

Relative effects of physical and small-scale nutrient factors on the distribution of tropical seagrasses in the Great White Heron National Wildlife Refuge, Lower Florida Keys

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ABSTRACT

We tested the relative effects of physical factors such as exposure time and water depth as well as nutrient availability on *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* distribution within the Great White Heron National Wildlife Refuge, Florida Keys. We quantified the percent cover of each seagrass species in 1-m² plots ($n = 325$) along intertidal and shallow subtidal flats adjacent to Upper Harbor Key Water Keys and Howe Key. We used model selection to evaluate the effects of physical parameters and water column nutrients on the percent cover and composition of seagrass species within plots. Best models were selected based on lowest Akaike's information criteria (AIC) values and maximum model weights (ω_i). We found that the presence of the other species, distance to nearest island and time of exposure during diurnal low tides best explained the distribution of *T. testudinum* ($\omega_i = 0.44$). Model averaged parameter estimates (β) showed that *H. wrightii* and *S. filiforme* had the greatest negative influence on *T. testudinum* ($\beta = -0.396, -0.278$, respectively). *H. wrightii* distribution was affected strongly by the presence of the other species, distance to Pine Channel, exposure time and mean lower low water (MLLW) ($\omega_i = 0.56$) with *T. testudinum* and *S. filiforme* exerting the greatest negative influences ($\beta = -0.450, -0.184$, respectively). The best model indicated that *S. filiforme* was strongly influenced by the other species, distance to Pine Channel and MLLW ($\omega_i = 0.5$). Model averaging indicated that *S. filiforme* was associated with deep water ($\beta_{\text{MLLW}} = -28.0.018$). Our study showcased that small scale (<100 m) habitat heterogeneity influenced the composition of seagrass communities.

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1. Introduction

Seagrass ecosystems are critically important because many species of threatened fish, reptiles and birds depend on them during some stage of their life cycle (Hughes et al., 2009). Understanding the factors that alter the abundance and distribution of species is an important focus of ecology particularly for foundation species such as seagrasses. For example, light as a function of water depth

is an established factor that determines habitat suitability for seagrasses (Robbins and Bell, 2000; Hale et al., 2004). Whereas, the risks associated with desiccation during low tide (Leuschner and Rees, 1993; Vermaat et al., 1993; Seddon and Cheshire, 2001) in structuring seagrass communities (Lan et al., 2005; Campbell et al., 2006) is less well understood. Fonseca and Bell (1998) showed that total seagrass percent cover tended to decrease while the ratio between *Halodule wrightii* and *Zostera marina* tended to increase with increased relative exposure index (REI) values. On the other hand, it is less clear how factors such as current speed (Fagherazzi and Wiberg, 2009) and erosion (Erftmeijer and Lewis III, 2006) may reduce habitat suitability for some seagrass species but not others. Understanding the relative influence of physical forces that act on seagrass community composition will provide resource managers with ecological insight that can be applied to maximize the success of seagrass restoration efforts and to predict the response of seagrasses by natural and anthropogenic changes in the physical environment over time.

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Degradation of seagrass beds is occurring worldwide (Lotze et al., 2006) with devastating impairment to ecosystem function (Coll et al., 2011) and reduction in coastal protection from waves (Koch et al., 2009). Nutrient enrichment is among the top threats to the ecosystem function of seagrass beds (McGlathery et al., 2013). Excessive input from sources such as fertilizers (Howarth et al., 2002) and sewage (Ward-Paige et al., 2005) stimulate phytoplankton blooms (Ferreira et al., 2011), macroalgae (Hauxwell et al., 2001; Kopecky and Dunton, 2006), and periphyton (Tomasko and Lapointe, 1991; Lapointe et al., 1994). These factors block light and reduce seagrass productivity (Nelson, 2009). Nutrient enrichment has been known to decrease habitat suitability for a theoretical climax community dominated by *Thalassia testudinum* (e.g., Thayer et al., 1994) to one dominated by *H. wrightii* (Fourqurean et al., 2005). Such changes also affect seagrass-dependent species at higher trophic levels. For example, Ferguson (2008, 2009), demonstrated that nutrient-driven changes in seagrass structural composition altered benthic invertebrate community composition and resulted in loss of larger bodied invertebrates. Studies that evaluate the role of nutrient enrichment and the extent of changes in seagrass community composition have wide application to the conservation of marine fauna and are critically needed for marine sanctuaries.

We applied Akaike's information criteria (AIC) to generalized linear models to evaluate the importance of physical factors and nutrient availability and on three species of seagrass: *T. testudinum*, *H. wrightii* and *Syringodium filiforme* within the Great White Heron National Wildlife Refuge, Florida Keys. We hypothesized that (i) seagrass plots closest to elevated concentrations of water column of nitrogen and phosphorus would be dominated by *H. wrightii* and *S. filiforme* (ii) seagrasses plots farther from elevated nutrient concentrations would be dominated by *T. testudinum* and affected most strongly by physical factors.

2. Methods

2.1. Study area

This study was conducted in intertidal and shallow subtidal (<3 m) seagrass flats adjacent to Upper Harbor Key (24°48'40.19"N, 81°26'26.67"W), Water Keys (24°46'40.28"N, 81°27'26.91"W) and Howe Key (24°43'48.22"N, 81°25'51.37"W) within the Great White Heron National Wildlife Refuge (hereafter referred to as: the refuge) and the Florida Keys National Marine Sanctuary (FKNMS), Florida, U. S. A. (Fig. 1). Data on water column nutrients, chlorophyll *a* concentrations, seagrass percent cover and periphyton percent cover were collected in April and May 2012 (spring), July 2012 (summer), October 2012 (fall), and February 2013 (winter). Additional seagrass and periphyton data were collected in April–May 2013 (spring). Assessments of sediment organic content were performed in October 2012 (fall) and February 2013 (winter). Furthermore, previous research suggested possible anthropogenic nitrogen and phosphorus concentration gradients from Howe Key to Upper Harbor Key (local sewage discharges) or from the Everglades (agricultural runoff) (Lapointe et al., 2004).

2.2. Quantification of seagrass abundance and distribution

From July 2012 to April 2013, a total of 325 plots were assessed (Fig. 1) and the percent cover of *T. testudinum* (turtle grass), *H. wrightii* (shoal grass), and *S. filiforme* (manatee grass) were quantified for each plot. In summer 2012, plots were selected by a snorkeler that swam approximately 15 meters from a boat. At each plot, the percent cover of each seagrass species was quantified using a 1 m² quadrat, gridded into 100, 10 cm cells. The presence of each

species was evaluated for each cell and percent cover was the sum of all cells. The snorkeler then haphazardly chose a direction and swam another ~15 m. This process was repeated five times per site. Additionally in summer 2012, we assessed percent cover on a wider area than could be covered by a swimming snorkeler. Plots were selected by anchoring a boat approximately every 200 m along four parallel transects which began 50–100 m from the mangrove islands. Snorkelers placed a quadrat on the benthos immediately off the starboard side. To map data, the coordinates of each plot were taken from the boat using a handheld Garmin GPSMap® 78 sc centered above the quadrat. Sixteen plots were assessed for Upper Harbor Key and Howe Key only. Due to time constraints, Water Keys was not assessed using a grid; only haphazard plots were collected during that time period. In fall 2012 and winter 2013, 30 GPS points spaced 50 m apart and forming a grid 250 m by 300 m were established using Google™ Earth. A boat was driven as close to the point as possible. Data and coordinates within each plot were collected as above.

To increase our sample size for seagrass and periphyton percent cover and take into account physical factors known to affect seagrass distribution we changed our seagrass plot selection methods in spring 2013. We sought to compare relative water depth across sites, thus we used mean lower low water (MLLW) from a digital elevation map (DEM) created in 1997 by the NOAA as part of the Florida Keys Benthic Habitat Mapping Project. Since updated maps were not available, we assumed that elevation did not change in the interim. Positive values represent points above sea level; whereas, negative values were below sea level. One hundred and twenty one plots along 21 transects were established along MLLW gradients. The origins of each transect were selected randomly from points that fell within 50 m of the channel and ran 400–700 m along depth gradients. Plots were spaced 100 m apart and percent cover of seagrasses and periphyton were quantified as above.

2.3. Quantification of periphyton percent cover

We quantified the percent cover of large periphyton (greater than 2 cm) and small periphyton (less than 2 cm long) by counting the number of cells within each 1 m² plot (see above) where large and small periphyton on seagrasses were observed even once within each cell. For 122 of the 325 total plots, percent cover was calculated as the sum of the number of cells for each periphyton class. We distinguished the two categories because large periphyton have been shown to uproot seagrass plants (Borowitzka and Lethbridge, 1989 as cited in Fong et al., 2000). In summer and fall 2012 and winter 2013 a subset of five random seagrass plots were selected and the percent cover of periphyton for those plots were quantified. In spring, 2013 at 102 plots where seagrass was quantified percent cover of large and small periphyton were also quantified.

2.4. Quantification of water column dissolved nutrients and chlorophyll *a*

2.4.1. Water column dissolved nutrients

To obtain a snapshot of nutrient concentrations for each site we quantified water column nutrient concentrations. The study area has four possible nutrient sources; the Gulf of Mexico (Gibson et al., 2008), Everglades discharges (Brand, 2002; Lapointe et al., 2004), sewage and aerobic treatment units near the inhabited Big Pine Key (Lapointe et al., 2004) and bird guano from roosting and nesting islands (Calle et al., 2014). We quantified the instantaneous nutrient concentrations of each site during four sampling seasons but we did not quantify nutrient concentrations with respect to distance to known roosting and nesting sites. Water samples were collected in May 2012 (spring), July 2012 (summer) October 2012 (fall), and

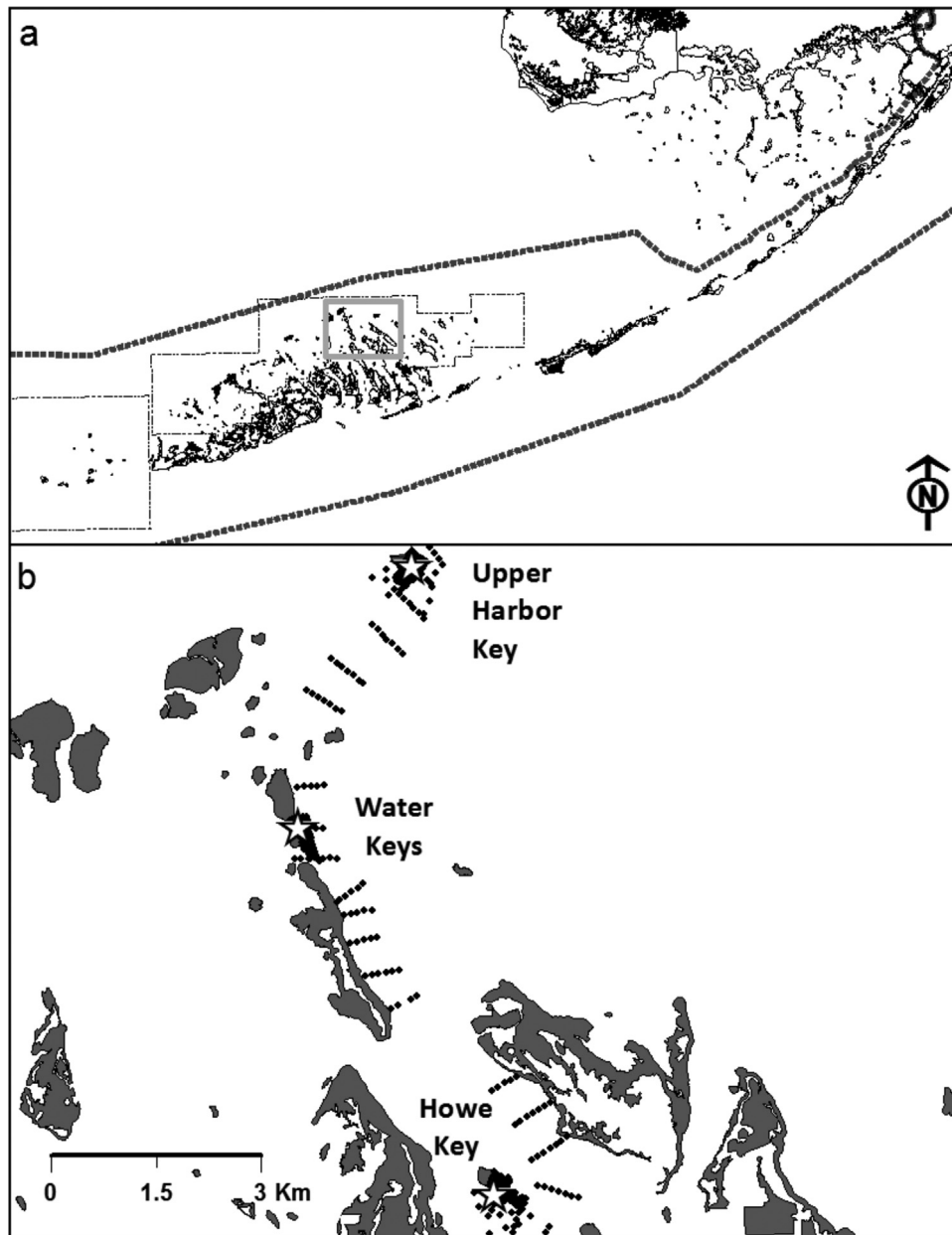


Fig. 1. Map of study area and plots visited within the Great White Heron National Wildlife Refuge. a: Dark dashed line represents the FKNMS boundary. Light dashed line represents the Great White Heron National Wildlife Refuge Boundary. Solid grey rectangle shows the extent of the study area within the refuge. b: Seagrass plot locations within each of our three study sites. Star icons represent approximate locations of water samples.

February 2013 (winter). Three grab-samples were collected per site during each season ($n = 12$ total per site) by collecting on-site water by dipping 500 ml high-density polyethylene bottles approximately 45 cm below the surface of the water. Samples were stored on ice in a dark cooler until returned to the laboratory. Within three hours of collection, samples were homogenized by inverting the bottle three times, and a 120 ml aliquot of sample water was withdrawn using a 60-cc acid washed syringe. Water was filtered through a Whatman™ 25 mm GF/F filter. The first 20 ml was discarded and the subsequent 100 ml aliquot was transferred to a 125 ml acid washed bottle and immediately frozen. Water samples and filter paper were kept frozen at -21°C until packed on dry ice in a cooler and sent to the Chesapeake Biological Laboratory for analysis. Water samples were analyzed for total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). Methodological details regarding nutrient analyses have been described elsewhere (Green et al., 2015).

2.4.2. Water column chlorophyll *a*

To estimate phytoplankton biomass, filter papers from the water column samples were analyzed for chlorophyll *a* ($n = 12$ per site). Chlorophyll *a* concentrations were determined fluorometrically according to the methods outlined in (Strickland and Parsons, 1972). For additional details regarding analytical methods please see: Green et al. (2015).

2.5. Quantification of sediment organic content

In fall (2012) and winter (2013), sediment organic content was quantified ($n = 20$ per site). At each site, 10 plots were haphazardly selected and one sawed-off 60-cc syringe (3 cm diameter, 5 cm deep) was used to collect sediments at each plot ($n = 10$). Sediments were dried at 60°C in a forced air oven then heated to 500°C in a

Table 1
Correlation matrix of all candidate physical and biotic environmental variables, as a screening tool prior to model construction. Only parameters within the bold box were included in the global models.

	Epi < 2	Epi > 2	<i>T. tes</i>	<i>H. wri</i>	<i>S. fil</i>	REI	MLLW	Dis Isl	Dis Pin	Expos	Sed org	Chl <i>a</i>	TDN	TDP
Epi < 2		0.47	0.13	−0.15	0.23	0.03	−0.25	0.45	−0.04	−0.19	0.09	0.14	−0.15	−0.09
Epi > 2	0.47		−0.09	−0.09	0.28	0.14	−0.23	0.37	0.12	−0.13	−0.06	0.06	−0.15	0.06
<i>T. tes</i>	0.13	−0.09		−0.38	−0.16	0.07	−0.11	0.27	0.09	−0.27	0.14	0.10	−0.05	−0.14
<i>H. wri</i>	−0.15	−0.09	−0.38		−0.14	−0.12	0.09	−0.07	−0.23	−0.04	0.10	0.10	−0.09	−0.10
<i>S. fil</i>	0.23	0.28	−0.16	−0.14		0.17	−0.31	0.15	0.10	−0.11	−0.05	0.04	−0.11	0.06
MLLW	−0.25	−0.23	−0.11	0.09	−0.31	−0.03		−0.35	0.15	0.64	−0.09	−0.09	0.36	0.09
Dis Isl	0.45	0.37	0.27	−0.07	0.15	−0.004	−0.35		−0.09	−0.28	0.27	0.37	−0.38	−0.25
Dis Pin	−0.04	0.12	0.09	−0.23	0.10	0.74	0.15	−0.09		0.1	0.26	−0.24	−0.01	0.52
Expos	−0.19	−0.13	−0.27	−0.04	−0.11	−0.18	0.64	−0.28	0.1		−0.3	−0.38	0.36	0.30
REI	0.03	0.14	0.07	−0.12	0.17		−0.03	−0.004	0.74	−0.18	0.013	0.33	−0.51	0.001
Sed org	0.01	−0.17	0.14	0.06	−0.14	−0.35	−0.06	0.05	−0.64	−0.11		0.39	−0.0002	−0.83
Chl <i>a</i>	0.14	0.06	0.10	0.10	0.04	0.33	−0.09	0.37	−0.24	−0.38	0.85		−0.92	−0.99
TDN	−0.15	−0.15	−0.05	−0.09	−0.11	−0.51	0.36	−0.38	−0.01	0.36	−0.58	−0.92		0.56
TDP	−0.09	0.06	−0.14	−0.10	0.06	0.001	0.09	−0.25	0.52	0.30	−0.99	−0.99	0.56	

Epi < 2 = % cover epiphytes less than 2 cm long, Epi > 2 = % cover epiphytes greater than 2 cm long, *T. tes* = % cover *T. testudinum*, *H. wri* = % cover *H. wrightii*, *S. fil* = % cover *S. filiforme*, REI = relative exposure index, MLLW = mean lower low water, Dis Isl = distance to nearest island, Dis Pin = distance to pine channel, Expos = diurnal exposure time, Sed org = sediment organic content, Chl *a* = chlorophyll *a*, TDN = total dissolved nitrogen, TDP = total dissolved phosphorus.

muffle furnace for 7 h. Organic content was quantified by loss on ignition (Heiri et al., 2001).

2.6. Physical parameters

We mapped the georeferenced seagrass plots in ArcMap™ and calculated the REI for each plot (Fonseca and Bell, 1998). To calculate the REI, we utilized spatial analysis tools to quantify effective fetch for 360 points around each plot in ArcMap™. This differed from Fonseca and Bell (1998) who calculated distance to island for 40 points around each plot. We incorporated wind speed data over 7 years (2005–2012). Wind speed data was obtained from NOAA's National Data Buoy Center Station VCAF1 at Vaca Key approximately 32 km from Howe Key.

Previous researchers documented halo effects around mangrove islands (Powell et al., 1991) attributed to guano from roosting birds (Fourqurean and Zieman, 1992) therefore we assessed the percent cover of seagrass with respect to distance to nearest island, which included both roosting islands and non-roosting islands (Calle et al., 2014).

Lapointe et al. (2004) found evidence of eutrophic conditions associated with septic tank leakage in seagrass communities in Spanish Harbor Channel on the east side of Big Pine Key and

approximately 5 km from our study area. To estimate the effects of eutrophication on seagrass abundance we calculated the distance of each plot from Pine Channel (24°41'32.712", −81°23'31.2"), a point in close proximity to a sampling station used by Lapointe et al. (2004). Distance to nearest island and distance to Pine Channel were quantified using the proximity tool in ArcMap™.

We quantified the relationship between water depth and seagrass abundance by mapping all georeferenced seagrass plots on the DEM in ArcMap™ and utilizing the extract multi-values to points tool. Negative MLLW values were below MLLW and indicated persistently deep water. Whereas, positive values were above MLLW on average and indicate dry land or intertidal zones.

Since these data were collected in intertidal and shallow subtidal seagrass flats, the duration of diurnal time that each plot was completely exposed to air was included as a parameter. Exposure time was estimated using a Tidal model of shallow water availability (TiMSA) (Calle et al., 2014). The TiMSA utilizes data from tidal gauges near the study area and approximates the rate of change over one year within Thiessen polygons for points across the study area. The exposure time was evaluated by extracting the mean exposure time for each seagrass plot using the extract multi-values to points tool in ArcMap™. Low values indicated plots that were rarely or never exposed during tidal fluctuation.

Table 2
Final set of models predicting percent cover for each seagrass species during 2012–2013 in the Lower Florida Keys: model averaged parameter estimates (β), 95% confidence intervals, variance inflation factors (VIF) and parameter weights ($\Sigma\omega_i$).

Species	Factor	β	2.50%	97.50%	VIF	$\Sigma\omega_i$
<i>T. testudinum</i>	% cover <i>H. wrightii</i>	−0.396	−0.5	−0.3	1.1	1.0
	% cover <i>S. filiforme</i>	−0.278	−0.4	−0.2	1.2	1.0
	Distance to nearest island (m)	0.033	0.0	0.0	1.2	1.0
	Distance to Pine Channel (m)	0.001	0.0	0.0	1.1	0.5
	Exposure time (min)	−0.063	−0.1	0.0	1.7	1.0
	Mean lower low water (m)	13.932	1.6	26.3	2.0	0.8
<i>H. wrightii</i>	% cover <i>T. testudinum</i>	−0.450	−0.56	−0.34	1.23	1.00
	% cover <i>S. filiforme</i>	−0.184	−0.31	−0.06	1.22	0.97
	Distance to nearest island (m)	0.009	−0.01	0.02	1.23	0.39
	Distance to Pine Channel (m)	−0.002	0.00	0.00	1.08	0.99
	Exposure time (min)	−0.055	−0.08	−0.03	1.81	1.00
	Mean lower low water (m)	19.963	6.58	33.35	2.00	0.97
<i>S. filiforme</i>	% cover <i>T. testudinum</i>	−0.265	−0.37	−0.16	1.39	1.00
	% cover <i>H. wrightii</i>	−0.158	−0.25	−0.06	1.30	0.98
	Distance to nearest island (m)	0.015	0.00	0.03	1.22	0.79
	Distance to Pine Channel (m)	0.001	0.00	0.00	1.09	0.94
	Exposure time (min)	0.007	−0.02	0.03	1.92	0.29
	Mean lower low water (m)	−28.018	−38.49	−17.55	1.92	1.00

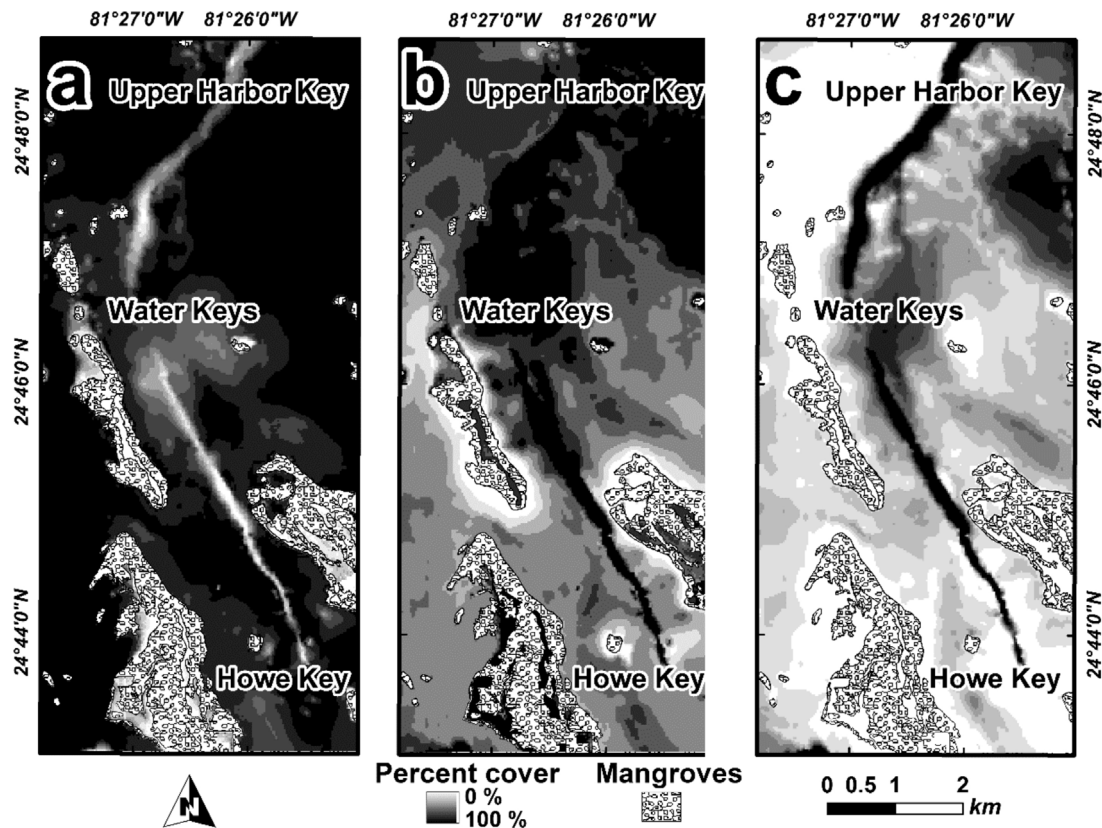


Fig. 2. Predictive maps of the percent cover for each seagrass species. a: *Thalassia testudinum*, b: *Halodule wrightii* and c: *Syringodium filiforme*.

2.7. Data analysis

While seagrass abundance may change seasonally in Florida (Robbins and Bell, 2000) seagrass populations within the FKNMS have tended to remain stable (Hall et al., 1999; Green et al., 2015). Therefore, we chose to evaluate data spatially and not temporally. Nutrient, chlorophyll *a* and sediment organic content data were averaged across all seasons for each site.

All parameters were initially screened based on their Pearson correlation coefficient (Table 1). Explanatory variables with a correlation coefficient ≥ 0.2 for at least one of the three seagrass species were retained (Table 1). When independent variables had correlation coefficients greater than 0.5 one of the variables are not included in model selection to reduce multicollinearity. This method is stricter than the 0.7 recommended by Burnham and Anderson (1998). One exception was the relationship between MLLW and exposure time at low tide (Table 1). We retained MLLW due to the well documented importance of water depth on influencing seagrass distribution (e.g., Fourqurean et al., 2003). Whereas, we wanted to evaluate the relative importance of a previously untested parameter (exposure time during diurnal low tide). Thus, we added both parameters to our models. Moreover, variance inflation factors (VIF) were less than 5 suggesting low multicollinearity among the parameters (Burnham and Anderson, 1998) (Table 2).

Model selection was applied to generalized linear models (GLM) with Gaussian distributions for each seagrass species. Best explaining models were identified using Akaike's information criteria corrected for small sample sizes (AICc) (Burnham and Anderson, 1998; Uhrin et al., 2011). This approach is based on the principle of parsimony used in linear regression (e.g., Soranno et al., 2008). However, it identifies the best approximating models through the evaluation of the maximum likelihood (e.g., Ralph et al., 2013) rather than reduction of error terms (Friedlander et al., 2007). We

used R version 3.0.1 (R Core Team, 2013) packages mcgv (Wood, 2000), MuMIn (Barton, 2013) and car (Fox and Weisberg, 2011). A global model was constructed for each seagrass species. Each species was tested against the other species as well as: the distance to nearest island (m), distance to Pine Channel (km), exposure time (min) and MLLW (m). A dredge function (Barton, 2013) was used to create subset of models from the global model. For each seagrass species, 64 models were developed. The null, best explaining, global and models with $\Delta_i < 5$ (Burnham and Anderson, 1998) are presented along with the best model that included only the physical parameters. Model averaging was used to generate model averaged parameter estimates; parameter estimates were considered significant when the 95% confidence intervals did not overlap zero. To estimate the degree of multicollinearity, variance inflation factors (VIF) were calculated. Parameter weights were calculated by summing the weights for all models where each factor appeared. Statistical differences for dissolved nutrients, chlorophyll *a* and periphyton among sites is discussed elsewhere (see: Green et al., 2015) and in Appendix A of Supplementary information for sediment organic content. Graphical evaluation of the relationship between the physical parameters and the percent cover of each species is presented in Appendix B of Supplementary information.

2.8. Maps

The best explaining model for each species were used to generate predictive percent cover maps (Fig. 2) of each seagrass species using the ESRI ArcToolbox™ Raster calculator. The coordinates of the sites were used to generate point shapefiles and projected into the UTM zone 17 projection with meter map units. Fifteen percent of the survey points ($n=49$) were reserved and the percent cover values were used to interpolate three preliminary independent percent cover rasters using the topo to raster method. Synoptic rasters

Table 3
Global, best explaining, null and physical models predicting percent cover for each of three seagrass species detected in the Lower Florida Keys during 2012–2013. Parameter estimates shown for each model term.

Species	Model	Intercept	% Cover	<i>T. testudinum</i>	% Cover	<i>H. wrightii</i>	% Cover	<i>S. filiforme</i>	Distance to nearest Island (m)	Distance to Pine Channel (m)	Exposure time (min)	Mean lower low water (m)	df	logLik	AICc	Δ_i	ω_i
<i>T. testudinum</i>	Null	83.32											2	-1603	3209	120.4	0.00
	Best explaining	92.64											7	-1537	3089	0.0	0.44
	Global	85.43											8	-1536	3089	0.3	0.37
	48	79.43											7	-1539	3092	2.7	0.11
<i>H. wrightii</i>	46	87.94											6	-1540	3092	3.5	0.08
	Physical	68.59											6	-1577	3166	77.3	0.00
	Null	19.53											2	-1610	3225	83.00	0.00
	Best explaining	85.43											7	-1564	3142	0.00	0.56
<i>S. filiforme</i>	Global	84.24											8	-1563	3143	0.85	0.37
	Physical	56.04											6	-1596	3204	62.45	0.00
	Null	11.48											2	-1567	3138	63.3	0.0
	Best explaining	10.54											7	-1530	3075	0.0	0.5
	Global	8.64											8	-1530	3077	1.8	0.2
	59	12.33											6	-1533	3078	2.7	0.1
	63	10.31											7	-1533	3080	4.5	0.1
	Physical	-18.07											6	-1543	3099	23.6	0.00

representing Euclidean distances to Pine Channel and to the nearest island were also generated. Existing bathymetry and exposure time rasters were also employed in the map algebra. The algorithms were executed in python syntax using the above rasters and their numerical modifiers in the raster calculator. The reserved points were used to extract values of each resulting raster corresponding to the location of each point. Survey percent cover values and the corresponding raster values were divided by to and rounded up for accuracy assessment in eleven class confusion matrices (Congalton and Green, 1993) (Appendix C of Supplementary information). One hundred percent accuracy was observed if presence or absence was assumed at greater or less than ten percent cover.

3. Results

3.1. Model selection

Across the study area, *T. testudinum* had the highest cover of all three species (83.3 ± 33.6 , mean $\pm$ SD). However, *T. testudinum* cover declined with very close proximity to islands and near the channel (Fig. 2). For *T. testudinum*, the model with the best support ($\omega_i = 0.44$) included the effects of the other two seagrass species, distance to nearest island, exposure time and MLLW (Table 3). The presence of each species, distance to nearest island and exposure time were in each of the best models suggesting that these parameters played a prominent role in determining *T. testudinum* distribution. As such, those parameters had strong model averaged weights ($\Sigma\omega_i > 0.9$) (Table 2). However, distance to nearest island and distance to Pine Channel had confidence intervals overlapping zero (Table 2), indicating unclear support for their inclusion as an explanatory variable. *H. wrightii*, *S. filiforme* and exposure time exerted negative effects on *T. testudinum*; whereas, distance to nearest island, distance to Pine Channel and MLLW had positive effects. Adding the effect of distance to Pine Channel decreased model support ($\omega_i = 0.37$) thus had low weight during model averaging ($\Sigma\omega_i = 0.5$). Mean lower low water was included in the top two models but averaged moderate support overall ($\Sigma\omega_i = 0.8$). The model that included only physical parameters and not the presence of *H. wrightii* or *S. filiforme* performed poorly ($\omega_i = 0.00$).

H. wrightii had lower cover than *T. testudinum* (19.5 ± 34.4) but tended to be slightly higher near islands (Fig. 2). Many factors influenced *H. wrightii* abundance and distribution (Table 3) across the study area. The best explaining model ($\omega_i = 0.56$) included all factors except distance to nearest island. When distance to nearest island was included, model support declined ($\omega_i = 0.37$). Confidence intervals for distance to nearest island overlapped zero (Table 2), which also indicated no support for this parameter. *T. testudinum*, *S. filiforme*, exposure time and distance to Pine Channel were included in each of the best models (Table 3) suggesting a strong influence on *H. wrightii* percent cover. Conversely, distance to Pine Channel had confidence intervals overlapping zero, which indicated that any potential effect on *H. wrightii* due to distance to Pine Channel was unclear. *T. testudinum*, *S. filiforme*, exposure time and distance to Pine Channel had negative effects on the percent cover of *H. wrightii*. Distance to nearest island exerted positive effects. The association between *H. wrightii* and positive MLLW values suggest that *H. wrightii* was often found in shallow intertidal areas rather than deep water regions. Model averaging showed that each factor except distance to nearest island had strong support (Table 2). Like *T. testudinum*, the model considering only physical parameters had no support ($\omega_i = 0.00$).

S. filiforme was sparsely distributed (11.8 ± 30.1) within the study area and occurred closer to the channel (Fig. 2). Like *H. wrightii*, many factors contributed to *S. filiforme* distribution and abundance in the refuge. The best explaining model ($\omega_i = 0.50$)

included the other seagrass species, distance to nearest island, distance to Pine Channel and MLLW (Table 2). The best models included each of these parameters except distance to nearest island. Note that distance to Pine Channel and exposure time had confidence intervals that included zero and showed unclear support for their inclusion in the best models. Model averaging showed that each of these parameters except distance to nearest island strongly influenced *S. filiforme* percent cover and distribution within the refuge (Table 2). The presence of *T. testudinum* and *H. wrightii* exerted negative effects on *S. filiforme* while the other factors had positive effects. The negative MLLW parameter value indicates that *S. filiforme* was associated with deeper water. The physical only model that lacked the presence of the other seagrass species had no support ($\omega_i = 0.00$).

4. Discussion

Physical factors alone did not have strong support among our models however a few factors emerged as having potentially important influence on seagrass distribution in the lower Florida Keys. For example, high current velocity may have influenced seagrass distribution near Upper Harbor Key. Upper Harbor Key has a long term and active wading bird colony (Calle et al., 2014) thus a persistent source of nutrients that should favor *H. wrightii* (Fourqurean et al., 1995). However, we did not document a halo of *H. wrightii* at that site as we found at Howe Key. Conversely, examining a shore-to-channel transect, Lapointe (2014) did find elevated nutrients and dominance of *H. wrightii* and macroalgae in a halo extending to ~40 m from Upper Harbor Key. The absence of *H. wrightii* from plots near UHK in our study may explain why the distance to nearest island was not an important factor in *H. wrightii* abundance within the refuge. One explanation for the absence of *H. wrightii* is high current velocity, evident from Google Earth™ images that show evidence of scouring within 100 m of the island (Google Earth, 3–7, 2013). High current velocities could dilute nutrient run off from bird guano and reduce habitat suitability for *H. wrightii*. Cabaco et al. (2008) showed that *T. testudinum* was resilient against erosion thus it may be favored over *H. wrightii* in locations where wind driven currents are strong. Despite the fact that REI did not meet the criteria to be included as a parameter in the global models for each species, Upper Harbor Key had significantly higher REI values than the other sites (L. Green, unpubl. data) suggesting faster wind driven currents near that site. Faster currents may have contributed to the scouring found around the island. No other work has implicated scouring or current velocity as factor affecting seagrass community composition and more research is needed to identify the degree to which it alters habitat suitability among seagrasses.

The negative relationship between water depth and light availability is known to influence the spatial segregation of seagrass species within intertidal and subtidal habitats. Spatial segregation based on water depth could contribute to the negative relationships we found between the species. Campbell and Fourqurean (2009) documented that *S. filiforme* generally grew in deeper waters than *T. testudinum* and *H. wrightii*. In our study, *S. filiforme* was the only species with a negative relationship to MLLW. This indicated that *S. filiforme* was predominantly in deep water; whereas, parameter values for *T. testudinum* and *H. wrightii* were positive and suggested these species were found in shallower water such as intertidal flats. Whereas, *T. testudinum* and *H. wrightii* were found in intertidal flats, both species had slight negative responses to exposure time. Lan et al. (2005) found that temperatures and desiccation impaired photosynthesis in *Thalassia hemprichii* and *Halodule uninervis*. Similarly, Vermaat et al. (1993) found greater variation in leaf loss for *Zostera noltii* growing in shallow waters (–16 cm relative to mean

sea level) compared to plants growing in intermediate (–32 cm) and deeper water (–46 cm). Moreover, *T. hemprichii* and *H. uninervis* had higher tolerance to thermal stress than *Syringodium isoetifolium* (Campbell et al., 2006), which supports our field observations that *S. filiforme* was found near channels and in deep water. Our results corroborated with previously published studies but showed how DEM and TiMSA models may enhance modeling efforts designed to predict changes in seagrass distribution with anthropogenic factors such as climate change and sea level rise.

Despite some evidence of nutrient enrichment in the refuge (Green et al., 2015), we only found mixed evidence that localized nutrient concentration influenced seagrass distribution. Small-scale nutrient availability at Howe Key may have resulted in a halo effect where *H. wrightii* dominated within 30 m of the island. Powell et al. (1991) showed that bird guano had a highly localized (<40 m) effect on seagrass communities that shifted habitat suitability in favor of *H. wrightii*. In fact, Howe Key is an established roosting site for wading birds (Calle et al., 2014). In addition to possible nutrient effects, the reduction in *T. testudinum* near Howe Key may have also contributed to a positive association between *H. wrightii* and the distance to nearest island because competition for resources may have been reduced in this locale. However, we did not see this relationship at Upper Harbor Key another known roosting and nesting site for wading birds (Calle et al., 2014) and likely weakened the importance of distance to nearest island in *H. wrightii* models. Whereas, we did not see a distinct change in *T. testudinum* abundance with proximity to Upper Harbor Key model averaging showed that distance to nearest island may affect the abundance and distribution of this species. However, the confidence intervals, which included zero, indicate unclear support for this factor to be important in influencing *T. testudinum*. Our study suggested that the effects of natural sources of localized nutrients such as bird guano on seagrass community composition are variable across intertidal landscapes and warrant further study.

Nutrient enrichment is among the leading causes of seagrass decline worldwide (Lotze et al., 2006) but our nutrient metrics (TDN, TDP, chlorophyll *a*, sediment organic content and periphyton percent cover) did not meet the criteria for inclusion in the global models. This may have been due to small sample sizes and restricted spatial distribution of our samples. It is possible that while water column nutrients and chlorophyll *a* (Boyer et al., 2009) slightly exceeded the numeric nutrient criteria established for the study area (Green et al., 2015), the concentrations may not have reached the thresholds proposed to negatively affect seagrasses in Florida (Janicki Environmental, 2011). Despite the fact that periphyton percent cover was not included as a parameter in our global models, small periphyton persistently covered greater than 80% of the seagrasses at each site during the study period (Green et al., 2015). Extensive and chronic macroalgal cover may result in future declines to seagrass health and distribution and suggests that temporal effects of nutrient availability and periphyton cover should be investigated within the refuge. However, we did find slight relationships between the abundance *H. wrightii* and *T. testudinum* and distance to Pine Channel (negative and positive, respectively, though the confidence intervals overlapped zero). It is worth noting that the negative relationship between nutrients, periphyton and seagrass in Florida is a topic of much debate (Tomasko and Lapointe, 1991; Lapointe et al., 1994; Franckovich and Fourqurean, 1997; Armitage et al., 2011). One reason for discrepancies in the effects of nutrients on seagrass may be the differential response by seagrasses to short term nutrient exposure in controlled experiments (Hessing-Lewis et al., 2014) and longer term exposure integrated in observational studies (Cabaco et al., 2013). Additionally, there are limited baseline data on seagrass community composition in our study area nor did we evaluate temporal effects of nutrient concentration on seagrass abundance. Establishing a clear connection

between nutrient enrichment and seagrass decline has proven to be increasingly complex since efforts to establish dose-dependent relationships between seagrasses and nutrient concentrations have been challenging (J. Kaldy, pers. comm.). To protect these critical ecosystems, it is evident that novel approaches (e.g., Schaeffer et al., 2012) may be needed to derive protective criteria thus effective management strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2015.03.005>.

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