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Light requirements of seagrasses determined from historical records of light attenuation along the Gulf coast of peninsular Florida

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ABSTRACT

Seagrasses around the world are threatened by human activities that degrade water quality and reduce light availability. In this study, light requirements were determined for four common and abundant seagrasses along the Gulf coast of peninsular Florida using a threshold detecting algorithm. Light requirements ranged from 8% to 10% of surface irradiance for *Halophila engelmannii* to 25–27% of surface irradiance for *Halodule wrightii*. Requirements for all species differed from previous reports generated at other locations. Variations were attributed to morphological and physiological differences, as well as adaptation to light histories at specific locations. In addition, seagrasses were absent from stations with significantly higher concentrations of total nitrogen, total phosphorus, chlorophyll *a* and color. These results confirm the need to address links between increased anthropogenic nutrient loads, eutrophication, reduced light penetration, and loss of seagrasses and the services they provide.

1. Introduction

Seagrasses around the world are threatened by human activities that result in degraded water quality and reduced light availability in particular. Many seagrass beds throughout the United States and globally have experienced declines in biomass and density since the middle 1900s (OSPAR, 2009; Waycott et al., 2009). As a consequence, the $3.8 trillion of ecosystem services provided by seagrasses have been degraded (Costanza et al., 1997). For example, seagrass loss results in decreased carbon storage; enhanced transfer of wave energy; increased suspended solids concentrations; and decreased refuge and foraging habitat for numerous marine and estuarine animals, such as fish, shellfish, birds and other wildlife (Duarte, 1995; Costanza et al., 1997; Hemminga and Duarte, 2000; Waycott et al., 2009; Fourqurean et al., 2012).

Due to their biology and physiology, survival and growth of seagrasses depend on a number of factors, including suitable substrate for roots and rhizomes, adequate periods of immersion, appropriate salinities and temperatures, and sufficient subsurface irradiance for photosynthesis (Hemminga and Duarte, 2000). Overall, light has been shown to be a key factor affecting the health of seagrass because it drives photosynthetic production of the energy that supports growth, respiration, reproduction, and responses to other stresses (Hemminga and Duarte, 2000). Due to the importance of light, management of human activities that reduce water clarity becomes essential for preserving valuable seagrass habitats.

Seagrasses are most prevalent in shallow waters with high light penetration and low concentrations of dissolved nutrients. In such conditions, seagrasses dominate because they can acquire substantial quantities of nutrients through their root systems and store nitrogen and phosphorus in their leaves, stems and rhizomes (Hocking et al., 1981; Valiela et al., 1997). As nutrient loading and water column concentrations increase, macroalgae, epiphytic algae and phytoplankton begin to outcompete seagrasses because these photoautotrophs are more efficient at acquiring nutrients from the water column and require less light (Williams and Ruckelshaus, 1993; Duarte, 1995; Biber et al., 2009). For example, macroalgae require a mere 1% of surface irradiance (SI); whereas, seagrasses require 11% SI or more on average (Duarte, 1991, 1995). Duarte et al. (2007) linked light requirements of seagrasses to the overall light regime at a location, with seagrasses in turbid waters apparently having higher light requirements than those growing in clearer waters. Previous studies have, in fact, demonstrated substantial variation in the minimum light requirements of seagrass species growing at different locations (Dennison,

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1987; Dunton, 1994; Dawes, 1998; Durako, 2007). For example, in the Indian River Lagoon in Florida, *Halodule wrightii*, *Syringodium filiforme* and *Thalassia testudinum* require approximately 33% of SI (Steward et al., 2005). In contrast, *T. testudinum* in Tampa Bay, Florida requires 20–25% SI (Tomasko and Hall, 1999), *H. wrightii* in Laguna Madre, Texas requires 15–18% SI (Williams and McRoy, 1982), and *S. filiforme* along the northwest coast of Cuba requires 19% SI (Dennison et al., 1993). These findings suggest that historical and current light regimes interact with other environmental influences to determine the light requirements of seagrasses, while also emphasizing the importance of estimating light requirements for multiple locations.

Historic and current light regimes are affected by nutrient loading and water column nutrient concentrations. In fact, nutrients have been shown to have a negative effect on water clarity in coastal systems, with Tomasko et al. (2001) demonstrating that a 45% increase in nitrogen in Lemon Bay, Florida resulted in a 29% increase in chlorophyll *a*, a 9% increase in the light attenuation coefficient, and a consequent 24% decrease in the maximum depth of seagrass occurrence. Similarly, Antón et al. (2011) showed that an increase in nutrients resulted in an increase in chlorophyll *a* and a 30% decrease in light available to seagrasses, and Onuf (1996) showed that a 50% decrease in light penetration caused by a brown tide event led to a 60% decrease in seagrass biomass in beds deeper than 1.4 meters. Excess nutrients also promote growth of macroalgae that can shade seagrasses (Valiela et al., 1997) and epiphytes that can absorb 30% or more of the light reaching seagrass blades (Dixon, 2000). Overall, increased nutrient delivery can generate negative effects on seagrasses by altering light regimes.

Given the links between increased inputs of nutrients, eutrophication, reduced light availability and detrimental impacts on seagrasses, managers of coastal systems will benefit from an improved understanding of the light requirements of seagrasses (Bricker et al., 2008). Therefore, we identified areas with and without seagrasses in eight coastal systems along Florida's Gulf coast; evaluated historical records of light attenuation to estimate the light requirements of seagrasses; and related estimated light requirements and light availability to variations in concentrations of chlorophyll *a*, total nitrogen, total phosphorus, and color. Through these efforts, we gained insights into the likely consequences of increased nitrogen and phosphorus loads, which often lead to eutrophication and altered light regimes in such systems (Duarte, 1995; Bricker et al., 2008). The resulting information can inform management actions, including the development of criteria for sustainable nutrient concentrations.

2. Methods

2.1. Study area

Sampling was conducted in eight coastal systems adjacent to the Steinhatchee, Suwannee, Wacasassa, Withlacoochee, Crystal, Homosassa, Chassahowitzka, and Weeki Wachee rivers along the Gulf coast of peninsular Florida (Fig. 1). These systems fall within the boundaries of Florida's second largest contiguous seagrass bed that covers approximately 3000 km^2 (Iverson and Bittaker, 1986; Zieman and Zieman, 1989; Hale et al., 2004). The shallow estuarine waters in the region are tidally dominated, with diurnal tides of approximately 1 m (Glancy et al., 2003). A significant amount of groundwater transported to these areas from springs and seeps generates relatively consistent inflows of freshwater and nutrient loads (Jones et al., 1997; Frazer et al., 2001, 2006). The sediments in these systems consist largely of clay and siliceous sand over limestone (Iverson and Bittaker, 1986).

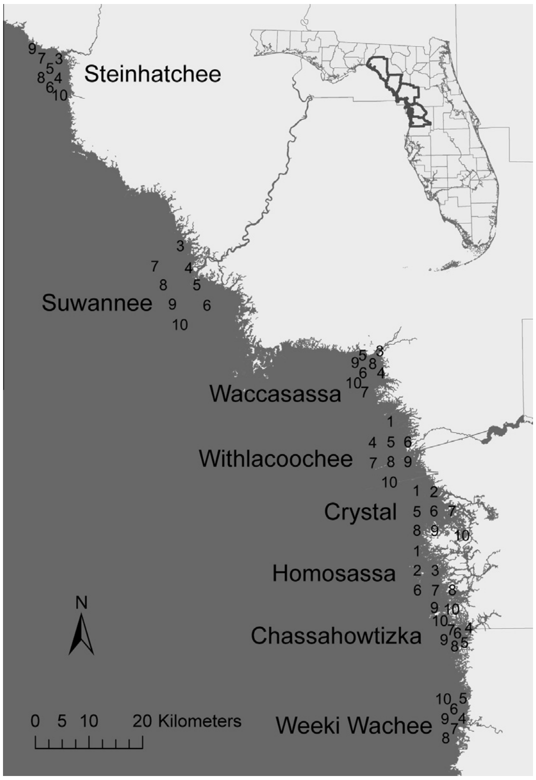

Fig. 1. Maps showing five counties in Florida (gray outlines in inset) and sampling stations (numbers) in eight coastal systems originally established by Frazer et al. (1998).

Within the study area, seagrass sampling took place at a subset of stations where water quality has been sampled since 1998 (Frazer et al., 1998). In each of the coastal systems, monthly sampling at ten stations located 0–11 km offshore (91% of stations were <6 km offshore) documented dissolved oxygen concentrations, salinities, temperatures, depths, light attenuation coefficients, chlorophyll *a* concentrations, color, and concentrations of total nitrogen and total phosphorus. Salinities were suitable (5–45) for seagrasses at 62 of the 80 stations (Doering et al., 2002; Lirman and Cropper, 2003; Touchette, 2007), and these stations were sampled to document seagrass cover and shoot density. Depths at selected stations ranged from 0.1 to 5.6 m, and mean salinities ranged from 10 to 30 between 1999 and 2011.

2.2. Light attenuation

Light attenuation was characterized with data collected between 1999 and 2011. During daylight hours, generally between 10:00 h and 15:00 h, two quantum light sensors (Li-Cor Instruments Inc.) were used with a data logger to simultaneously measure surface and subsurface flux of photosynthetically active radiation (PAR, $\mu E\ m^{-2}\ s^{-1}$). For each sampling event at each station, a light attenuation coefficient (K_d) was calculated as:

$$K_d = [\ln(I_0/I_z)]/z \quad (1)$$

where I_0 is incident irradiance at the surface and I_z is light intensity at depth (z) in meters (Kirk, 1994). When feasible, light readings were recorded at three different depths (all $\geqslant 0.5$ m) and an average K_d was calculated for use in subsequent analyses. Light attenuation coefficients were not corrected for cloud cover or sun angle. Given K_d values from monthly sampling events at each of the selected stations, the historical light regimes were characterized by calculating the percentage of incident light reaching the bottom (% SI) as:

$$\%\ \mathrm{SI} = (I_z/I_0) \times 100 = e^{(-K_d z)} \times 100 \tag{2}$$

2.3. Water quality and environmental data

Thirteen years of data from the long-term water quality monitoring program (1999–2011) were used to characterize key properties of the eight systems. Sampling took place during daylight hours, generally between 10:00 h and 15:00 h. Maximum depth was measured to the nearest 0.1 m at each station with a surveyor's pole. Water temperature, salinity, pH, and the concentration of dissolved oxygen (DO) were recorded at each station with either a YSI model 85 or Y600QS meter. Temperature was recorded to the nearest 0.1 °C, salinity to the nearest 0.1, pH to the nearest 0.01, and dissolved oxygen to the nearest 0.1 mg L^{-1}.

In addition, at each station, a surface water sample was collected in an acid-washed Nalgene bottle that was first rinsed with ambient water. Water samples were stored on ice, transported to the laboratory and frozen. A second water sample collected at each station was filtered through a 47-mm diameter Whatman Grade GF/F glass fiber filter. The filter and accompanying material were placed over silica gel desiccant, while the filtrate was collected in an acid cleaned Nalgene bottle that was first rinsed with filtrate. These samples were transported to the laboratory on ice and refrigerated.

All frozen water samples were analyzed to yield concentrations of total nitrogen (TN) and total phosphorus (TP). Total phosphorus concentrations (μg L^{-1}) were determined using the procedures of Murphy and Riley (1962) with persulfate digestion (Menzel and Corwin, 1965). Total nitrogen concentrations (μg L^{-1}) were determined by oxidizing water samples with persulfate and measuring nitrate–nitrogen concentrations with second-derivative spectroscopy (Bachmann and Canfield, 1996).

Filtered material and filtrates were analyzed to generate chlorophyll *a* concentrations (μg L^{-1}) and color (Pt–Co units), respectively. Chlorophyll *a* concentrations were determined spectrophotometrically (Method 10200 H; American Public Health Association, 1989) following pigment extraction with ethanol (Sartory and Grobbelaar, 1984). Color was measured with a spectrophotometer (American Public Health Association, 1989).

2.4. Seagrass distribution and abundance

In decreasing order, *Thalassia testudinum, Halodule wrightii, Syringodium filiforme, Halophila engelmannii,* and *Ruppia maritima* were the five most common and abundant seagrass species found in the eight coastal systems. During 2010 and 2011, at the beginning (May–June) and end (August–September) of each growing season, seagrasses were sampled at the seven to eight stations selected within each system.

To perform this sampling, a marker was placed at each station's coordinates and four quadrants were established (northwest, southwest, southeast, and northeast). In each quadrant, SCUBA divers tossed three 0.5 m × 0.5 m quadrats within 10 m of the center point to yield 12 samples of total percent cover of all seagrasses and percent cover by species recorded to the nearest 5% (Fourqurean et al., 2002). Shoots of *T. testudinum, H. wrightii, S. filiforme, H. engelmannii*, and *R. maritima* were counted in 0.25 m × 0.25 m subquadrats within each quadrat. Shoot counts were scaled to number of shoots m^{-2}. Mean shoot densities and mean percentage covers were calculated for stations by combining data from the four sampling periods.

2.5. Statistical analyses

A boundary analysis was performed to identify thresholds in light regimes linked to increases in percent cover or shoot density for common and abundant seagrass species. All thresholds were based on estimates of the median % SI reaching the bottom at each seagrass station as derived from all K_d values recorded between 1999 and 2011 (90–148 months, with 85% of stations having records from 120 or more months). The seagrass data used in the boundary analysis comprised mean percentage covers or mean shoot densities for each species as calculated from values for the 12 quadrats or subquadrats deployed at each station during the two sampling periods in both 2010 and 2011.

For each seagrass species, mean percentage covers and mean shoot densities were associated with median % SI values from the appropriate stations after the latter values were placed in ascending order. If a median % SI value was associated with a percentage cover or shoot density of zero and that median % SI was greater than the first median % SI associated with a percentage cover or shoot density greater than zero, the datapoint was excluded because it was assumed that other factors besides light limited establishment and survival of seagrasses. Once the data were organized, a moving split-window was applied and a dissimilarity index was calculated using percentage covers or shoot densities falling in the two halves of the split window (Ludwig and Tongway, 1995). In other words, the moving split-window of 6 median % SI values was split into 2 groups with 3 values each. The percentage covers or shoot densities in each group were averaged, and a squared Euclidean distance (SED) was computed as:

$$\mathrm{SED} = [(\mathrm{Mean}\ L_1)] - [(\mathrm{Mean}\ L_2)]^2 \tag{3}$$

where, Mean L_1 and Mean L_2 represent the means of the three percentage covers or shoot densities associated with the first and second groups of three median % SI values within the window of six values. After each dissimilarity index was calculated, the split-window was moved one position further along the ordered series of median % SI values, and another dissimilarity index was calculated. This process was repeated until each median % SI value was included within a split-window. Thresholds were identified as occurring within the range of median % SI values associated with the first large increases in squared Euclidean distances (for our data values from 200 to 4000).

The consistency of differences in seagrass metrics, i.e., percentage covers and shoot densities, were evaluated relative to these thresholds with Welch's *t*-tests. All mean percentage cover values and mean shoot densities equal to and below each threshold were compared to the mean percentage cover values and mean shoot densities above that threshold, with significant relationships indicated by p-values $\leqslant 0.05$.

Welch's *t*-tests also were performed on other relevant environmental and water quality data, i.e., depth, temperature, salinity, pH, color, and concentrations of DO, TP, TN, and chlorophyll *a*. For each parameter, separate *t*-tests were performed using data from stations parsed by the species of seagrasses that occurred there and by % SI values. For stations with long-term median % SI values greater than the estimated threshold for the relevant species of seagrass, Welch's *t*-tests compared depths, temperatures, salinities, pH values, and DO concentrations from stations where seagrasses were found to data from stations where seagrasses were not found. In contrast, *t*-tests performed on color values and concentrations of TP, TN, and chlorophyll *a* compared data from stations where seagrasses were found to data from stations where seagrasses were not found, regardless of the historical light regime. The different approaches reflected direct effects on seagrass survival and productivity exerted by the first set of parameters and indirect effects mediated through light attenuation associated with the second set of parameters. Although depth could have had an indirect affect on seagrasses through light attenuation, it was characterized as a parameter that directly affected seagrasses because seagrasses in shallow water could have been killed by prolonged exposure to air. If they were a limiting factor, concentrations of TN and TP could have influenced the health of seagrasses directly, but concentrations did not appear to be limiting. In fact, 8% of TN records and 23% of TP records in the study area exceeded criteria associated with healthy seagrasses in coastal bays of Maryland (640 $\mu g\,L^{-1}$ for TN and 37 $\mu g\,L^{-1}$ for TP; Wazniak et al., 2007). Therefore, we focused on indirect effects through stimulation of phytoplankton, epiphytes and macroalgae that shaded seagrasses.

3. Results

3.1. Light regimes

Calculations based on K_d values indicated that between 1999 and 2011 the amount of light reaching the bottom at the 62 sampling stations varied from <0.001% to >99% SI over the 13-year period of record. Stations off the Suwannee River consistently received the least light, with an overall median of 3% SI during the period of record (Table 1). In contrast, stations off the Homosassa River consistently received the most light, with an overall median of 33% SI during the period of record (Table 1). Light regimes not only varied among systems, but median % SI values also varied among stations within each system (Table 1). The systems with the largest range of median % SI values over the thirteen years were off the Crystal and Chassahowitzka rivers, with ranges of 35% and 33% SI, respectively (Table 1). In contrast, the Suwannee River system had the least variable values and the least amount of light reaching the bottom, with a range of 6% SI calculated from a maximum median of 7% SI at station 3 and a minimum median of 1% SI at stations 7 and 8 (Table 1). As anticipated due to spatial variation in water chemistry and productivity in the water column, light penetration varied greatly among systems and stations, which created the basis for a natural experiment.

3.2. Seagrass distribution and abundance

At least one species of seagrass was found at 35 of the 62 sampling stations during at least one of the 4 sampling periods (i.e., 56% of stations), and 30 of the 35 stations where seagrass was found supported more than one species (i.e., 86%; Table 2). *Thalassia testudinum* and *H. wrightii* were the only species that occurred in monospecific beds, and a mixture of these two species occurred at 21 stations. Three or more species were present at 18 stations that supported seagrasses, with the most common mixture comprising *T. testudinum, H. wrightii,* and *S. filiforme.*

Table 1
Variation in median percent surface irradiance reaching the bottom at stations in the eight systems from 1999 to 2011. % SI = percent surface irradiance.

System	Overall median %SI	Station	Median % SI	Range
Steinhatchee	15	8	6	24
		9	30	
Suwannee	3	7, 8	1	6
		3	7	
Wacasassa	7	3	1	22
		7	23	
Withlacoochee	5	7	2	11
		6, 9	13	
Crystal	16	1	6	35
		9	41	
Homosassa	33	8	19	33
		2	52	
Chassahowitzka	21	4	3	29
		10	32	
Weeki Wachee	31	9	21	23
		8	44	

The stations off the mouths of the Weeki Wachee and Homosassa rivers, two of the southernmost systems, had the broadest distributions of seagrass (Table 2). At least one species was found at each of the 7 sampling stations off the Weeki Wachee River and at 7 of 8 stations off the Homosassa River (Table 2). In contrast the Suwannee, Wacasassa and Withlacoochee systems, three northern systems, had less extensive coverage, with seagrass found at only 1 or 2 of the 8 sampling stations in each system (Table 2).

Thalassia testudinum and *H. wrightii* were the most common and abundant seagrasses found in the study, and *R. maritima* was the least common and abundant. In the Weeki Wachee system, *T. testudinum* and *H. wrightii* were found in up to 90.5% and up to 57.4% of the deployed quadrats, respectively (Table 2). *Thalassia testudinum* had maximum mean shoot densities ± standard deviations (SDs) of 464.9 ± 489.4 shoots m^{-2} off the Weeki Wachee River, and *H. wrightii* reached maximum mean shoot densities of 373.1 ± 1167.1 shoots m^{-2} off the Chassahowitzka River. Similarly, maximum mean percentage covers ± SDs of 19.8 ± 22.6% for *T. testudinum* and 6.5 ± 18.3% for *H. wrightii* were recorded off the Weeki Wachee and Chassahowitzka rivers, respectively (Table 2). *Ruppia maritima* was found in no more than 10.4% of the deployed quadrats in any system, with a maximum mean shoot density ± SD of 72.7 ± 377.0 shoots m^{-2} and a maximum mean percentage cover ± SD of 1.9 ± 7.8% (Table 2).

3.3. Light thresholds

Thresholds were estimated for four of the five seagrass species. Due to its limited distribution and abundance, thresholds were not estimated for *R. maritima.*

Light requirements varied among species (Table 3). *Halodule wrightii* had the highest light requirement at 25–27% SI, and *H. engelmannii* exhibited the lowest light requirement at 8–10% SI. *Syringodium filiforme* and *T. testudinum* required intermediate amounts of light, with thresholds of 8–16% SI and 18–25% SI, respectively. These thresholds showed that although seagrass species resided in the same environment and were exposed to the same temporal variation in light and water chemistry, their physiologies and growth strategies generated differing light requirements.

In general, *t*-tests confirmed differences in the abundance and distribution of seagrasses among stations where the median percent of surface irradiance at the bottom met or exceeded the threshold and stations where light penetration was less (Table 3). The tests based on percentage cover of *H. wrightii* and shoot densities of *H. engelmannii* were non-significant (Table 3).

3.4. Relationships among seagrass light thresholds and environmental conditions

In ten cases, parameters considered to directly affect seagrasses differed significantly among stations that had seagrasses and sufficient light reaching the bottom versus stations that had sufficient light penetration but lacked seagrasses (Table 4). Although statistically significant, these differences appeared unlikely to be biologically significant because they did not exceed the tolerances of seagrasses (Table 5). In addition, the directionality of the differences was not consistent across species. For example, *T. testudinum* and *H. engelmannii* were more common at deeper sites, whereas *S. filiforme* was more common at shallow sites (Table 4).

In contrast, a consistent pattern of significant differences was observed for water quality characteristics that primarily affected seagrasses by altering light availability (Table 6). In all cases, seag-

Table 2
Distribution and abundance of seagrass species. SD = standard deviation; *T. testudinum* = *Thalassia testudinum*; *H. wrightii* = *Halodule wrightii*; *S. filiforme* = *Syringodium filiforme*; *H. engelmannii* = *Halophila engelmannii*; *R. maritima* = *Ruppia maritima*.

System species	Stations with seagrass/stations sampled	Percent of quadrats with seagrass	Mean cover ± SD (%)	Mean shoot density ± SD (shoots m^{-2})
Steinhatchee				
T. testudinum	5/8	34.1	18.5 ± 30.5	215.2 ± 372.0
H. wrightii	5/8	9.6	<1.0	20.1 ± 154.9
S. filiforme	3/8	21.1	5.9 ± 16.0	154.1 ± 419.1
H. engelmannii	4/8	2.3	<1.0	7.3 ± 90.0
R. maritima	1/8	1.6	<1.0	1.9 ± 30.6
Suwannee				
H. wrightii	1/8	0.3	<1.0	<1.0
Wacasassa				
T. testudinum	1/8	9.6	<1.0	6.0 ± 32.1
H. wrightii	2/8	6.8	<1.0	6.5 ± 34.4
S. filiforme	1/8	11.7	4.6 ± 15.2	123.4 ± 425.8
H. engelmannii	1/8	0.3	<1.0	<1.0
Withlacoochee				
H. wrightii	1/8	6.8	<1.0	5.0 ± 27.3
S. filiforme	1/8	3.9	<1.0	3.5 ± 21.3
H. engelmannii	2/8	0.5	<1.0	<1.0
Crystal				
T. testudinum	4/8	18.2	7.0 ± 19.2	101.5 ± 286.9
H. wrightii	5/8	21.4	3.1 ± 11.0	158.0 ± 735.6
S. filiforme	3/8	34.9	10.9 ± 19.5	300.2 ± 516.1
H. engelmannii	4/8	11.7	1.1 ± 4.1	30.3 ± 139.4
R. maritima	1/8	1.0	<1.0	<1.0
Homosassa				
T. testudinum	5/8	34.1	11.4 ± 20.6	157.4 ± 269.4
H. wrightii	7/8	25.3	6.5 ± 18.3	253.3 ± 865.7
S. filiforme	3/8	11.5	2.4 ± 8.4	75.4 ± 287.7
H. engelmannii	2/8	4.4	1.0 ± 6.2	38.0 ± 263.0
R. maritima	2/8	3.9	<1.0	2.3 ± 18.8
Chassahowitzka				
T. testudinum	1/7	0.6	<1.0	<1.0
H. wrightii	3/7	21.1	6.4 ± 17.6	373.1 ± 1167.1
H. engelmannii	3/7	19.6	4.8 ± 12.8	182.3 ± 558.7
R. maritima	3/7	10.4	1.9 (7.8	72.7 (377.0
Weeki Wachee				
T. testudinum	7/7	90.5	19.8 ± 22.6	464.9 ± 489.4
H. wrightii	7/7	57.4	5.5 ± 9.8	331.1 ± 1173.4
R. maritima	1/7	4.8	<1.0	16.3 ± 113.6

Table 3
Estimated threshold light requirements for seagrasses and results of *t*-tests assessing differences in percentage covers and shoot densities. % SI = percent of surface irradiance; SE = standard error; * = significant at $0.01 < p \leqslant 0.05$; ** = significant at $p \leqslant 0.01$; *T. testudinum* = *Thalassia testudinum*; *H. wrightii* = *Halodule wrightii*; *S. filiforme* = *Syringodium filiforme*; *H. engelmannii* = *Halophila engelmannii*.

Species	Portion of moving window	Cover			Density		
		Threshold (% SI)	Mean (%)	SE (%)	Threshold (% SI)	Mean (shoots m^{-2})	SE (shoots m^{-2})
T. testudinum	Below threshold	18–23	0.20^{**}	0.02	20–25	0.40^{**}	0.36
	Above threshold		22.00^{**}	4.25		393.00^{**}	65.20
H. wrightii	Below threshold	25–27	2.00	0.68	25–27	32.40^{*}	13.66
	Above threshold		7.10	2.29		400.10^{*}	141.73
S. filiforme	Below threshold	8–16	0.00^{**}	0.00	8–16	0.00^{**}	0.00
	Above threshold		17.30^{**}	5.13		525.50^{**}	140.72
H. engelmannii	Below threshold	8–10	0.10^{*}	0.05	8–10	1.90	1.86
	Above threshold		3.50^{*}	1.52		142.80	65.93

rasses were present at stations with significantly lower concentrations of TN, TP, chlorophyll *a* and color.

4. Discussion

4.1. Seagrass distribution and abundance

Seagrass distribution and abundance in the study region showed a direct relationship with the percent of surface irradiance (% SI) reaching the bottom. Systems where median light penetration over 13 years was greater than 20% SI (Homosassa and Weeki Wachee) had the most abundant and diverse seagrass beds, with all species found and a maximum of 90% of quadrats containing seagrasses. Systems such as Suwannee, Wacasassa, and Withlacoochee, with overall median values of 3–7% SI, had little to no seagrass. At a maximum, only 11% of quadrats contained seagrasses in these systems. Systems that were more variable, i.e., stations exhibited both low and high median % SI values, yielded seagrass abundances between the two extremes.

Table 4
Means for water quality parameters with direct effects on seagrasses and results of *t*-tests comparing those parameters at stations with seagrass and stations with suitable light but no seagrass. * = significant at $0.01 < p \leqslant 0.05$; ** = significant at $p \leqslant 0.01$; Temp = water temperature; Sal = salinity; DO = dissolved oxygen concentration; *T. testudinum* = *Thalassia testudinum*; *H. wrightii* = *Halodule wrightii*; *S. filiforme* = *Syringodium filiforme*; *H. engelmannii* = *Halophila engelmannii*.

Species	Seagrass	Light	Mean				
			Depth (m)	Temp. (°C)	Sal	DO (mg L^{-1})	pH
T. testudinum	Present		1.4^{**}	23.0	24.2^{**}	7.1^{*}	8.07^{**}
	Absent	⩾Threshold	1.0^{**}	23.2	19.1^{**}	7.0^{*}	7.97^{**}
H. wrightii	Present		1.3	23.1	22.3^{**}	7.1	8.03^{*}
	Absent	⩾Threshold	1.3	22.5	29.6^{**}	7.0	8.07^{*}
S. filiforme	Present		1.2^{**}	22.8	25.2^{**}	7.1	8.02
	Absent	⩾Threshold	1.3^{**}	23.1	21.3^{**}	7.0	8.01
H. engelmannii	Present		1.5^{**}	22.9	22.3	7.0	7.98^{**}
	Absent	⩾Threshold	1.2^{**}	23.1	22.3	7.0	8.02^{**}

Table 5
Values of water quality parameters that may stress seagrasses. DO = dissolved oxygen concentration; *T. testudinum* = *Thalassia testudinum*; *H. wrightii* = *Halodule wrightii*; *S. filiforme* = *Syringodium filiforme*; *H. engelmannii* = *Halophila engelmannii*.

Species	Characteristic	Values of concern	References
T. testudinum	Salinity	Requires > 17, optimum 30	[a]
	Depth	Deeper than mean low tide (0.4 m here)	[b,c]
	pH	7.8–9.0	[d]
	Temperature	Optimum 30 °C	[a]
	DO	Requires > 5 mg L^{-1}	[e]
H. wrightii	Salinity	Requires > 3.5, optimum 30	[a]
	Depth	Deeper than mean low tide (0.4 m here)	[b,c]
		Can survive short periods of exposure	[f]
	pH	7.8–9.0	[d]
	Temperature	Optimum 30 °C	[a]
	DO	Requires > 5 mg L^{-1}	[e]
S. filiforme	Salinity	Requires > 17, optimum 35	[a,g]
	Depth	Deeper than mean low tide (0.4 m here)	[b,c]
		Can survive short periods of exposure	[h]
	pH	7.8–9.0	[d]
	Temperature	Optimum 30 °C	[a]
	DO	Requires > 5 mg L^{-1}	[e]
H. engelmannii	Salinity	Survives 9–35, optimum 25	[i]
	Depth	Deeper than mean low tide (0.4 m here)	[b,c]
	pH	7.8–9.0	[d]
	Temperature	Optimum 30 °C	[a]
	DO	Requires > 5 mg L^{-1}	[e]

[a] Iverson and Bittaker (1986).
[b] Hemminga and Duarte (2000).
[c] National Oceanic and Atmospheric Administration (2012).
[d] Invers et al. (1997).
[e] Wazniak et al. (2007).
[f] Zieman and Zieman (1989).
[g] McMahan (1968).
[h] Moore (1963).
[i] Dawes et al. (1987).

In these systems, i.e., Steinhatchee, Crystal, and Chassahowitzka, a maximum of 35% of quadrats contained seagrasses. Water quality in systems with abundant seagrasses and systems with less seagrass varied as expected. Systems with low amounts of seagrass (Suwannee, Wacasassa, and Withlacoochee) had higher color and concentrations of nitrogen, phosphorus, and chlorophyll *a*.

Although threshold % SI values accurately predicted systems where seagrass were found, there were stations within these systems that had sufficient light but no seagrasses. This observation highlighted the fact that although light was often a limiting factor, it was not the only factor affecting seagrasses. The absence of a suitable substrate represented another key influence because, for example, seagrasses would not have grown on limestone outcrops. Temperature, salinity, and DO could have had a profound influence on seagrass distribution and abundance (Lee et al., 2007; Wazniak et al., 2007); however, analyses did not yield consistent evidence for effects from these parameters.

In contrast, analyses of water quality characteristics considered to indirectly affect seagrasses by altering light regimes did yield a consistent pattern. In all cases, results highlighted the likelihood that increased nutrient concentrations were related to increased chlorophyll *a* concentrations, which in combination with high levels of color, led to shading of seagrasses. In fact, Jacoby et al. (2011) showed that chlorophyll concentrations in these systems were positively correlated with concentrations of total nitrogen and total phosphorus ($r^2 = 0.33$ and 0.85, respectively, for $\log_{10}$-transformed data). Similar relationships have been reported previously, with Tomasko et al. (2001) having documented 45% and 29% increases in nitrogen and chlorophyll *a* concentrations, respectively, in Lemon Bay, Florida, which caused light attenuation coefficients to increase by 9%.

Table 6
Means for water quality parameters with indirect effects on seagrasses and results of *t*-tests comparing those parameters at stations with seagrass and stations with suitable light but no seagrass. ** = significant at $p \leqslant 0.01$; TN = total nitrogen concentration; TP = total phosphorus concentration; Chl *a* = chlorophyll *a* concentration.

Species	Seagrass	Mean			
		TN ($\mu g\ L^{-1}$)	TP ($\mu g\ L^{-1}$)	Chl *a* ($\mu g\ L^{-1}$)	Color (Pt–Co units)
T. testudinum	Present	424.5^{**}	13.5^{**}	2.4^{**}	14.8^{**}
	Absent	477.3^{**}	34.3^{**}	6.1^{**}	26.5^{**}
H. wrightii	Present	439.5^{**}	17.0^{**}	3.1^{**}	16.3^{**}
	Absent	480.1^{**}	35.0^{**}	6.6^{**}	28.9^{**}
S. filiforme	Present	404.7^{**}	18.6^{**}	3.3^{**}	17.0^{**}
	Absent	469.5^{**}	28.0^{**}	5.0^{**}	23.1^{**}
H. engelmannii	Present	426.4^{**}	17.8^{**}	3.6^{**}	16.8^{**}
	Absent	467.1^{**}	28.8^{**}	5.0^{**}	23.5^{**}

4.2. Seagrass light requirements

Light thresholds varied among species and across the systems studied, and they differed from previously reported thresholds for the same species at other locations. Light equivalent to 18–25% SI was required by the most prominent seagrass in the region, *T. testudinum*. This result was very similar to previously reported values: 18.2% SI in Lemon Bay, Florida found by taking the average of the % SI reaching the deepest parts of the study region where *T. testudinum* was found (Tomasko et al., 2001); 20–25% SI in Tampa Bay, Florida calculated in the same manner (Tomasko and Hall, 1999); and 20% SI in Corpus Christi Bay, Texas found by calculating the effects of an in situ light reduction experiment (Czerny and Dunton, 1995). In contrast, thresholds reported for *H. wrightii* differed by up to 19% SI: 33% SI reported in the Indian River Lagoon, Florida based on the median % SI at the depth limit of beds (Steward et al., 2005); 18% SI in San Antonio Bay, Texas based on a whole plant model that assumed light was the dominant factor affecting seagrass production and growth (Dunton, 1994); 14% SI in Perdido Bay, Alabama based on the effects of in situ shading (Shafer, 1999); and 24–27% SI in this study. The threshold for *S. filiforme* reported here, 8–15% SI, is lower than 20% SI calculated for the Indian River Lagoon, Florida by combining seagrass depth limits and an optical model that calculated absorption and scattering coefficients (Gallegos and Kenworthy, 1996) and 19.2% SI documented for northwest Cuba as the mean percent light at the maximum depth limit of *S. filiforme* (Dennison et al., 1993). Limited research on the light requirements of *H. engelmannii* suggested that this species was an understory plant with small rhizomes and a lower respiratory demand that allowed it to survive under lower irradiances (Duarte, 1991). Dawes et al. (1987) showed that *H. engelmannii* at Indian Bluff Island, Florida had a compensation point of $60\ \mu E\ m^{-2}\ s^{-1}$. Given that the compensation point essentially represented the minimum amount of light required for survival, light intensities capable of supporting the growth of *H. engelmannii* were expected to be higher. In fact, combining average surface irradiance for the stations where *H. engelmannii* was found in the study area and the threshold estimated for this species, 8–10% SI, equated to photosynthetically active radiation fluxes of 104–131 $\mu E\ m^{-2}\ s^{-1}$, which is 1.75–2.00 times the estimated compensation point. An even higher threshold, 23.7% SI, was reported for *H. engelmannii* in northwest Cuba (Dennison et al., 1993). Spatial variation in estimated light thresholds may have reflected adaptation to light regimes at the specific locations (Duarte, 1991).

In addition to spatial variation in threshold light requirements, other data suggested that historical and current light regimes interacted with seagrass physiology (especially growth and respiration) and diverse environmental influences to determine the light requirements of seagrasses. Duarte (1991) showed how growth strategies and architecture of seagrass species differed, which led to varying patterns in abundance in different environments. In fact, he distinguished two main growth strategies, pioneer species that grew quickly and climax species that were long-lived. He also explained how larger rhizomes increased respiratory demands of seagrasses, and how these increased demands consequently increased requirements for light. Duarte et al. (2007) subsequently demonstrated how environmental factors can have an effect on light requirements of seagrasses. In particular, he indicated that seagrasses colonizing deeper areas in turbid waters did not grow at depths predicted by equations derived from data collected in clearer waters. Thus, species subjected to different levels of turbidity may have received not only less light, but also light that was less suitable for photosynthesis. Additionally, salinity could have affected light requirements of seagrasses, with most species displaying optimum productivity in oceanic salinity and reduced photosynthesis in suboptimal salinities (Torquemada et al., 2005; Lirman and Cropper, 2003). For example, *Halophila johnsonii* displayed lower light compensation and saturation points and elevated photosynthetic efficiency at optimal salinities; but efficiency decreased significantly and light requirements rose at points above and below this optimal level (Torquemada et al., 2005). Nutrient availability also has been shown to affect growth and potentially the light requirements of seagrasses, with Udy and Dennison (1997) having documented that fertilization led to different growth rates for seagrass species due to different amino acid compositions and nutrient content in tissues. In addition to water quality, physical conditions also could have affected the abundance and distribution of seagrasses. For example, Fonseca and Bell (1998) showed that percent cover declined with increasing wave exposure and current speed due to disturbance of sediment and negative effects on seagrass rooting and colonization. Larkum et al. (2006) linked longer residence times to increased retention of nutrients, which made the affected systems more susceptible to eutrophication and a subsequent reduction in the light available to seagrasses. Regardless of the complexity of interactions, knowledge of light requirements for seagrasses represents a valuable element in managing coastal systems sustainably.

4.3. Management of seagrasses

Although threshold light requirements for seagrasses vary, knowing those requirements remains important for managing and protecting seagrass habitats and the ecosystem services they deliver. Seagrasses exhibit higher light requirements than other photoautotrophs (Duarte, 1995); therefore, managing habitats to meet their light requirements will not only benefit seagrasses, but also ensure sufficient light for other estuarine primary producers. Protecting seagrasses also benefits numerous other organisms because seagrass habitats support high densities of fauna by providing protection and food (Orth et al., 1984). In large part, due to their sensitivity and ecological importance, seagrasses can and do play a central role in current management approaches to protecting coastal systems.

Seagrass light requirements can serve as a valuable metric of a system's health and a basis for estimating sustainable nutrient concentrations. For example, seagrass light requirements can be used to identify non-detrimental chlorophyll levels that can be linked to appropriate nutrient concentrations. In fact, light requirements of seagrasses can be incorporated into two primary approaches to setting nutrient criteria: the reference comparison and response based approaches (USEPA, 2009). The reference comparison approach uses nutrient concentrations from an area with healthy seagrass as a guide for reductions in an area in need of restoration based on the fact that nutrients affect chlorophyll *a* concentrations and alter water transparency. The response based approach determines maximum allowable nutrient concentrations from rigorous cause-effect relationships between nutrients and both an initial biological response, chlorophyll *a* concentrations, and a subsequent biological response, healthy seagrasses.

At this time, seagrass light requirements are being used to manage water quality in coastal systems. Wazniak et al. (2007) and Stevenson et al. (1993) demonstrated how knowledge of seagrasses light requirements determined water quality thresholds for Chesapeake Bay, Virginia and how improving water quality to meet these thresholds led to improvement in seagrasses and the system as a whole. In the Indian River Lagoon, management targets for nutrient loads were based on data collected from reference sites and times that supported robust amounts of seagrass (Steward et al., 2005). In Tampa Bay, managers have used seagrass light requirements and reference periods to develop numeric nutrient criteria by relating nutrient loading, ambient nutrient concentrations, chlorophyll *a* concentrations, and seagrass light requirements (Janicki Environmental Incorporated, 2011).

5. Conclusions

Light requirements are a key determinant of the distribution and abundance of seagrasses, although other factors can play important roles. Light requirements vary among species and locations, with light history playing an integral role in the expression of a threshold. Furthermore, seagrasses were less common and abundant at locations where higher concentrations of phosphorus, nitrogen, chlorophyll *a*, and color indicated reduced water quality. Applying and improving knowledge of the interactions among water quality, light attenuation and seagrass health will be critical for conservation and restoration efforts.

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