sound had the lowest values (0.41 g/m^2/d and 1.0). Principal component analysis suggested that St. Andrew Bay, Big Lagoon and Santa Rosa Sound were the most similar, with higher values for shoot densities and leaf turnover and lower salinities and watershed:water ratios. St. Joseph Bay had high aboveground productivity and salinity, and low turbidity. St. George Sound had low aboveground productivity, high total suspended solids and the highest watershed:water ratio. These baseline productivity estimates will be useful to assess the success of restoration efforts targeting seagrasses in the Florida panhandle and evaluate impacts of climate change on seagrasses.

KEY WORDS: seagrasses, water quality, leaf area index, shoot counts

INTRODUCTION

Seagrasses, flowering marine plants that live in shallow coastal waters worldwide, provide habitat for fish and invertebrates. Many economically important fish and shellfish species depend on this habitat during critical stages of their life histories (Williams and Heck 2001, Hughes et al. 2009). Seagrasses also play a significant role in the global carbon and nutrient cycles (Larkum et al. 2006). They stabilize sediment, maintain coastal biodiversity, and provide food for waterfowl, as well as endangered mammal and turtle species (Orth et al. 2006, Waycott et al. 2009). Seagrasses are particularly vulnerable to human impacts such as eutrophication and other processes that reduce water clarity (Burkholder et al. 2007). The response of seagrasses to climate change including increasing temperature, sea level rise, CO_2 concentrations, and precipitation events is complex (Harley et al. 2006, Zimmerman 2021). Thus, there is a need for baseline information about seagrass productivity.

Seagrasses can serve as indicators of health in estuarine and nearshore waters because of their sensitivity to poor water quality conditions (Orth et al. 2006). Efforts to improve water quality to mitigate seagrass losses have been successful in Florida estuaries such as Tampa and Sarasota Bays (Tomasko et al. 2005, Greening et al. 2011). Management efforts to protect or restore seagrass habitat often include recommendations to improve environmental conditions that increase light availability or create 'no motor zones' to reduce destructive activities such as propeller scarring from boating (O'Brien et al. 2018). Restoration activities by planting seagrass shoots or spreading seeds have become increasingly more common (Orth et al. 2020). Understanding the conditions of existing beds is key before restoration occurs since transplantation of seagrass is costly and unsuccessful without the appropriate water quality (Bayraktarov et al. 2015, Rezek et al. 2019; Valdez et al. 2020).

Thalassia testudinum Banks & Soland ex Koenig is a tropical/subtropical marine angiosperm common in the shallow waters of the Gulf of Mexico (GOM), ranging from the Florida Keys to Mexico. Optimal growth occurs in salinities of 24–35, temperatures of 27–30°C, and irradiance at the seagrass canopy of at least 18% of surface irradiance (Zieman 1975, Irlandi et al. 2002, Lee et al. 2007, Garrote—Moreno et al. 2014, McDonald et al. 2016). However, survival outside of these ranges occurs with wide phenotypic variations (Manuel et al. 2013, Garrote—Moreno et al. 2014, McDonald et al. 2016). *Thalassia testudinum* spatial distribution is variable across the northern GOM. As the dominant seagrass in the barrier lagoons of St. Joseph Bay, Santa Rosa Sound and Big Lagoon, FL, *T. testudinum* occurs as continuous, sometimes monospecific beds near the inlet to the GOM in St. Andrew Bay and on shoals (Lanark Reef, Dog Island Reef) in St. George Sound (Yarbro and Carlson 2016). These areas are euryhaline and receive little freshwater directly, resulting in less variation of the environmental conditions leading to optimal growth. *Thalassia testudinum* is largely absent from mesohaline regions of the Florida Panhan-

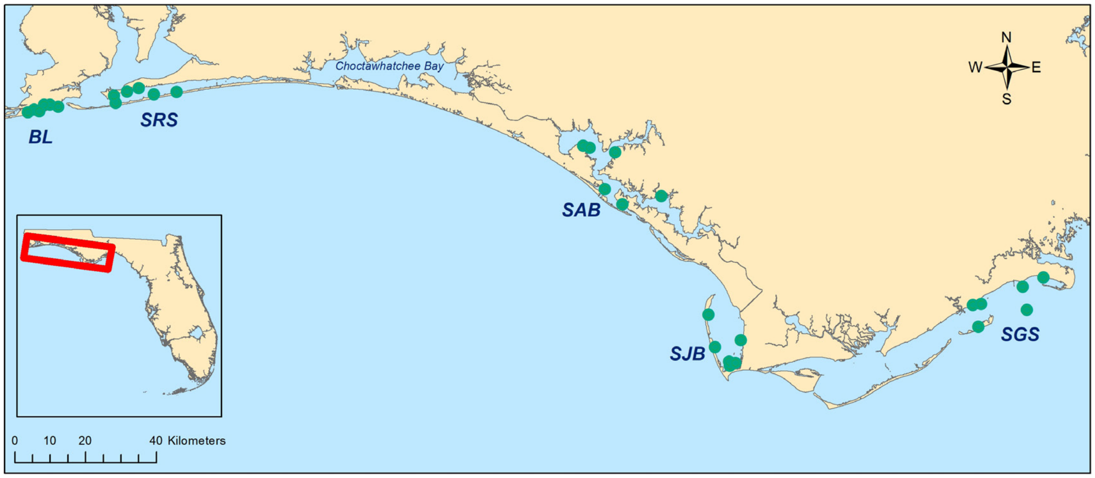

FIGURE 1. *Map of the locations of productivity measurements along the northern Gulf coast of Florida. BL–Big Lagoon; SRS–Santa Rosa Sound; SAB–St. Andrew Bay; SJB–St. Joseph Bay; SGS–St. George Sound.*

dle in the river–dominated estuaries, including Perdido Bay, Escambia Bay, East Bay of Pensacola Bay, Choctawhatchee Bay, and Apalachicola Bay.

Many estuaries of the Florida panhandle have experienced large losses of seagrasses over the past 50 years or more (Handley et al. 2006, Yarbro and Carlson 2016). Following the Deepwater Horizon oil spill in 2010, agencies had the opportunity to improve or restore seagrass beds using penalty funds from Natural Resource Damage Assessments and RESTORE Act funding (DHNRDAT 2021). A collaborative partnership consisting of state and local researchers across the Florida panhandle was established with a primary object of examining the factors preventing recovery in panhandle estuarine areas that had contained seagrass in the 1940s and 1950s but were currently devoid of seagrasses (Florida Fish and Wildlife Conservation Commission 2019). Measurements of aboveground productivity of *T. testudinum* in 5 estuaries in the Florida panhandle where it was the only or dominant seagrass species present were one component of this study. Because all the study sites were nearly at the same latitude with similar temperature ranges, we hypothesized that productivity would not vary significantly among estuaries unless there were differences in salinity and light availability, 2 key factors influencing *T. testudinum* growth and survival (Lee et al. 2007). Only a few measurements of *T. testudinum* biomass or aboveground production have been made in the Florida Panhandle, predominantly in St. Joseph Bay and St. George Sound (Iverson and Bittaker 1986, Rodriguez and Heck 2021). Thus, this study provides key information on the spatial variability of *T. testudinum* productivity at its northern limit in the northeastern GOM as well as baseline information to evaluate how climate change such as warming temperatures and increased precipitation intensity affect this species.

Materials and Methods

Study areas

Measurements were made in 5 estuaries of similar latitude in the Florida panhandle with *T. testudinum*–dominated meadows (Figure 1). These estuaries are aligned from west to east and include Big Lagoon, Santa Rosa Sound, St. Andrew Bay, St. Joseph Bay, and St. George Sound. Big Lagoon, the smallest and westernmost water body (Table 1), is a barrier lagoon located between Perdido and Pensacola Bays. Water exchange with these adjacent bays is limited (Livingston 2015). It receives freshwater surface runoff from the watershed but has no direct riverine source of freshwater. Santa Rosa Sound is also a barrier lagoon connected to the Pensacola Bay system at its western end and Choctawhatchee Bay at its eastern end. Like Big Lagoon, freshwater surface runoff is predominantly from local sources. St. Andrew Bay is in the central panhandle with extensive beds of *T. testudinum* and *Halodule wrightii*. Major freshwater sources to this system are Econfina Creek and direct runoff from the watershed. St. Joseph Bay is a barrier lagoon east of St. Andrew Bay. Seagrass beds in this bay were almost all continuous, monospecific beds of *T. testudinum*. Direct runoff from the watershed is the major surface freshwater source in this system. St. George Sound is located east of the mouth of the Apalachicola River, which has a 53,500 km^2 watershed in Florida, Alabama, and Georgia (Table 1). *Halodule wrightii* is the only seagrass species in found in small beds in the western sound, but *T. testudinum*, *H. wrightii*, and *Syringodium filiforme* are common in the central and eastern parts of St. George Sound (Yarbro and Carlson

TABLE 1. *Centroids of latitude and longitude, water and watershed areas, and the ratio of watershed area to water area for Florida panhandle estuaries.*

Estuary	Centroid	Water area (km^2)	Watershed area (km^2)	Watershed: water ratio
Big Lagoon[1,2]	30.32ºN; -87.37ºW	13	27	2
Santa Rosa Sound[1,2,4]	30.37ºN; -87.02ºW	101	177	2
St. Andrew Bay[3]	30.21ºN; -85.72ºW	243	2,980	12
St. Joseph Bay[1,3]	29.78ºN; -85.35ºW	170	1,995	12
St. George Sound[3]	29.78ºN; -84.71ºW	550	53,520	97

[1]Coastal lagoon, isolated from direct riverine discharge

[2] Water and watershed area provided by T. Eriksen (pers. comm., University of West Florida)

[3] Data from the Northwest Florida Water Management District Surface Water Improvement and Management Plans (Northwest Florida Water Management District 2017a, b).

[4]Water and watershed area are only for western Santa Rosa Sound (west of 86.75 W) where the study was conducted

2016). All systems except St. George Sound have relatively low watershed:water area ratios (Table 1). The watershed:water area ratio in St. George Sound is 8 times greater than those of St. Andrew and St. Joseph Bays and 30 times greater than Big Lagoon or Santa Rosa Sound.

Environmental conditions

Salinity and temperature measurements were made using a calibrated Eureka Manta—2 model sub2 sonde or a YSI Pro Plus multimeter, depending on the group making the measurements. Light profiles were measured using a LI—COR spherical quantum sensor in all systems except St. George Sound. Light attenuation coefficient, k_d was calculated from light profiles as

$$\frac{I_z}{I_0} = e^{-k_d z} ; \qquad \text{(equation 1)}$$

where I_z is irradiance at depth z, I_0 is surface irradiance and k_d is attenuation coefficient. Grab water samples were collected in bottles triple rinsed with site water and kept on ice until analysis for color, turbidity and total suspended solids (TSS). Triplicate 60 mL water samples were filtered through GF/F filters (nominal pore size 0.7µm) in the field and frozen until analysis for chlorophyll *a*.

Plant measurements

In each estuary, aboveground productivity of *T. testudinum* was measured at 6 sites at least 2 times in 2016, once in June and once later in the growing season. Measurements were made 3 times in Santa Rosa Sound at 6 sites in June, 2 sites in July and 6 sites in September. Late season measurements were made in July in St. Andrew Bay, in August in Big Lagoon and St. Joseph Bay, and in October in St. George Sound. Locations were selected based on a visual cover survey made in 2014 (Yarbro and Carlson 2016) where *T. testudinum* was the dominant or sole species present. At each location, 4 quadrats, 0.2 m on a side (0.04 m^2), were anchored on the sediment using 0.15 m sod staples. Each *T. testudinum* shoot in the quadrat was punched just above the end of the short shoot at the basal meristem with a 20—gauge hypodermic needle, following Zieman and Zieman (1989). After about 10 days, all seagrass material within the quadrat, both above and below the sediment surface, was carefully harvested and stored on ice for transport to the laboratory for processing.

In the laboratory, punched shoots were separated from the collected materials, and the length, width, and punch translocation distance were measured for each leaf in the shoot, with up to 20 punched shoots assessed for each quadrat. The location of the hole in the oldest blade was used as the zero or reference position against which to measure extension of the remaining younger leaves. The oldest blade had the hole nearest the end of the short shoot and was usually covered with the most epiphytes and damaged. The remaining seagrass tissues were separated into leaves, roots and rhizomes, and into live or dead fractions of each. Tissues were gently rinsed with tap water and dried for 5–7 days at a minimum of 50°C and then weighed. Productivity was calculated from the dry weights of new leaf growth in each quadrat divided by the elapsed time in days between punch and harvest and the area of the quadrat (0.04 m^2).

The total number of shoots, both live and dead, of each species of seagrass in each quadrat was also recorded, as was the presence of macroalgae. We measured live biomass (g/m^2), density of *T. testudinum* shoots (#/m^2), 1—sided leaf area index (LAI, unitless), shoot specific leaf growth (SSBG) in cm^2/d, leaf turnover on a leaf—area basis (%/d), and productivity on a g/m^2/d basis. Species—specific live biomass included above and belowground fractions. The LAI of *T. testudinum* was calculated by multiplying the mean total leaf area per shoot times the number of shoots/m^2 calculated for each quadrat. The SSBG was calculated by summing the area of new growth (cm^2) for all the leaves in a shoot divided by the number of days between punching and harvesting. Leaf turnover (%/d) was calculated by dividing SSBG by the total leaf area of the shoot. Root:shoot ratio was calculated by dividing root and rhizome biomass by aboveground biomass.

Laboratory analysis

Chlorophyll *a* was measured with a methanol extraction (Yarbro and Carlson 2018) except in Santa Rosa Sound where a 90% acetone extraction was used (Welschmeyer 1994, Presley and Caffrey 2021). The TSS is a gravimetric estimate of the number of particles in the water and was determined using method 2540 D of Standard Methods for the Examination of Water and Wastewater (APHA 1985). Turbidity, which estimates light scattering by particles as well as the number of particles present, was measured nephelometrically on a Hach 2100Q turbidimeter using calibrated standards as described in Standard Methods for the Examination of Water and Wastewater (APHA 1985). Color of the water column was determined from filtered water samples at 440 nm in a Hitachi U—2900 spectrophotometer after Kirk (1976) and Gallegos et al. (1990).

Other data sources

Data collected for this study were supplemented with data from the Florida Department of Environmental Protection Impaired Waters Rule (https://floridadep.gov/dear/watershed—assessment—section) for St. George Sound and Big Lagoon. Parameters used included salinity, temperature, TSS, turbidity and chlorophyll *a*. Data were evaluated to ensure they were within the normal ranges found at these locations.

Statistical analysis

We examined correlations among plant parameters: total live biomass, shoot density, leaf productivity, LAI, shoot specific leaf growth and root:shoot ratio. We also examined correlations among environmental variables: salinity, temperature, chlorophyll *a*, turbidity, TSS, color, and k_d. Correlation analyses were done using R (version 3.6.0) and the GG*ally* package (Schloerke et al. 2022) with the Spearman method. A principal component analysis was conducted using watershed:water ratio, average summer environmental variables (salinity, chlorophyll *a*, TSS, and turbidity) and the average plant metrics (SSBG, leaf productivity, LAI, and number of live shoots) for each system. Primer Version 7 (Clarke and Gorley 2015) was used for the principal component analysis. Data were normalized prior to analysis. Means $\pm$ sd are reported for all measurements.

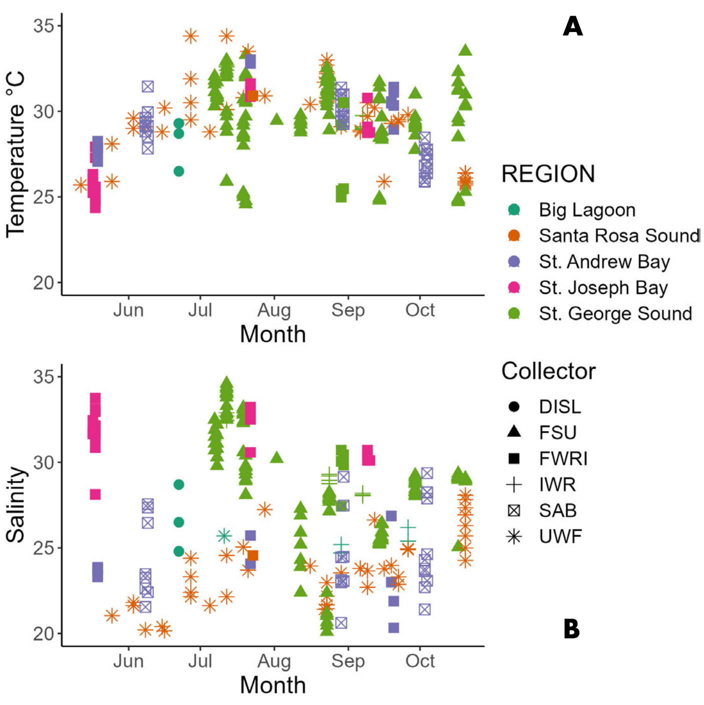

FIGURE 2. *Water quality parameters measured between May and October 2016 in 5 Florida panhandle estuaries. A. Temperature. B. Salinity. DISL—Dauphin Island Sea Lab; FSU—Florida State University; FWRI—Florida Fish and Wildlife Research Institute; IWR—Florida Department of Environmental Protection Impaired Water Rule; SAB—St. Andrew Bay Resource Management Association Inc; UWF—University of West Florida.*

Results

Environmental data

Temperature ranged from 24.4°C in May to 36.4 °C in July across all systems (Figure 2A). The seasonal pattern in temperature was similar across all systems. Salinity ranged from 12 to 35 across all systems with no consistent seasonal differences across systems (Figure 2B). Mean salinities were lowest in Santa Rosa Sound (21.91 ± 2.52) and St. Andrew Bay (22.01 ± 4.08) (Table 2). Mean salinity was 25.77 ± 1.44 in Big Lagoon and was highest in St. Joseph Bay (31.47 ± 1.32) and St. George Sound (31.19 ± 3.16; Table 2). Chlorophyll *a* concentrations ranged from 0.36 to 15.22 μg/L with the highest reported value in St. Andrew Bay. However, Big Lagoon had the highest mean chlorophyll *a* value and Santa Rosa Sound had the lowest while levels were similar across St. Andrew Bay, St. Joseph Bay and St. George Sound (Table 2). Color was highest in St. Andrew Bay and was negatively correlated with salinity ($r = -0.70$, $p < 0.001$). Turbidity and TSS were highest in St. George Sound and were positively correlated with each other ($r = 0.68$, $p < 0.001$), but only turbidity was negatively correlated with salinity ($r = -0.34$, $p < 0.001$; Supplemental Figure S1).

Light attenuation integrates chlorophyll *a*, color, turbidity, and TSS, and each can reduce light availability to seagrasses. Mean light attenuation was lowest in Santa Rosa Sound. St. Joseph Bay also had low light attenuation. No light attenuation measurements were made in St. George Sound. Salinity and light attenuation from the other 4 systems were negatively correlated ($r = -0.45$, $p < 0.001$). Light attenuation was positively correlated with chlorophyll *a* ($r = 0.69$, $p < 0.001$), color ($r = 0.85$, $p < 0.001$) and turbidity ($r = 0.70$, $p < 0.001$; Supplemental Figure S1). In St. Andrew Bay and Santa Rosa Sound, where light attenuation was measured in more than one season, values decreased between spring and fall (Supplemental Figure S2).

Shoot and leaf metrics

Mean live biomass of *T. testudinum* (above— and belowground) ranged from 175–872 g/m^2 for all locations (Table 3). Biomass was greatest in St. Andrew Bay, followed by St. Joseph Bay, while sites in St. George Sound had the least biomass. Biomass increased between June and later sampling periods in all estuaries except St. George Sound. Variability was high among quadrats and sites in each estuary. Dead biomass, as a fraction of live biomass, was greatest in Santa Rosa Sound in June (0.42) and ranged from 0.04–0.25 for other estuaries and sampling periods. *Thalassia testudinum* shoot density varied 7—fold among estuaries (Table 4). Highest shoot density occurred in Santa Rosa Sound and St. Andrew Bay, and the lowest density occurred in St. George Sound. In all systems except St. Joseph Bay, mean shoot density increased between early and later measurement periods.

While monospecific *T. testudinum* beds were targeted for this study, small amounts of *H. wrightii* occurred in some quadrats in Big Lagoon, Santa Rosa Sound (June only), St. Andrew Bay, and St. George Sound (Table 3). However, *H. wrightii* represented less than 7% of the biomass from Big Lagoon, Santa Rosa Sound and St. Andrew Bay, but between 11 and 35% in St. George Sound. In addition, *S. filiforme* was also present in St. George Sound, where it was 19% and 32% of all seagrass biomass in June and October, respectively. Mean counts of *H. wrightii* shoots in Big Lagoon were 3,440 ± 3,210 in June and 4,390 ± 3,160/m^2 in August (Table 4). Variability in shoot counts

TABLE 2. *Mean (± sd) of surface salinity, temperature, light attenuation (K_d), chlorophyll a, color, turbidity and total suspended solids (TSS) between June and August 2016 for estuaries in the Florida panhandle where productivity measurements were made. n.d. – no data.*

Estuary	Surface Salinity	Surface Temperature °C	K_d/m	Chlorophyll *a* μg/L	COLOR PCU	Turbidity NTU	TSS mg/L
Big Lagoon	25.77 ± 1.44	28.45 ± 1.33	0.65 ± 0.06	6.00 ± 1.27	n.d.	1.67 ± 0.08	5.00 ± 1.00
Santa Rosa Sound	21.91 ± 2.52	30.95 ± 1.65	0.49 ± 0.08	1.26 ± 0.65	9.72	1.36 ± 0.49	4.95 ± 1.81
St. Andrew Bay	22.01 ± 4.08	30.05 ± 1.18	0.87 ± 0.36	4.67 ± 3.36	40.56 ± 24.48	1.30 ± 1.04	2.32 ± 1.54
St. Joseph Bay	31.47 ± 1.32	30.36 ± 1.15	0.56 ± 0.31	4.03 ± 3.42	6.52 ± 4.61	0.94 ± 0.63	2.32 ± 0.99
St. George Sound	31.19 ± 3.16	29.94 ± 2.37	n.d.	4.46 ± 2.98	14.31 ± 6.03	2.68 ± 2.65	6.45 ± 6.38

TABLE 3. *Mean ± sd of live seagrass biomass (above- and belowground) harvested from quadrats in 5 estuaries from the Florida panhandle during productivity measurements. N—number of quadrats; Dead/Live—weight of dead biomass/weight of live biomass.*

		Live biomass (g/m²)						
		Thalassia testudinum			***Halodule wrightii***		***Syringodium filiforme***	
Estuary	**Month**	**Mean ± sd.**	**N**	**Dead /live**	**Mean ± sd**	**N**	**Mean ± sd.**	**N**
Big Lagoon	June	366 ± 244	23	0.10	26.8 ± 31.1	7		
	August	453 ± 312	24	0.15	0.91 ± 0.58	6		
Santa Rosa Sound	June	261 ± 170	24	0.42	18.9 ± 15.5	2		
	July	373 ± 122	7					
	September	625 ± 164	24	0.14				
St. Andrew Bay	June	867 ± 622	24	0.25	31.8 ± 31.3	8		
	July	872 ± 406	24	0.04	31.0 ± 43.5	16		
St. Joseph Bay	June	759 ± 405	23	0.16				
	August	778 ± 369	24	0.21				
St. George Sound	June	268 ± 175	23	0.05	43.7 ± 29.5	5	73.5 ± 58.3	17
	October	175 ± 166	24	0.16	186 ± 210	7	173 ± 120	19

TABLE 4. *Means ± sd of seagrass species density harvested from quadrats in 5 estuaries from the Florida panhandle during productivity measurements. N—number of quadrats.*

		Live Shoots (#/m²)					
		Thalassia testudinum		***Halodule wrightii***		***Syringodium filiforme***	
Estuary	**Month**	**Mean ± sd.**	**N**	**Mean ± sd**	**N**	**Mean ± sd.**	**N**
Big Lagoon	June	839 ± 378	22	3,440 ± 3,210	15		
	August	1,090 ± 649	23	4,390 ± 3,160	22		
Santa Rosa Sound	June	984 ± 477	24	1,750 ± 1,029	3		
	July	1,303 ± 533	7				
	September	1,720 ± 652	24				
St. Andrew Bay	June	1,130 ± 345	24				
	July	1,280 ± 330	24				
St. Joseph Bay	June	885 ± 382	23				
	August	755 ± 301	24				
St. George Sound	June	229 ± 112	20	446 ± 422	7	414 ± 370	14
	October	253 ± 164	24	632 ± 736	7	1,260 ± 513	20

among sites and quadrats was high (Table 4). Mean counts of *H. wrightii* were lower in Santa Rosa Sound in June and in St. George Sound than counts in Big Lagoon. Mean shoot counts of *S. filiforme* in St. George Sound were 414 ± 370 and 1,260 ± 513/m² in June and October, respectively.

Mean *T. testudinum* leaf length and width were highest in St. Joseph Bay and St. George Sound in the eastern panhandle with lower mean values in the estuaries to the west (Table 5). The fraction of each leaf that was green (% green) was high (81–89%) in Santa Rosa Sound, lowest in St. Andrew Bay in July (49%), and similar (60–71%) elsewhere. One—sided LAI for *T. testudinum* was greatest in St. Joseph Bay, where longer and wider blades combined with 755–885 shoots/m² created the highest leaf surface area across the estuaries. The lowest mean 1—sided LAI was measured in St. George Sound where the density of *T. testudinum* shoots was very low.

Productivity

Indices of growth (leaf productivity, SSBG, and turnover on a leaf area basis) varied among regions and sampling periods (Figure 3). Leaf productivity was also greater during the latter sampling periods in all regions, but the variation within the sites within a region was also much greater during this time (Figure 3A). Sites in St. Joseph Bay had the greatest productivity during both sampling periods, with means of 2.3 and 5.1 g/m²/d for June and August, respectively. Sites in St. George Sound, just to the east, had the lowest productivity, with means of 0.57 and 0.41 g/m²/d for June and October, respectively.

The growth response of individual shoots to environmental conditions (SSBG) ranged from 0.34−0.66 cm²/d in June and increased across the panhandle from west to east (Figure 3B). Mean SSBG values from the later sampling period were greater than June values in all estuaries except Santa Rosa Sound. The highest SSBG value, 1.6 cm²/d, occurred in St. Joseph Bay in August. Leaf turnover was also greater during the second sampling period, July—September, in all regions but Santa Rosa Sound (Figure 3C). Greatest leaf turnover occurred in St. Andrew Bay in July.

Leaf productivity was significantly positively correlated with

TABLE 5. *Mean ± sd of blade length and blade width of T. testudinum shoots and 1-sided leaf area index (LAI) in 5 estuaries from the Florida panhandle. % green—mean percent of blade that was green; N—number of quadrats.*

		Blade characteristics			1-sided LAI	
Estuary	**Month**	**Length (cm)**	**% Green**	**Width (cm)**		**N**
Big Lagoon	June	15 ± 7.3	60%	0.40 ± 0.08	2.06 ± 0.91	22
	August	16 ± 8.3	65%	0.41 ± 0.07	2.28 ± 1.05	23
Santa Rosa Sound	June	12 ± 6.5	89%	0.36 ± 0.07	1.16 ± 0.60	24
	July	13 ± 6.7	91%	0.43 ± 0.08	1.78 + 0.80	7
	September	11 ± 6.8	81%	0.38 ± 0.07	1.85 ± 0.71	24
St. Andrew Bay	June	11 ± 5.3	69%	0.40 ± 0.10	1.87 ± 0.53	24
	July	14 ± 6.2	49%	0.46 ± 0.12	2.30 ± 0.54	24
St. Joseph Bay	June	18 ± 10.5	61%	0.67 ± 0.15	4.18 ± 2.15	23
	August	25 ± 15.4	71%	0.67 ± 0.18	4.06 ± 1.60	24
St. George Sound	June	18 ± 12.5	67%	0.62 ± 0.16	1.18 ± 0.63	20
	October	21 ± 14.3	68%	0.67 ± 0.15	1.04 ± 0.47	24

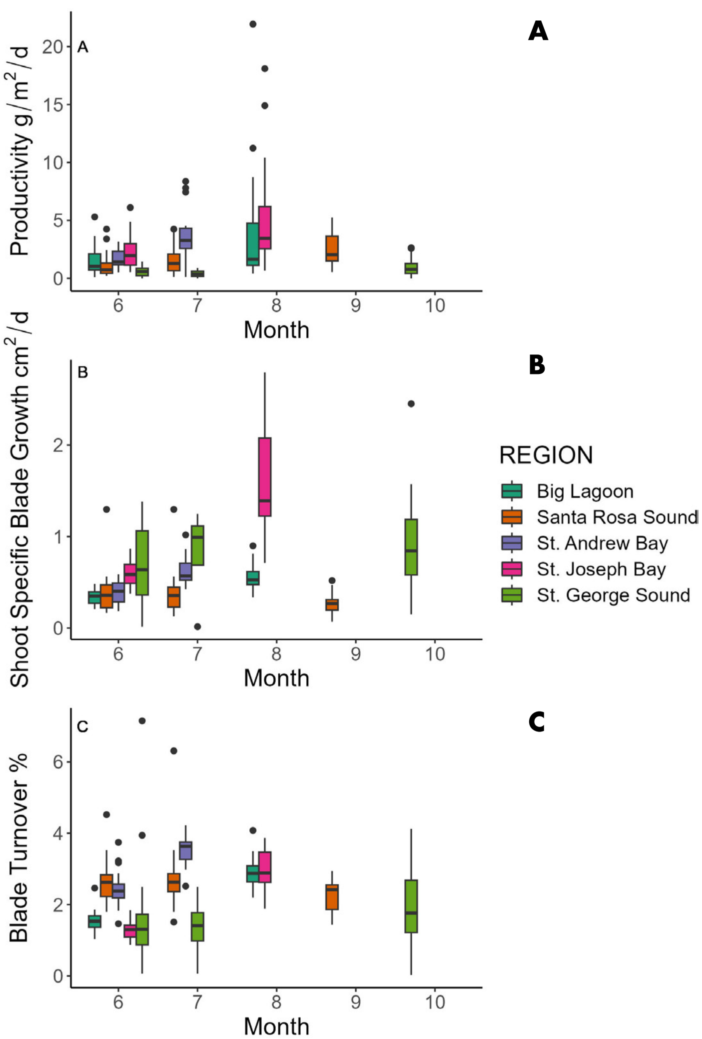

FIGURE 3. *Box plots of T. testudinum productivity between June and October 2016 in 5 Florida panhandle estuaries. A. Aboveground productivity (g/m²/d). B. Shoot specific blade growth (SSBG). C. Blade turnover (%/d). Solid line—median; box—Interquartile range; vertical lines—highest and lowest values excluding outliers; dots—outliers.*

T. testudinum shoot density (r = 0.51, p < 0.001), LAI (r = 0.69, p < 0.001), and total live biomass (r = 0.51, p < 0.001). While SSBG was significantly (p < 0.001) positively correlated with leaf productivity, leaf turnover and LAI, the correlation coefficients were < 0.4 (Supplemental Figure S3). Total live biomass was significantly positively correlated with LAI (r = 0.53, p < 0.001) and the root:shoot ratio (r = 0.56, p < 0.001). Principal component analysis revealed that the first 2 components explained 79.5% of the variation in the data (Supplemental Table S1). The first principal component explained 49% of the variability in the data, with the watershed:water ratio, leaf turnover, live shoot number and turbidity having the most influence on this component (Figure 4). The second component explained 30.4% of the variability and was dominated by SSBG, leaf productivity, LAI and salinity (Figure 4, Supplemental Table S1).

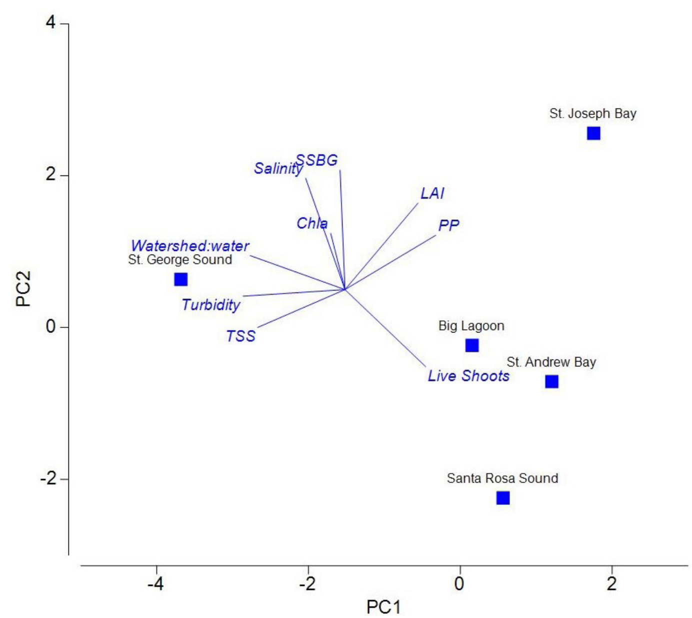

FIGURE 4. *Principal Component Analysis showing differences among 5 Florida panhandle estuaries based on mean environmental data and T. testudinum metrics. SSBG—shoot specific blade growth; LAI—leaf area index; PP—blade productivity; Chla—chlorophyll a; TSS—total suspended solids.*

Discussion

This study was the first effort to compare the biomass, shoot density, and leaf productivity of *T. testudinum* across the 5 estuaries of the Florida panhandle where *T. testudinum* can be found. *Thalassia testudinum* biomass estimates were in the low to middle range of values measured in the Caribbean Sea (Cortes et al. 2019, van Tussenbroek et al. 2014) and the Laguna Madre, TX (Kaldy and Dunton 2000), but were similar to values measured in Florida Bay (Herbert and Fourqurean 2009), East Flats, TX (Darnell and Dunton 2016), and Tobago (Juman 2005). The SSBG was higher in our study than in the eastern GOM near Homosassa, FL (Barry et al. 2018).

Leaf turnover in June in Big Lagoon, St. Joseph Bay and St. George Sound was similar to June values from Rabbit Key in Florida Bay (Frankovich and Zieman 2005). However, leaf turnover from later in the growing season in this study was considerably greater than comparable months from Florida Bay (Frankovich and Zieman 2005). Productivity values were consistent with other summer measurements from St. Joseph Bay where July productivity was 3.34 $g/m^2/d$ (Roderiguez and Heck 2021). Daily growing season productivity has been reported in Tobago (Juman 2005) and the Laguna Madre, TX (Kaldy and Dunton 2000), and rates are similar to estimates from this study. Productivity in panhandle *T. testudinum* beds likely declines outside of the growing season due to lower water temperatures and diminished light availability resulting from shorter day lengths, lower sun angles, and reduced water clarity during the winter and spring high river flow periods. Declining growth rates over the growing season were also observed in St. Joseph Bay where *T. testudinum* productivity declined from 1.55 to 0.66 $g/m^2/d$ between fall and winter (Rodriguez and Heck 2021).

Mean shoot densities were similar to densities reported in other estuaries in the GOM (Tomasko et al. 1996, Kaldy and Dunton 2000, Darnell and Dunton 2016, Barry et al. 2018) and in coastal regions of the Caribbean Sea (Gallegos et al. 1993, Herbert and Fourqurean 2009). Lowest shoot densities were measured in St. George Sound where sampling sites were not monospecific, with *H. wrightii* and *S. filiforme* also present. *Halodule wrightii* was also present in quadrats in Big Lagoon, Santa Rosa Sound, and St. Andrews Bay, but were not co—dominant like in St. George Sound.

Analysis of the possible effects of estuary, sampling period, and physical factors, such as salinity and light availability, was limited because physical data were not always matched to seagrass sampling locations or collected during the same time period as productivity measurements. The principal component analysis indicates that St. Andrew Bay, Big Lagoon and Santa Rosa Sound were the most similar to each other with higher values for live shoots and leaf turnover and lower values for salinity and watershed:water ratio. St. Joseph Bay had high leaf productivity, high salinity and low turbidity. St. George Sound had low leaf productivity, high TSS and the highest watershed:water ratio.

All sampling locations were in long—established *T. testudinum* beds (Yarbro and Carlson 2016), but differences among the 5 estuaries are apparent. Big Lagoon, Santa Rosa Sound, and St. Joseph Bay are coastal lagoons with limited freshwater input, whereas St. Andrew Bay and St. George Sound are more directly influenced by freshwater discharge (Northwest Florida Water Management District 2017a, b). However, productivity measures showed little relationship to freshwater input or salinity; the highest productivity occurred in July and August during a period of highest temperature, regardless of the location of the estuary. Teasing apart temporal patterns is a challenge because the later sampling periods varied among estuaries due to logistical constraints. Big Lagoon, St. Andrew Bay, and St. Joseph Bay were sampled twice in the summer: June and then in July or August. All 3 estuaries had higher SSBG, leaf productivity, and leaf turnover during the second sampling period. While these metrics were similar in Santa Rosa Sound in June and July, leaf productivity was higher in September than in the other 2 months.

The LAI was less variable between sampling periods than other plant metrics. These differences may result from allocation of resources to reproduction in June. While long days and warm water temperatures create excellent conditions for growth in June, allocation of fixed carbon to flowering structures might reduce the rate of leaf growth. *Thalassia testudinum* in the GOM most commonly flowers from April through June (Durako and Moffler 1987). Kaldy and Dunton (2000) found that about 15% of the aboveground biomass of *T. testudinum* was allocated to reproduction in the Laguna Madre, TX. If biomass allocation to reproductive structures occurred primarily in May and June, this might contribute to lower productivity measures in June compared with those collected later in the season.

Several metrics were calculated to estimate biomass and productivity, and each metric provided a different assessment of growth. The SSBG and leaf turnover metrics provided an estimate of shoot—level productivity, while LAI and blade productivity provided information on the productivity of the seagrass bed. The LAI is less commonly reported but provides information about the potential photosynthetic area of leaves and is increasingly used to calibrate remotely sensed data (Dierssen et al. 2010, Hill et al. 2014, Hedley et al. 2017). Measures of biomass and shoot density provided estimates of the standing stocks of seagrass tissues. In multi—species meadows, such as those in St. George Sound, biomass estimates for all species are necessary to provide context for productivity measurements of one species.

Based on productivity and biomass measurements, *T. testudinum* was most productive in St. Joseph Bay. Monitoring data from 2008 through 2016 (Johnsey et al. 2018) showed that *T. testudinum* was dominant in this bay, often occurring in large monospecific beds. In St. George Sound, SSBG was highest of all estuaries, except for St. Joseph Bay in August, but productivity of *T. testudinum* in St. George Sound was the lowest of all estuaries. While sites in Big Lagoon, Santa Rosa Sound, St. Andrew Bay and St. George Sound were selected to be in monospecific *T. testudinum* beds, other species were present. Quadrats in Big Lagoon and Santa Rosa Sound had 1,750–4,390 shoots/m^2 of *H. wrightii* but had *T. testudinum* shoot densities greater than those measured in St. Joseph Bay, where daily productivity and SSBG were greater overall. In St. George Sound, *T. testudinum* shoots had much lower densities in other estuaries, and quadrats contained numerous *S. filiforme* and *H. wrightii* shoots. However, the high rate of SSBG might have reflected efforts by *T. testudinum* shoots to outgrow shoots of other species to reach adequate light. Determining the effects of competition with other seagrass species on *T. testudinum* productivity will require further research by examining productivity in mixed beds.

These data on standing stocks and productivity of *T. testudinum* in 5 estuaries of the Florida panhandle provide information for estuaries not previously studied. Differences in blade productivity, biomass and other plant metrics were generally similar among estuaries, with higher values in the clear marine waters of St. Joseph Bay and lowest values in the relatively more turbid waters of St. George Sound. This study at the northern extent of the Caribbean basin also puts *T. testudinum* productivity in context with work done across the Caribbean region (van Tussenbroek et al. 2014, e.g. Cortes et al. 2019). Results provide baseline estimates useful for assessing the success of restoration activities targeting *T. testudinum* beds in the region, particularly as climate change in the region leads to increased sea level rise, higher temperatures and more extreme precipitation events.

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Literature Cited

APHA (America Public Health Association). 1985. Standard methods for the examination of water and wastewater. 16th edition. American Public Health Association, Washington, D.C., USA, 1268 p.

Barry, S.C., C.A. Jacoby, and T.K. Frazer. 2018. Resilience to shading influenced by differential allocation of biomass in *Thalassia testudinum*. Limnology and Oceanography 63:1817–1831. https://doi.org/10.1002/lno.10810

Bayraktarov, E., M.I. Saunders, S. Abdullah, M. Mills, J. Beher, H.P. Possingham, P.J. Mumby, and C.E. Lovelock. 2015. The cost and feasibility of marine coastal restoration. Ecological Applications 26:1055—1074. https://doi.org/10.1890/15—1077

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

Clarke, K.R. and R.N. Gorley, 2015. PRIMER v7: User Manual/Tutorial. PRIMER—E Plymouth, UK. https://www.primer—e.com/

Cortés, J., H.A. Oxenford, B.I. van Tussenbroek, E. Jordán—Dahlgren, A. Cróquer, C. Bastidas, and J.C. Ogden. 2019. The CARICOMP network of Caribbean marine laboratories (1985—2007): History, key findings, and lessons learned. Frontiers in Marine Science 5:519. https://doi.org/10.3389/fmars.2018.00519

Darnell, K.M. and K.H. Dunton. 2016. Reproductive phenology of the subtropical seagrasses *Thalassia testudinum* (turtle grass) and *Halodule wrightii* (shoal grass) in the northwest Gulf of Mexico. Botanica Marina 59:473–483. https://doi.org/10.1515/bot—2016—0080

DHNRDAT (Deepwater Horizon Natural Resource Damage Assessment Trustees). 2021. Deepwater Horizon Natural Resource Damage Assessment Programmatic Review. November. Available: www.gulfspillrestoration.noaa.gov/sites/default/files/2021—11_Deepwater_Horizon_TC_Final_2021_Programmatic_Review.pdf. (viewed on 4/24/23).

Dierssen, H.M., R.C. Zimmerman, L.A. Drake, and D. Burdige. 2010. Benthic ecology from space: Optics and net primary production in seagrass and benthic algae across the Great Bahama Bank. Marine Ecology Progress Series 411:1–15. https://

doi.org/10.3354/meps08665

Durako, M.J. and M.D. Moffler. 1987. Factors affecting the reproductive ecology of *Thalassia testudinum* (Hydrocharitaceae). Aquatic Botany 27:79–95. https://doi.org/10.1016/0304—3770(87)90087—8

Frankovich, T.A. and J.C. Zieman. 2005. A temporal investigation of grazer dynamics, nutrients, seagrass leaf productivity, and epiphyte standing stock. Estuaries 28:41–52. https://doi.org/10.1007/BF02732752

Florida Fish and Wildlife Conservation Commission. 2019. Roadblocks to seagrass recovery. GEBF Project ID: 49540. FWC Project ID FN003. Final Report. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA. 26 p. https://myfwc.com/research/habitat/seagrasses/projects/roadblocks Downloaded 4/24/23.

Gallegos, C.L., D.L. Correll, and J.W. Pierce. 1990. Modelling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. Limnology and Oceanography 35:1486–1502. https://doi.org/10.4319/lo.1990.35.7.1486

Gallegos, M.E., M. Merino, N. Marbá, and C.M. Duarte. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: Elucidating rhizome growth. Marine Ecology Progress Series 95:185–192. https://www.int—res.com/articles/meps/95/m095p185.pdf

Garrote—Moreno, A., A. McDonald, T. Sherman, J.L. Sanchez—Lizaso, K. Heck, and J. Cebrian. 2014. Short—term impacts of salinity pulses on ionic ratios of the seagrasses *Thalassia testudinum* and *Halodule wrightii*. Aquatic Botany 120:315–321. https://doi.org/10.1016/j.aquabot.2014.09.011

Greening, H.S., L.M. Cross, and E.T. Sherwood. 2011. A multiscale approach to seagrass recovery in Tampa Bay, Florida. Ecological Restoration 29:82—93. https://doi.org/10.3368/er.29.1—2.82

Handley, L.R., D. Altsman and R. DeMay. 2006. Seagrass status and trends in the northern Gulf of Mexico: 1940–2002. Scientific Investigations Report 2009—5287, U.S. Geological Survey, Washington, D.C., and Report 855—R—04—003, U.S. Environmental Protection Agency, Washington, D.C., USA. 267 p.

Harley, C. D., A. R. Hughes, K.M. Hultgren, B.G. Miner, C.J. Sorte, C.S. Thornber, L.R. Rodriguez, L. Tomanek, and S.L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228—241. https://doi.org/10.1111/j.1461—0248.2005.00871.x

Hedley, J.D., J. Brandon, K. Randolph, M.Á. Pérez—Castro, R.M. Vásquez—Elizondo, S. Enríquez, and H.M Dierssen. 2017. Remote sensing of seagrass leaf area index and species: The capability of a model inversion method assessed by sensitivity analysis and hyperspectral data of Florida Bay. Frontiers in Marine Science 4:362. https://doi.org/10.3389/fmars.2017.00362.

Herbert, D.A. and J.W. Fourqurean. 2009. Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinum* in Florida Bay. Estuaries and Coasts 32:188–201. https://doi.org/10.1007/s12237—008—9116—x

Hill, V.J., R.C. Zimmerman, W.P. Bissett, H. Dierssen, and D.D.R. Kohler. 2014. Evaluating light availability, seagrass biomass, and productivity using hyperspectral airborne remote sensing in Saint Joseph's Bay, Florida. Estuaries and Coasts 37:1467–1489. https://doi.org/10.1007/s12237—013—9764—3

Hughes, A.R., S.L. Williams, C.M. Duarte, K.L. Heck, Jr., and M. Waycott. 2009. Associations of concern: Declining seagrasses and threatened dependent species. Frontiers of Ecology and the Environment 7:242–246. https://doi.org/10.1890/080041

Irlandi, E., B. Orlando, S. Maciá, P. Biber, T. Jones, L. Kaufman, D. Lirman, and E.T. Patterson. 2002. The influence of freshwater runoff on biomass, morphometrics, and production of *Thalassia testudinum*. Aquatic Botany 72:67–78. https://doi.org/10.1016/S0304—3770(01)00217—0

Iverson, R.L. and H.F. Bittaker. 1986. Seagrass distribution and abundance in Eastern Gulf of Mexico coastal waters. Estuarine, Coastal and Shelf Science 22:577–602. https://doi.org/10.1016/0272—7714(86)90015—6

Johnsey, E., P.R. Carlson, D. Byron, K. Heck, J. Brucker, and K. Kebart. 2018. Summary report for St. Joseph Bay. In L. Yarbro and P.R. Carlson, eds. Seagrass Integrated Mapping and Monitoring Report No. 3. Fish and Wildlife Research Institute Technical Report TR—17 version 3, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA, p. 1—17.

Juman, R.A. 2005. The structure and productivity of the *Thalassia testudinum* community in Bon Accord Lagoon, Tobago. Revista de Biología Tropical 53 (suppl. 1):219—227.

Kaldy, J.E. and K. H. Dunton. 2000. Above and below—ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. Marine Ecology Progress Series 193:271–283. https://doi.org/10.3354/meps193271

Kirk, J.T.O. 1976. Yellow substance (gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south—eastern Australia waters. Australian Journal of Marine and Freshwater Research 27:61–71. https://doi.org/10.1071/MF9760061

Larkum, A.W.D, R.J. Orth, and C.M. Duarte. 2006. Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, 676 p. https://doi.org/10.1007/978—1—4020—2983—7

Lee, K.S., S.R. Park, and Y.K. Kim. 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses, a review. Journal of Experimental Marine Biology and Ecology 350:144–175. https://doi.org/10.1016/j.jembe.2007.06.016

Livingston, R.J. 2015. Climate Change and Coastal Ecosystems. CRC Marine Science Series, Volume 18, CRC Press, Boca Raton, FL, USA, 572 p. https://doi.org/10.1201/b17607

Manuel, S.A., K.A. Coates, W.J. Kenworthy, and J.W. Fourqurean. 2013. Tropical species at the northern limit of their range: Composition and distribution in Bermuda's benthic habitats in relation to depth and light availability. Marine Environmental Research 89:63–75. https://doi.org/10.1016/j.marenvres.2013.05.003

McDonald, A.M., P. Prado, K.L. Heck, Jr., J.W. Fourqurean, T.A. Frankovich, K.H. Dunton, and J. Cebrian. 2016. Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale. Aquatic Botany 134:87–96. https://doi.org/10.1016/j.aquabot.2016.07.007

Northwest Florida Water Management District. 2017a. Pensacola Bay System Surface Water Improvement and Management Plan. Program Development Series 17—06, Havana, FL, USA, 132 p. https://nwfwater.com/water—resources/surface—water—improvement—and—management/pensacola—bay—system/

Northwest Florida Water Management District. 2017b. St. Andrew Bay System Surface Water Improvement and Management Plan. Program Development Series 17—08, Havana, FL, USA, 136 p. https://nwfwater.com/water—resources/surface—water—improvement—and—management/st—andrew—bay/

O'Brien, K.R., M. Waycott, P. Maxwell, G.A. Kendrick, J.W. Udy, A.J. Ferguson, K. Kilminster, P. Scanes, L.J. McKenzie, K. McMahon, M.P. Adams, J. Samper—Villarreal, C. Collier, M. Lyons, P.J. Mumby, L. Radke, M.J.A. Christianen, and W.C. Dennison. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Marine Pollution Bulletin 134:166—176. https://doi.org/10.1016/j.marpolbul.2017.09.006

Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck, A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, S, Olyarnik, F.T. Short, M. Waycott, and S.L. Williams. 2006. A global crisis for seagrass ecosystems. Bioscience 56:987–996. https://doi.org/10.1641/0006—3568(2006)56[987:AGCFSE]2.0.CO;2

Orth, R.J., J.S. Lefcheck, K.S. McGlathery, L. Aoki, M.W. Luckenbach, K.A. Moore, M.P.J. Oreska, R. Snyder, D.J. Wilcox, and B. Lusk. 2020. Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. Science Advances 6:eabc6434. https://doi.org/10.1126/sciadv.abc6434

Presley, R. and J.M. Caffrey. 2021. Nitrogen fixation in subtropical seagrass sediments: Seasonal patterns in activity in Santa Rosa Sound, Florida, USA. Journal of Marine Science and Engineering 9:766. https://doi.org/10.3390/jmse9070766.

Rezek, R.J., B.T. Furman, R.P. Jung, M.O. Hall, and S.S. Bell. 2019. Long—term performance of seagrass restoration projects in Florida, USA. Nature Scientific Reports 9:15514 https://doi.org/10.1038/s41598—019—51856—9.

Rodriguez, A.R. and K.L. Heck. 2021. Approaching a tipping point? Herbivore carrying capacity estimates in a rapidly changing, seagrass—dominated Florida Bay. Estuaries and Coasts, 44:522—534. https://doi.org/10.1007/s12237—020—00866—2

Schloerke B., D. Cook, J. Larmarange, F. Briatte, M. Marbach, E. Thoen, A. Elberg, and J. Crowley. 2022. GGally: Extension to 'ggplot2'. https://ggobi.github.io/ggally/ (viewed on 5/27/22).

Tomasko, D.A., C.J. Dawes, and M.O. Hall. 1996. The effects of anthropogenic nutrient enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. Estuaries 19:448–456. https://doi.org/10.2307/1352462

Tomasko, D., C.A. Corbett, H.S. Greening, and G. Raulerson. 2005. Spatial and temporal variation in seagrass coverage in Southwest Florida: Assessing the relative effects of anthropogenic nutrient load reductions and rainfall in four contiguous estuaries. Marine Pollution Bulletin 50:797–805. https://doi.org/10.1016/j.marpolbul.2005.02.010

Valdez, S.R., Y.S Zhang, T. van der Heide, M.A Vanderflift, F. Tarquinio, R.J. Orth, and B.R. Silliman. 2020. Positive ecological interactions and the success of seagrass restoration. Frontiers in Marine Science 7:91. https://doi.org/10.3389/fmars.2020.00091

Van Tussenbroek, B.I., J. Cortés, R. Collin, A.C. Fonseca, P.M.H. Gayle, H.M. Guzmán, G.E. Jácome, R. Juman, K.H. Koltes, H.A. Oxenford, A. Rodríguez—Ramirez, J. Samper—Villarreal, S.R. Smith, J.J. Tschirky, and E. Wei. 2014. Caribbean—wide, long—term study of seagrass beds reveals local variations, shifts in community structure and occasional collapse. PLOS One 9(3): e90600. https://doi.org/10.1371/journal.pone.0090600

Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworth, F.T. Short, and S.L. Williams 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106:12377–12381. https://doi.org/10.1073/pnas.0905620106

Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and phaeopigments. Limnology and Oceanography 39:1985–1992. https://doi.org/10.4319/lo.1994.39.8.1985

Williams, S.L. and K.L. Heck, Jr. 2001. Seagrass community ecology. In M.D. Bertness, S.D. Gaines, and M.E. Hay, eds. Marine Community Ecology. Sinauer Associates, Sunderland, MA, USA, p. 317—337.

Yarbro, L.A. and P.R. Carlson. 2016. Seagrass Integrated Mapping and Monitoring Program mapping and monitoring report No. 2. FWRI Technical Report TR—17, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA, 281 p.

Yarbro L.A. and P.R. Carlson. 2018. Seagrass Integrated Mapping and Monitoring Report No. 3. FWRI Technical Report TR—17 version 3, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA. https://myfwc.com/research/habitat/seagrasses/projects/completed/simm/simm—reports/

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

Zieman, J.C., and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: A community profile. Biological report 85—7.25. U.S. Minerals Management Service, Washington, D.C., USA, 155 p.

Zimmerman, R. C. 2021. Scaling up: Predicting the impacts of climate change on seagrass ecosystems. Estuaries and Coasts, 44(2), 558—576. https://doi.org/10.1007/s12237—020—00837—7