Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization

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**Abstract**

Depth of colonization (*Zc*) is a useful seagrass growth metric that describes seagrass response to light availability. Similarly, percent surface irradiance (% SI) at *Zc* is a measure of seagrass light requirements with applications in seagrass ecology and management. Methods for estimating *Zc* and % SI are highly variable making meaningful comparisons difficult. A new algorithm is presented to compute maps of median and maximum *Zc*, *Zc, med* and *Zc,max*, respectively, for four Florida coastal areas (Big Bend, Tampa Bay, Choctawhatchee Bay, Indian River Lagoon). Maps of light attenuation (*Kd*) based on MODIS satellite imagery, PAR profiles, and Secchi depth measurements were combined to produce maps of % SI at *Zc,med* and *Zc,max*. Among estuary segments, mean *Zc,med* varied from (±s.e.) 0.86±0.08 m for Old Tampa Bay to 1.96±0.10 m for Western Choctawhatchee Bay. Coefficients of variation for *Zc,med* were 1-10%. Percent SI at *Zc,med* averaged 18% for Indian River Lagoon (range = 9-24%), 42% for Tampa Bay (36-49%) and 55% for Choctawhatchee Bay (46-75%). Estimated light requirements were significantly lower in Indian River Lagoon than in the other estuaries, while estimates for Tampa Bay and Choctawhatchee Bay were higher than the often cited estimate of 20%. Spatial gradients in depth of colonization and % SI were apparent in all estuaries. The analytical approach, implemented in R, could be applied easily to new data from these estuaries or to other estuaries and could be incorporated routinely in assessments of seagrass status and condition.

**Key words**: seagrass, depth of colonization, light requirements, remote sensing**Introduction**

Seagrasses are ecologically valuable components of aquatic ecosystems that have a critical role in shaping aquatic habitat. These ‘ecosystem engineers’ influence multiple characteristics of aquatic systems through interactions with many biological and abiotic components (Jones *et al*. 1994; Koch 2001). For example, seagrasses reduce wave action, stabilize sediments, and provide habitat and refuge for invertebrates and juvenile fish (Williams and Heck 2001; Hughes *et al*. 2009). Seagrasses also respond to changes in light attenuation through the water column via physiological light requirements. Seagrass coverage declines with water depth due to light attenuation, and declines more rapidly in systems with high water column production where light attenuation is relatively high (Duarte 1995). The light-limited maximum depth to which seagrass grows is variously called “depth limits” or “depth of colonization.” Empirical relationships between nutrient loading, light attenuation, light requirements, and depth of colonization have been identified (Duarte 1991; Kenworthy and Fonseca 1996; Choice *et al*. 2014) and have been used to characterize light regimes and other water quality requirements to maintain seagrass habitat (Janicki and Wade 1996; Steward *et al*. 2005). Seagrasses may be particularly useful in this respect because they respond to water quality over relatively long time scales, “integrating” their exposure to stress. Thus, time scales of seagrass response better match time scales for monitoring, assessment and nutrient management motivated by policy (Duarte 1995; Burkholder *et al*. 2007).

A variety of approaches have been used to estimate seagrass depth of colonization. A common *in situ* approach is to sample seagrass along depth transects until the maximum depth is adequately characterized (e.g., Spears *et al*. 2009; Choice *et al*. 2014). Alternative techniques include underwater photos or videos, aquascope identification, or hydroacoustic assessments (Zhu *et al*. 2007; Søndergaard *et al*. 2013). These are especially useful for site-specific evaluations where the analysis needs are driven by local questions (e.g., Iverson and Bittaker 1986; Hale *et al*. 2004). Availability of estuary-scale geospatial data for seagrass coverage, based on photo-interpretation of aerial imagery, suggests that standardized techniques can be applied at different spatial scales and would be valuable for a variety of scientific and policy applications. For large scale evaluation, it is often useful to subdivide water bodies into segments for the purpose of analysis and policy development (e.g., Steward *et al*. 2005; Schaeffer *et al*. 2012; US EPA 2012). One challenge in doing so is that estuaries are often characterized by gradients in water quality, such that any segmentation scheme is likely to include within-segment gradients in water quality and associated seagrass depth of colonization. Local conditions may require adaptive assessment approaches that can address interactive effects of environmental variables at different spatial scales.

An example from the Big Bend region of Florida illustrates the issue of scale in analyzing seagrass depth of colonization (Fig. 1a). In a segment from this region, the highest depth of colonization largely occurs around the outer perimeter of the mapped seagrass coverage (red line in Fig. 1a). However, depth-dependent seagrass growth patterns are also evident at smaller spatial scales within the segment, wherein the segment-scale depth of colonization overestimates the depth distribution near the outflow of the Steinhatchee River, where high concentrations of colored dissolved organic matter reduce water clarity locally (personal communication, N. Wellendorf, Florida Department of Environmental Protection). An improved method for estimating depth of colonization should have sufficient flexibility to characterize seagrass responses at a large scale, such as the segment average, while still resolving important patterns at smaller scales, such as the local impact of a river outflow. Developing and demonstrating this capability was one objective of this study.

Another objective of this study was to combine spatially-resolved estimates of depth of colonization with light attenuation measures at the same spatial scales to characterize the pattern and range of seagrass light requirements in estuaries. Although not always the case, the spatial distribution of submerged aquatic plants is often associated with light availability (Barko *et al*. 1982; Hall *et al*. 1999; Dennison *et al*. 1993), wherein depth of colonization is controlled by light requirements needed and average light attenuation. Published estimates of seagrass light requirements are species-specific and quite variable. Duarte (1991) reported that seagrasses can extend to depths receiving an average of 11% of surface irradiance, while estimates of light requirements for seagrass in Chesapeake Bay were about 20% (Batiuk *et al*. 1992). Dennison *et al*. (1993) reported minimum light requirements, defined as the percent light at the maximum depth limit, ranging from less than 5% to greater than 30% depending on site conditions. Estimates of ~20% are common in the literature, approximating a value in the middle of published estimates (see also Kemp *et al*. 2004). An estimate of ~ 20% for seagrass in Florida estuaries has been applied for management purposes in Tampa Bay, Choctawhatchee Bay, and elsewhere in Florida (e.g., FDEP 2012; US EPA 2012) and can be traced to the estimate of 22.5% for lower Tampa Bay from Dixon and Leverone (1995).

Sources of variation in estimates of seagrass light requirements are numerous and include physiological differences among seagrass species, differences in attenuation of light on the surface of seagrass leaves, and variations in other physiological stressors such as salinity or water temperature (Kenworthy and Haunert 1991; Kemp *et al*. 2004; Choice *et al*. 2014). Differences in operational definitions and method of estimation are also likely to contribute to differences in reported values. For example, Dennison *et al*. (1993) defined minimal light requirements as the percent light at the maximal depth limit for seagrass – where depth limit was defined variously by different included studies. Choice *et al*. (2014) applied a statistical method to data from individual stations seeking to find the percentage of surface irradiance linked to seagrass percent cover or shoot density of zero. In this study, we sought to generate more comparable estimates by broadly applying the same method to characterize seagrass depth of colonization and relating it to estimates of light attenuation at similar scales. We defined light requirements following Dennison et al. (1993), except that we operationally defined depth of colonization in terms of our approach. To quantify light attenuation at temporal and spatial scales relevant to understanding seagrass distributions in coastal ecosystems, we used estimates derived from satellite remote sensing along with more conventional observations of water clarity (light profiles, Secchi depth). Ocean color data from satellite remote sensing can provide consistent estimates of light attenuation across a large spatial extent, often with a high return frequency and sustained data collection, which is ideal for characterizing average attenuation (Woodruff *et al*. 1999; Chen *et al*. 2007).

The overall goal of this study is to present an algorithm for estimating seagrass depth of colonization and light requirements using geospatial datasets describing seagrass coverage and satellite remote sensing data of light attenuation in the water column. The approach allowed us to more accurately estimate and compare light requirements by using a standardized method that was applied to multiple spatial scales. By doing so, we address a general management need to provide locally-relevant estimates of depth of colonization and the amount of light estimated to be present at the depth where seagrass abundance is declining most quickly. The specific objectives were to 1) describe the method for estimating seagrass depth of colonization, 2) apply the technique to target locations in four Florida estuaries to illustrate quantification of seagrass growth patterns, and 3) develop a spatial description of relationships among depth limits and light attenuation, characterizing patterns in light requirements in each case study and between regions. The analytical approach was also automated for use in the R statistical programming language (RDCT 2016), which allowed us to evaluate changes in seagrass light requirements in Tampa Bay over twenty years.

**Methods**

*Study sites and data sources*

Study sites included four coastal areas in Florida: the Big Bend region (northeast Gulf coast), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf coast), and Indian River Lagoon (Atlantic coast; Table 1 and Fig. 2). Florida’s estuaries and coastal waters are partitioned into segments following a scheme developed by the US Environmental Protection Agency for numeric nutrient criteria. The method for estimating depth of colonization was evaluated initially using one segment in each of our 4 areas, chosen based on geographic coverage in Florida coastal areas and availability of seagrass data. These segments included Big Bend (BB), Western Choctawhatchee Bay (WCB), Old Tampa Bay (OTB), and Upper Indian River Lagoon (UIRL). The analysis was then expanded to quantify spatially-resolved seagrass depth limits and associated light requirements for all the segments in three of the estuaries, omitting the Big Bend from further analysis due to insufficient light attenuation data.

Geospatial data describing seagrass coverage and bathymetry were used to estimate depth of colonization. These data are available for coastal regions of Florida from the US Geological Survey, Florida Department of Environmental Protection, Florida Fish and Wildlife Conservation Commission, and Florida’s watershed management districts. Seagrass coverage maps were obtained for a recent year in each of the study sites (Table 1). The original coverage maps were produced by photo-interpreting aerial images to categorize seagrass as absent, discontinuous (patchy), or continuous. We aggregated to two categories, present (continuous and patchy) and absent.

Bathymetry data were obtained from the National Oceanic and Atmospheric Administration’s (NOAA) National Geophysical Data Center (<http://www.ngdc.noaa.gov/>) as either Digital Elevation Models (DEMs) or as bathymetric sounding data from hydroacoustic or other surveys. Tampa Bay bathymetry provided by the Tampa Bay National Estuary Program are described in Tyler *et al*. (2007). Bathymetry for the Indian River Lagoon was obtained from the St. John’s Water Management District (CPE 1997). Because the vertical datum (i.e., MLLW, NAVD88, etc.) varied, all bathymetric data were vertically adjusted to local mean sea level using the NOAA VDatum tool (<http://vdatum.noaa.gov/>). Adjusted data were combined with seagrass coverage layers using standard union techniques for raster and vector layers in ArcMap 10.1 (ESRI 2012). To reduce computation time, bathymetry layers were first masked using a 1 km buffer of the seagrass coverage layer. Raster bathymetric layers were converted to point layers to combine with seagrass coverage maps, described below.

*Quantifying light attenuation*

Satellite remote sensing imagery was used to create a gridded 1 km2 map of estimated light attenuation for Tampa Bay and Choctawhatchee Bay. Secchi depth measurements were used to quantify attenuation for the Indian River Lagoon because light scattering from bottom reflectance and insufficient grid resolution prevented use of satellite remote sensing measurements.

For Tampa Bay and Choctawhatchee Bay, daily MODIS (Aqua level-2) satellite data were downloaded from the NASA website (<http://oceancolor.gsfc.nasa.gov/>) for the five years preceding the year the seagrass imagery was acquired. Images were reprocessed using the SeaWiFS Data Analysis System software (SeaDAS, Version 7.0). For Tampa Bay, light attenuation was derived from daily MODIS images using a previously-developed algorithm that estimates Secchi depth using a regression relating field observations and satellite-derived estimates of the diffuse attenuation coefficient at 490 nm (*Kd* (490), Chen *et al*. 2007). Monthly and annual mean Secchi depth was estimated from the daily images and then averaged to create a single layer. Similarly, *Kd* for Choctawhatchee Bay was derived from MODIS using the QAA algorithm (Lee *et al*. 2005), which was also used by Chen *et al*. 2007 to estimate *Kd* (490). Monthly field measurements of *Kd*obtained in 2010 at ten locations in Choctawhatchee Bay were used to correct annual means of the un-validated satellite values (*Kd, MODIS*) to match annual means of *in situ* measurements (model II regression: *Kd*=0.65*Kd,MODIS*, r2=0.93). Field *Kd* estimates were estimated as the slope between irradiance and depth (i.e., log*IZ* = log*IO* – *Kd* Z) from underwater PAR measurements (4 pi Biospherical PAR sensor on SBE25 CTD profiler). The empirical relationship for the 2010 data was applied to all five years of annual mean satellite-derived *Kd* data prior to averaging to create a single layer for further analysis. In summary, the same algorithm was applied to both locations to estimate light attenuation, where estimates were previously validated for Tampa Bay and validated herein for Choctawhatchee Bay.

For Indian River Lagoon, secchi depth data (meters, *ZSecchi*) collected within ten years prior to the seagrass coverage data (i.e., 1999–2009) were obtained from the state of Florida’s impaired waters rule (IWR) database, update 40. A 10-year averaging period was used for Indian River Lagoon to compensate for uneven temporal coverage, whereas 5-year averages were used for the other estuaries. Stations with less than five observations were removed as were observations flagged as the detection limit (i.e., Secchi disk visible on bottom). As an additional data quality screen, Secchi data were compared with bathymetry to ensure that the reported Secchi depth was less than water depth.

*Estimating seagrass depth of colonization*

Seagrass depth of colonization (*Zc*) was computed by overlaying seagrass coverage maps and bathymetry data to generate a point shapefile with attributes of location, depth (m), and seagrass presence or absence. The proportion of points with seagrass present was computed within discrete depth bins, spanning the full range of depths. Depth bins were dynamically selected, ensuring that bins were no larger than 0.5 m and contained no more than 50 bathymetric soundings. For whole segments using a large radius, these limits were changed to 0.1 m and 1000 points. If a very large number of soundings were present, this approach generated a larger number of narrower bins, while producing the opposite given a smaller number of observations. Three depth of colonization metrics were derived from the empirical pattern of seagrass presence vs. depth. These included minimum (*Zc,min*), median (*Zc,med*), and maximum (*Zc,max*) depth of colonization. These terms each describe meaningful points on the depth distribution of the seagrass coverage map. *Zc, max* is the deepest depth at which mappable seagrasses occurred in coverage maps, excluding isolated patches (or outliers) at deeper depths. *Zc,med* is the median depth of the deep water edge of seagrass. Finally, *Zc,min* approximates the depth at which seagrass percent cover begins to decline with increasing depth, which may occur at *Z=*0 m.

The algorithm for estimating *Zc* was implemented recursively for locations on a grid covering the study area, resulting in a map of depth of colonization. It was also implemented at a single central location in estuary segments with a radius large enough to encompass all observations in the segment. At each location, the seagrass-depth data (i.e., merged bathymetric and seagrass coverage data) was extracted within a radius from the chosen location (Fig. 1). Geospatial data were imported and processed using functions in the rgeos and sp packages in R (Bivand *et al*. 2008; Bivand and Rundel 2014). A *Zc* estimate for each location was then quantified by computing the proportions of points containing seagrass as a function of depth. The chosen radius depends on the information desired about a location. In general, a sufficient radius will result in a plot illustrating a decreasing proportion of points with seagrass with increasing depth (Fig. 3). The radius should also change depending on whether an estimate at a single location is preferred or if a sampling grid is used. In the former, the radius depends on an expected area of influence given a priori knowledge of a location. As an example, the radius to characterize depth of colonization at the outflow of the Steinhatchee River in Fig. 1 was large enough to describe variation in growth affected by local conditions, while small enough to not over-sample beyond the expected influence of river outflow. In the latter, an appropriate radius will provide complete coverage of the grid while minimizing redundancy of information through overlap of the sampled area by each point.

At each sampled location, a logistic function was fitted to the extracted depth points using non-linear regression, quantifying the decrease in seagrass cover with respect to depth (Equation 1; Fig. 3):

 (1)

where the proportion of points with seagrass present, *P*, within each depth bin, centered at *Z*, was defined by a logistic curve with an upper asymptote *α*, an inflection point *β*, and a scale parameter *γ*. The curve was fitted by minimizing the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992). Initial parameter values for fitting were estimated as **max(*P*), **=median(*Z*) and **=75th percentile(*Z*) - median(*Z*). The maximum rate of decrease in seagrass coverage respect to *Z* is and occurs at *Z*=**. The tangent at *Z*=** passes through the line *P=* at *Z=*** and through *P*=0 at *Z=***The three seagrass depth of colonization metrics were defined in terms of these reference values as follows:

(2)

(3)

(4)

Several quality control measures were implemented to reduce spurious estimates. First, *Zc* parameters (i.e., depth of colonization) were estimated only if the number of seagrass depth points was sufficient for the logistic curve to be estimable. Second, estimates were provided only if the fitted value for **, the inflection point on the logistic curve, was within the range of depth, *Z*, in the data. It was possible for *-*2** to be less than zero, and this was common when seagrass cover declined immediately as depth increased from zero (Fig. 3B). In these cases, *Zc,min*= 0 and *Zc,med* is half the depth from zero to *Zc,max* (Fig. 3b).

Estimates of parameter uncertainty from the logistic model were also used to evaluate the quality and variability associated with individual depth of colonization estimates. Elements of the model-estimated variance-covariance matrix for the model parameters ,  and  were used to estimate the variance of the depth of colonization parameters using equations for sums and differences of normal random variables (Ku 1966):

(5)

(6)

(7)

We then estimated 95% prediction intervals for each parameter as the estimate where 2 is the appropriate estimate from eq. 5, 6 or 7. The value of is not defined when *-* 2**< 0 because *Zc,min* is fixed at zero (Fig. 3b). Given the estimated prediction intervals, we also considered depth of colonization to be inestimable if the 95% prediction interval for *Zc, max* included zero.

*Estimate of spatial distribution and mean depth of colonization*

Depth of colonization within estuary segments was estimated using (1) a single central point in the segment and a large sampling radius, and (2) a grid of sample points. For the first approach, a segment mean was generated using all the depth vs. seagrass observations within the segment. The variance of *Zc* was computed using eqs. 5, 6 and 7. For the second approach, *Zc* was estimated at each node on a regular grid of sample points distributed throughout each estuary segment. Nodes were spaced at an interval of 0.01 degrees latitude and longitude (≈ 0.6 x 0.5 km at 30° N) and the sampling radius for each location was set to 0.02 degrees. To account for spatial correlation among the estimates, segment means and standard errors were computed from the gridded estimates using an intercept-only spatial mixed model, implemented using the nlme package in R. An isotropic Gaussian correlation structure with a nugget effect was selected from among other options based on the Akaike Information Criterion. These examples demonstrated application of the algorithm to individual segments of the four target estuaries, and more importantly, how it can be used to discern between uncertainty and variability in seagrass growth patterns. Estimates at a single point for the whole segment provided an evaluation of uncertainty at a relatively coarse scale, whereas means of the gridded estimates demonstrated variability at increased resolution.

*Seagrass Light Requirements*

Seagrass light requirements were computed as the average fraction of surface irradiance (PAR) reaching the depth of colonization, which was quantified for this purpose as *Zc,med*. The same calculations using *Zc,max* are included as supplemental information. Depth of colonization and light attenuation were quantified on identical grids. Grid size was selected to maximize the number of matches between depth of colonization and light attenuation measurements, resulting in grid radii of 0.04 degrees for Choctawhatchee Bay, 0.1 degrees for Tampa Bay and 0.15 degrees for Indian River Lagoon. Grid cells centered more than 1 km from seagrass were not included, preventing spurious comparison of seagrass depth of colonization with light attenuation far from shorelines. The percentage of surface irradiance (% SI) at the median depth of colonization was computed using

 (8)

where the light extinction coefficient (*Kd*) was obtained as a remote sensing product (Choctawhatchee Bay, Tampa Bay) or from field-based Secchi depth measurements (Indian River Lagoon). Where *Kd* was derived from Secchi depth (*ZSecchi*), it was computed using (Poole and Atkins 1929; Idso and Gilbert 1974). The empirical link between *Kd* and Secchi depth has been the focus of more recent work and the estimate can vary by location and time (e.g., 1.1 – 2.0, Liu et al. 2005). While we acknowledge that the specific value is a concern, the chosen value of 1.7 is widely used and is appropriate for estuaries with moderate to clear waters typical of Florida coastal areas (Smith et al. 2006). The % SI at the maximum depth of colonization (*Zc,max*) was also estimated and is reported as supplemental information.

Segment means and standard errors for light requirements were computed from the spatially-correlated gridded estimates using an intercept-only spatial mixed model, as for depth of colonization. Tests for differences in mean light requirements between estuary segments were also implemented using a spatial mixed model using the nlme package in R, in this case with a single categorical fixed effect (estuary segment) and a Gaussian spatial correlation structure with a nugget effect.

*Trends in seagrass light requirements in Tampa Bay*

As a final analysis, we applied the seagrass algorithm to estimate changes in light requirements from 1988 to 2010 in Tampa Bay. This demonstrated how the algorithm can be applied to evaluate trends over large areas using Tampa Bay as an example where seagrass recovery has been a focus of management efforts over several decades (Greening *et al*. 2014)*.* Monthly observations of Secchi depth were obtained from routine monitoring stations maintained by the Tampa Bay Estuary Program (TBEP 2011, Fig. S1). Satellite estimates of light attenuation were not used for the comparison because of limited temporal coverage relative to availability of seagrass data. Secchi data at each sampling station were averaged within years and then converted to estimates of light attenuation (, as above) for comparison with seagrass coverage data. Seagrass data for Tampa Bay were obtained from sources noted above at approximate biennial intervals for the period of record (1988, 1990, 1992, 1994, 1996, 1999, 2001, 2004, 2006, 2008, and 2010). Seagrass light requirements were estimated for each year of seagrass coverage data at each monitoring station to describe general trends over the last twenty years.

**Results**

*Segment characteristics and seagrass depth estimates*

The study areas varied in size and depth (Table 1). Area ranged from 59 km2 for Western Choctawhatchee Bay (WCB) to 271 km2 for the Big Bend (BB). Mean depth was less than 5 meters in each segment, except for WCB, which was slightly deeper (5.3 m). Maximum depth was greater in WCB (11.9 m) and Old Tampa Bay (OTB, 10.4 m) compared to BB (3.6 m) and Upper Indian River Lagoon (UIRL, 3.7 m) segments. Seagrass coverage was extensive in BB (74.8 % of total segment area), less in UIRL (32.8 %) and OTB (11.9 %), and very sparse in WCB (5.9 %), where most seagrass was in a large patch located just west of the inlet to the Gulf of Mexico (Fig. 2). Seagrasses were distributed throughout BB except for a noticeable area of decreased coverage near the outflow of the Steinhatchee River (Fig. 2, upper left). Seagrasses in OTB and UIRL were distributed narrowly along the shorelines, consistent with strong depth-dependence. Seagrass coverage declined toward the northern ends of both OTB and UIRL.

Whole segment estimates (± prediction interval) based on single locations with large radii for *Zc,med* varied from 0.95±0.07 m in OTB to 2.29±0.19 m in BB, with 95% prediction intervals equal to ±1% to 10% of the estimate (Table 2). Estimates of *Zc,max* varied from 1.1 m to 3.8 m and were somewhat less precise, with 95% prediction intervals equal to 3 to 20% of the estimate (Table 2). Means of spatially-resolved estimates of *Zc,med* for a grid of points in each segment varied from 2% more than to 15% less than the whole-segment estimates (Table 2), within the margin of uncertainty for each, suggesting that the two approaches gave comparable results. The difference was largest for BB, where the gridded estimates of depth of colonization had a bi-modal distribution (i.e., lower estimates near the Steinhatchee outflow vs. higher values distant from the river outflow, Fig. 4 upper left). The whole segment estimate of *Zc,max* for BB was 3.8 m, 65% more than the 2.3 m average of the gridded estimates, reflecting a greater influence of the deeper-distributed seagrass on the whole segment calculation (Table 2; Fig. 4). Estimates for *Zc,min* were as low as zero in BB and OTB (Table 2), indicating that seagrass coverage decreased immediately with any increase in depth. The highest values for *Zc,min* were associated with relatively deep seagrass distributions, as in WCB. In these cases, coverage did not decrease initially with depth. Seagrass percent cover often increased initially with increasing depth, likely reflecting stressors such as wave energy or desiccation during extreme low tides affecting the shallow margin of the seagrass bed.

Spatial heterogeneity of the gridded estimates in depth of colonization was particularly apparent for segments BB and UIRL (Fig. 4). As previously mentioned, depth of colonization in the Big Bend segment was reduced in the vicinity of the Steinhatchee River discharge. Seagrasses were also limited to shallower depths at the north end of the Upper Indian River Lagoon segment, but grew at maximum depths up to 2.2 m on the eastern portion of the Upper Indian River Lagoon segment near the Merritt Island National Wildlife Refuge (Fig. 2). Seagrasses in Old Tampa Bay grew slightly deeper in the eastern and southern portion of the segment and declined to shallower depths near freshwater inflow channels on the northern margin (Fig. 4, Fig. 8). The deepest growing seagrass in western Choctawhatchee Bay was closest to Destin Pass, where regular tidal exchange with Gulf of Mexico waters maintains relatively low light attenuation (Fig. 4). *Zc* could not be estimated where seagrasses were sparse or absent as in the center of Old Tampa Bay and western Choctawhatchee Bay, or where there was an insufficient gradient in water depth, as in several areas of the Big Bend segment (Fig. 4). Conversely, individual points absent of seagrass can be assigned a depth estimate if the radius of the sample area satisfies the above criteria. This can produce gridded maps that may not resemble the original coverage maps because they do not describe the same information (i.e., Fig. 4 does not always resemble coverage in Fig. 2).

Gridded estimates for all segments in each bay (excluding Big Bend) provided further information on the distribution of seagrasses between segments and the average depth of colonization in each estuary (Table 3; Figs. 7, 8, 9). Seagrass *Zc* estimates were computed for 338 locations in Choctawhatchee Bay, 252 locations in Tampa Bay, and 47 locations in the Indian River Lagoon. Mean *Zc,med* (±s.e.) for the bays were 1.43±0.38, 0.91±0.31, and 1.12±0.26 m for Choctawhatchee Bay, Tampa Bay, and Indian River Lagoon, respectively. Mean *Zc,med* was not significantly different between any of the bays. Segment means within estuaries varied, although statistical differences were difficult to determine in some locations due to low sample size (i.e., Indian River Lagoon segments, Table 3). In Tampa Bay, *Zc,med* was ~0.5 m less in Old Tampa Bay than in the Lower or Middle Tampa Bay segments, but was only significantly different (*p* < 0.05) compared with the latter. Similarly, *Zc,med* in the eastern segment of Choctawhatchee Bay was 1.1 m and 1.5 m less than *Zc,med* in the central and western bay, respectively, although only the eastern and western estimates were significantly different (*p* < 0.05). No statistical differences were observed between segments of the Indian River Lagoon despite higher *Zc,med* in more southern segments (Fig. 9).

*Seagrass light requirements*

Estimates of light attenuation, seagrass depth of colonization, and corresponding light requirements for all locations in Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon indicated substantial variation, both between and within the different bays. Satellite-derived estimates for Choctawhatchee Bay and Tampa Bay resolved spatial variation in average light attenuation (Figs. 5 and 6). For Choctawhatchee Bay, *Kd* increased from the western and central segments toward the eastern segment, which is adjacent to the Choctawhatchee River discharge (Fig. 5). Similarly, attenuation increased from lower and central Tampa Bay into Old Tampa Bay and Hillsborough Bay. Attenuation was also less in the central area of the lower bay segments (Fig. 6). Secchi depth was highest in the southern Indian River Lagoon and decreased to the north. Relatively few Secchi depth measurements were available for the Upper Indian River Lagoon and Banana River segments, likely because maximum water clarity exceeded the maximum depth in shallow areas, resulting in right-censored measurements.

Whole-estuary means for percent surface irradiance (% SI) at *Zc,med* (i.e., seagrass light requirement) was (mean±s.e.) 55±3.2 % SI for Choctawhatchee Bay, 42±2.6 % SI for Tampa Bay, and 18±3.0 % SI for Indian River Lagoon. Based on Tukey contrasts, average light requirements for seagrass were significantly different between all estuaries, particularly for Indian River Lagoon. Despite some apparent spatial patterns in seagrass light requirements (Fig. 7, 8, 9), significant differences were not found between segments of a single estuary, except for a marginally significant difference between eastern and western Choctawhatchee Bay (*p* = 0.04). In Tampa Bay, the segment mean (±s.e.) % SI at *Zc,med* ranged from 36±4.7% to 49±4.9 % (Table 3, Fig. 8). For Choctawhatchee Bay, segment means were 46±6.4 % SI to 75±10.0 % SI, with the apparently higher values in eastern Choctawhatchee Bay (Table 3, Fig. 7). For Indian River Lagoon, segment averages ranged from 9±7.1 % SI to 24±8.6 % SI (Table 3, Fig. 9). Either small sample sizes, as for Indian River Lagoon, or a small number of effectively independent samples given the spatial correlation of residuals, reduced the statistical significance of apparent spatial differences in light requirements between segments.

The final analysis comparing trends in light requirements from 1988 to 2010 in Tampa Bay demonstrated variation over time with notable differences by Bay segment. Although trends varied between years, light requirements were generally lowest for Hillsborough Bay in the northeast and highest for Lower Tampa Bay near the outflow in the southern portion of the Bay (Fig. 10, top). These apparent trends in light requirements were explained by overall deeper median depths of colonization and lower light attenuation in Lower Tampa Bay, whereas Hillsborough bay had shallower depth of colonization and higher light attenuation (Fig. 10, bottom). Between years, variation in light requirements between segments was most apparent earlier and later in the time series, whereas segments were most similar in 1999 in the middle of the time series. Hillsborough Bay was most variable between years with median light requirements ranging from 25% (1988) to 42% (2006). As a final note, the distribution of boxplots in 2010 shows a slightly different pattern from results in the same year in Fig. 8 that are based on satellite estimates of *Kd*. This discrepancy is explained by differences in sampling location where those in the former are based on a finite group of monitoring stations (Fig. S1) and those in the latter are based on multiple sampling locations in a uniform grid that better characterizes coverage of nearshore seagrasses (Fig. 8).

**Discussion**

Seagrass depth of colonization is an important measure of the status and condition of seagrass communities in estuaries because it relates to light attenuation and related anthropogenic water quality changes, especially eutrophication caused by excess nutrient loading (Dennison *et al*. 1993; Short and Wyllie-Echeverria 1996; Burkholder *et al*. 2007). Because seagrasses are ecologically important and sensitive to water quality changes, both seagrass coverage and depth of colonization have been used to define water quality management objectives (Steward *et al*. 2005; US EPA 2012; Greening *et al*. 2014). The methods developed and demonstrated in this study are a rigorous, yet efficient and practical approach for computing seagrass depth of colonization at a large scale using widely-available geospatial data sets describing seagrass areal extent and bathymetry. The method is automated via R code, and thus not especially labor-intensive. Because it is automated, it is reproducible and could be applied to new data from the studied estuaries or other estuaries with appropriate data. The method provides maps of depth of colonization, resolving both means and spatial gradients at a range of scales from an individual measurement to the whole estuary. Uncertainty is estimated for individual estimates of depth of colonization, while both variability (s.d.) and uncertainty (s.e.) are quantified for segments of estuaries and whole estuaries. Given these characteristics, our approach is a novel tool for assessment of seagrass distribution with respect to water depth at different spatial scales. Moreover, resolving spatial differences in depth of colonization and light requirements provides valuable information to support further investigation of the causes and mechanisms affecting the extent and spatial distribution of seagrass habitats. These products have the potential to more effectively address management needs based on eutrophication endpoints given comparability of estimates using a standardized approach.

Maps illustrating spatial patterns in depth of colonization quantified expected distributions, wherein seagrasses grew to greater depth when closer to ocean passes, where water was clearer (Figs. 7, 8, 9). Differences among segment means were mostly not statistically different, reflecting both variability in estimates at the scale of estuary segments and spatial correlation of residuals, which reduced the effective number of degrees of freedom. For example, if the seagrass distribution within a segment includes two areas with homogeneous depth of colonization within but differences among them, this will tend to inflate uncertainty regarding the segment means, leading to poor resolution of differences among segments. Possible solutions could include a different segmentation approach or analysis of pattern without segmentation. If the objective was to resolve changes in average depth of colonization over time, which would be of interest ecologically, a statistically powerful approach could be an evaluation of pairwise changes at each grid node. While we have not yet evaluated a time series of coverages in this way it would be a useful extension of our research.

For the first time, we also combined estimates of light attenuation for estuaries based on satellite remote sensing and Secchi depth measurements to resolve spatial patterns in seagrass light requirements. Like depth of colonization, maps of these values quantify gradients in light requirements, even if “segments” delineated for management purposes did not clearly identify regions that differed by light requirements. We would expect light requirements, as we defined them, to be higher at locations closer to freshwater and nutrient sources because epiphytic algal growth, salinity variations, color, or other factors such as sediment geochemistry could impose constraints on seagrass growth beyond those imposed by light attenuation in the water column (Hemminga 1998; Kemp *et al*. 2004). The results neither conflicted with nor definitively supported this expectation. For example, the highest light requirements in each of the estuaries were furthest from tidal exchange and closest to sources of freshwater and nutrients (Fig. 7, 8, 9). But, the differences were subtle and, given variations within segments, did not emerge as significant differences among segment means. On the other hand, light requirements for seagrass in Indian River Lagoon was significantly less than for seagrass in Choctawhatchee Bay and Tampa Bay. Light requirements for Choctawhatchee Bay and Tampa Bay were both more than the 20% estimate that has been referenced broadly in water quality management (Batiuk *et al*. 1992; Dennison *et al*. 1993; Kemp *et al*. 2004) and locally within Florida (Dixon and Leverone 1995; US EPA 2012). Light requirements for Tampa Bay were similar to 20% in only a few areas of the Bay. We further note the differences in light requirements for Tampa Bay using grid-based estimates at a uniform and fine spatial scale in Fig. 8, compared to those based on relatively few locations at routine monitoring stations (Figs. 10 and S1). This highlights the need to consider sampling regime and relevant scales for estimates of light requirements that apply to an entire estuary. Regardless, our estimates are not outside the norm given the broad range in published estimates of seagrass light requirements (Dennison *et al.* 1993).

Some of the differences in light requirements that we observed may relate to species composition, since the physiology of seagrass species is far from invariant. For example, *Halodule wrightii* is the most abundant seagrass in western Choctawhatchee Bay (Yarbro and Carlson 2015) andhas higher light requirements than several other abundant species in Florida (Choice *et al*. 2014) including *Thalassia testudinum*, which dominates the more oceanic areas of Tampa Bay. Choice *et al*. (2014) found that light requirements for *Syringodium filiforme* were much less, as low as 8-15 % SI, although Kenworthy and Fonseca (1996) found that the depth distribution of *H. wrightii* and *S. filiforme* were similar in the lower Indian River Lagoon, implying their light requirements may be similar. Estimates of light requirements for several species of *Halophila* indicate a potential to grow at 5% SI or less (Kenworthy and Haunert 1991), consistent with some of our lowest estimates from Lower Indian River Lagoon (Fig. 9). Neither *S. filiforme* nor any of the *Halophila* spp. appear to be dominant species in Tampa Bay or Choctawhatchee Bay, perhaps limiting seagrass distributions in those estuaries to higher light environments compared with lower Indian River Lagoon. Although we cannot be certain the extent to which species composition can explain the differences that we observed in %SI at the depth of colonization, the key observation is that differences were observed, that seagrass species vary in their physiology and responses to a range of factors, and therefore, that it may be useful to understand and manage seagrass habitats utilizing local information where possible. Another consideration related to species composition is that our estimates are likely to be driven by the deepest growing species. Light attenuation changes could alter competitive relationships among species within the mappable seagrass area, which would not be apparent in our analysis.

Our estimates of % SI at the depth of colonization necessarily also depend on our approach to estimating depth of colonization, as do others in the literature. Depth of colonization is a reference point along a gradient of decreasing seagrass cover (presumably) associated with increasing light limitation and related physiological stress (e.g., Fig. 3 in Hemminga 1998). In some studies, percent cover was estimated by diver observation (Choice *et al*. 2014), enabling a statistical approach (e.g., moving split window) that directly resolves a threshold for rapid decline in percent cover with respect to % SI at the scale of a single quadrat. To scale up the analysis, we needed to use seagrass coverage maps based on photointerpretation which necessarily imposes a binary classification (present/absent). By inferring the probability of seagrass presence conditional on depth, however, we obtained an estimate analogous to that of Choice *et al*. (2014), with the parameter β (Fig. 3) estimating the threshold for most rapid decline in seagrass presence. However, it is still unavoidable that seagrass will be both present at greater depths and stressed by light limitation at lesser depths. In this regard, a strength of our approach is that we can estimate the % SI associated with both the local extremes of the mappable seagrass distribution (i.e., *Zc,max*; Figs. S2, S3, S4) and the center of that depth distribution (i.e., *Zc,med*). Moreover, by being linked to aerial coverage data, the estimates are available for a range of spatial scales, are comparable across all those scales, and can be quickly re-computed when new surveys are completed.

Our estimates also depend on an accurate characterization of average light attenuation, something that will always be challenging in the context of seagrass ecology. For example, since and and *ksd* ~ 1.7, Secchi depth in seagrass habitats is often similar to the depth of colonization, potentially leading to right censoring of Secchi measurements when the disk would be visible on the bottom. Accurate light profiling is possible but also more difficult in shallow water than in deeper water. Limitations on boat operations also favor sampling during periods of calm winds, perhaps leading to under-sampling of periods when sediment resuspension is above average. Quantifying light attenuation via satellite remote sensing has advantages but also presents both similar and new challenges. For example, concern regarding bottom reflectance led Chen *et al*. (2007) to exclude data if water depth was <2 m, excluding nearly all seagrass areas. Light attenuation estimates are therefore based on nearby, but deeper waters. If attenuation is lower in open water, this will tend to increase the estimate of % SI at the depth of colonization. On the other hand, the uniform and sustained spatial and temporal coverage provided by satellite remote sensing is an advantage. Such uniform coverage may reduce spurious small-scale variability.

Sustained trends in water quality are another factor that can affect estimates of light requirements because seagrasses can be both slow to recover following disturbance and resistant to stress in the first place. In particular, species such as *Thalassia testudinum* display a phalanx growth strategy and buffer against periods of low light by tapping into below ground reserves, making them slow to achieve a light-limited equilibrium distribution in the presence of water quality trends. Improving trends in light attenuation could lead to higher estimates of light requirements, whereas the opposite may be true with declining trends in clarity. As a result, considering both depth of colonization and changes in the apparent light requirements may be useful for understanding the status and trends related to seagrass habitats.

This study has implications for both seagrass ecology and environmental management. Scientifically, the ability to resolve patterns in several parameters related to depth of colonization as well as % SI at the depth of colonization could be useful for generating testable hypotheses. For example, persistent differences in spatial patterns of depth distributions may suggest hypotheses regarding the causes and could stimulate research to identify local drivers. Similarly, we could seek to better understand temporal changes in depth of colonization, but without a consistent approach to quantifying it, we may not be aware of such changes. For example, despite extensive documentation of changes in the area of seagrass habitat in Tampa Bay since 1950 (Greening *et al*. 2014), little attention has been given to trends in the depth distribution during the same period. Results in Fig. 10 demonstrate the novelty of our approach and its potential to describe previously undocumented changes in seagrass recovery from eutrophication impacts.

There are several important management implications related to our method and results. Localized patterns in depth of colonization, such as in the case of the Steinhatchee River outflow, illustrate that management goals related to seagrass depth distribution and light attenuation may not be applicable in water quality segments that are drawn without considering local drivers. At a slightly larger scale, differences among segments and among entire estuaries show that it can be both important and (fortunately) possible to consider local differences in the water quality requirements for seagrasses when developing and evaluating water quality goals over time. Even though seagrasses are affected by factors other than light attenuation, resistance and resilience in the face of multiple stressors can be influenced by the physiological and energetic changes affected by light availability (Burkholder *et al*. 2007). In the case of Tampa Bay, light availability generally exceeds seagrass light requirements estimated in the early 1990s. This may have sustained the seagrass recovery, which accelerated following a brief ENSO-related period of increased river flow and increased light attenuation in the late 1990s (Greening *et al*. 2014).

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Figure Captions

**Fig.1** Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. (a) seagrass coverage and depth contours at 2 meter intervals, including the whole segment estimate for depth of colonization; (b) a grid of sampling locations with sampling radii for estimating *Zc* and seagrass depth points derived from bathymetry and seagrass coverage layers; (c) an example of sampled seagrass depth points for a test location

**Fig. 2** Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay). SR= Steinhatchee River outflow; MI= Merritt Island National Wildlife Refuge

**Fig. 3** Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Three depth estimates (*Zc,min*, *Zc,med*, *Zc,max*) are based on a linear curve through the inflection point of a logistic growth curve. The logistic curve is defined by the parameters α, β, and γ and describes the decrease in the proportion of sample points with seagrass as a function of depth below mean tide level (MTL). (a) The estimation method when the linear curve intercepts α at a depth greater than zero. (b) The alternative method when the linear curve intercepts α at depth less than zero

**Fig. 4** Spatially-resolved estimates of maximum seagrass depth of colonization (m) for four coastal segments of Florida. Estimates are assigned to grid locations for each segment, where grid spacing was fixed at 0.01 decimal degrees. Radii for sampling seagrass bathymetric data around each grid location were fixed at 0.02 decimal degrees. From left to right, top to bottom: Big Bend, Old Tampa Bay, Upper Indian R. Lagoon, Western Choctawhatchee Bay

**Fig. 5** Satellite estimated light attenuation for Choctawhatchee Bay as an average of years from 2003 to 2007. See Fig. 7 for segment identification

**Fig. 6** Satellite estimated light attenuation for Tampa Bay as an average of years from 2006 to 2010. See Fig. 8 for segment identification

**Fig. 7** Median depth of seagrass colonization (*Zc,med*, m) and light requirements (% surface irradiance at *Zc,med*) for multiple locations in Choctawhatchee Bay, Florida. Each location has light attenuation from satellite observations and an estimate of seagrass depth of colonization with a search radius of 0.04 degrees. Box plots show the 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. CCB: Central Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay

**Fig. 8** Median depth of seagrass colonization (*Zc,med*, m) and light requirements (% surface irradiance at *Zc,med*) for multiple locations in Tampa Bay, Florida. Each location has light attenuation from satellite observations and an estimate of seagrass depth of colonization with a search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

**Fig. 9** Median depth of seagrass colonization (*Zc,med*, m) and light requirements (% surface irradiance at *Zc,med*) for multiple locations in Indian River Lagoon, Florida. Each location has an average Secchi depth observation and an estimate of seagrass depth of colonization with a search radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth. Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon

**Fig. 10** Summary of light requirements of seagrasses in segments of Tampa Bay from 1988 to 2010. Estimates are based on Secchi observations at routine monitoring stations and median depth of colonization estimates from coverage maps. Boxplot distributions of light requirements are shown in the top plot and median changes of *Zc,med* (m) and light attenuation in each year are shown as continuous paths in the bottom plot. See Fig. S1 for locations of stations in each segment. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

Supplementary figures

**Fig. S1** Locations of selected water quality stations monitored by the Hillsborough County Environmental Protection Commission (TBEP 2011). Secchi observations at each station were used to evaluate changes in light requirements of seagrass at approximate biennial intervals from 1988 to 2010. Stations were chosen based on continuity of data for the period of interest. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

**Fig. S2** Maximum depth of seagrass colonization (*Zc,max*, m) and light requirements (% surface irradiance at *Zc,max*) for multiple locations in Choctawhatchee Bay, Florida. Each location has light attenuation from satellite observations and an estimate of seagrass depth of colonization with a search radius of 0.04 degrees. Box plots show the 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. CCB: Central Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay

**Fig. S3** Maximum depth of seagrass colonization (*Zc,max*, m) and light requirements (% surface irradiance at *Zc,max*) for multiple locations in Tampa Bay, Florida. Each location has light attenuation from satellite observations and an estimate of seagrass depth of colonization with a search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

**Fig. S4** Maximum depth of seagrass colonization (*Zc,max*, m) and light requirements (% surface irradiance at *Zc,max*) for multiple locations in Indian River Lagoon, Florida. Each location has an average Secchi depth observation and an estimate of seagrass depth of colonization with a search radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth. Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon

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| **Table 1** Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates (see Fig. 2 for spatial distribution). Year is the date of the seagrass coverage and bathymetric data. Latitude and longitude are the geographic centers of each segment. Area and depth values are square kilometers and meters, respectively. Secchi measurements (m) were obtained from the Florida Department of Environmental Protection's Impaired Waters Rule (IWR) database, update number 40. Secchi mean and standard errors are based on all observations within the ten years preceding each seagrass survey | | | | |
|  | BB*a* | OTB | UIRL | WCB |
| Year*b* | 2006 | 2010 | 2009 | 2007 |
| Latitude | 29.61 | 27.94 | 28.61 | 30.43 |
| Longitude | -83.48 | -82.62 | -80.77 | -86.54 |
| Surface area | 271.37 | 205.5 | 228.52 | 59.41 |
| Seagrass area | 203.02 | 24.48 | 74.89 | 3.51 |
| Depth (mean) | 1.41 | 2.56 | 1.4 | 5.31 |
| Depth (max) | 3.6 | 10.4 | 3.7 | 11.9 |
| Secchi (mean) | 1.34 | 1.41 | 1.3 | 2.14 |
| Secchi (se) | 0.19 | 0.02 | 0.02 | 0.08 |
| *a*BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Western Choctawhatchee Bay | | | | |
| *b*Seagrass coverage data sources, see methods for bathymetry data sources | | | | |
| BB, WCB: http://geodata.myfwc.com/ | | | | |
| OTB: http://data.swfwmd.opendata.arcgis.com/ | | | | |
| UIRL: http://www.sjrwmd.com/gisdevelopment/docs/themes.html | | | | |
| BB, WCB: http://geodata.myfwc.com/ | | | | |

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| **Table 2** Summary of seagrass depth estimates (m) for each segment in Fig. 4. Whole segment estimates and prediction intervals were obtained from a single point estimate that included all seagrass depth data for the segment. Mean, standard error, standard deviation, minimum, and maximum values are for multiple grid points within each segment in Fig. 4. Mean and standard error estimates were from intercept-only models that included Gaussian correlation structures to account for spatial dependencies between points | | | | | | | |
| Segment*a* | Whole segment | Pred. Int. (+/-) | Mean | St. Err. | St. Dev. | Min | Max |
| BB |  |  |  |  |  |  |  |
| *Zc,min* | 0.75 | 0.25 | 1.56 | 0.18 | 0.79 | 0 | 2.72 |
| *Zc,med* | 2.29 | 0.19 | 1.94 | 0.17 | 0.76 | 0.55 | 2.97 |
| *Zc,max* | 3.84 | 0.43 | 2.29 | 0.19 | 0.81 | 0.74 | 3.48 |
| OTB |  |  |  |  |  |  |  |
| *Zc,min* | 0.83 | 0.16 | 0.58 | 0.07 | 0.28 | 0.05 | 1.48 |
| *Zc,med* | 0.95 | 0.07 | 0.86 | 0.08 | 0.3 | 0.33 | 1.74 |
| *Zc,max* | 1.07 | 0.21 | 1.17 | 0.12 | 0.4 | 0.34 | 2.04 |
| UIRL |  |  |  |  |  |  |  |
| *Zc,min* | 1.19 | 0.04 | 1.36 | 0.06 | 0.27 | 0.75 | 2.01 |
| *Zc,med* | 1.48 | 0.02 | 1.51 | 0.08 | 0.23 | 0.98 | 2.08 |
| *Zc,max* | 1.77 | 0.05 | 1.63 | 0.08 | 0.23 | 1.11 | 2.16 |
| WCB |  |  |  |  |  |  |  |
| *Zc,min* | 1.84 | 0.42 | 1.58 | 0.11 | 0.34 | 0.78 | 2.29 |
| *Zc,med* | 2.17 | 0.22 | 1.96 | 0.1 | 0.31 | 1.51 | 2.51 |
| *Zc,max* | 2.5 | 0.47 | 2.36 | 0.14 | 0.39 | 1.75 | 3.1 |
| *a*BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon, WCB: Western Choctawhatchee Bay | | | | | | | |

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| **Table 3** Summary of median depth of colonization (*Zc,med*, m) and light requirements (%) for all bay segments of Choctawhatchee Bay, Indian River Lagoon, and Tampa Bay. Superscripts for mean *Zc,med* denote significant differences of segments within estuaries. See Figs. 7 to 9 for spatial distribution of the results | | | | | | | | | | |
| **Segment*a*** |  | *Zc,med* | | | |  | % light | | | |
|  | *n* | Mean | St. Err. | Min | Max |  | Mean | St. Err. | Min | Max |
| **Choctawhatchee Bay** |  |  |  |  |  |  |  |  |  |  |
| CCB | 171 | 1.9ab | 0.2 | 0.5 | 4.2 |  | 56.4 | 5.2 | 19.5 | 91.7 |
| ECB | 16 | 0.8a | 0.4 | 0.4 | 0.9 |  | 74.7 | 10.0 | 58.0 | 88.6 |
| WCB | 151 | 2.3b | 0.3 | 1.6 | 2.8 |  | 46.4 | 6.4 | 22.3 | 77.9 |
| **Indian River Lagoon** |  |  |  |  |  |  |  |  |  |  |
| BR | 2 | 1.0c | 0.4 | 1.0 | 1.1 |  | 20.7 | 7.5 | 20.2 | 21.3 |
| LCIRL | 14 | 1.2c | 0.3 | 0.9 | 1.6 |  | 13.6 | 6.4 | 5.8 | 24.7 |
| LIRL | 3 | 1.6c | 0.4 | 1.5 | 1.6 |  | 9.2 | 7.1 | 6.0 | 11.2 |
| LML | 4 | 1.0c | 0.4 | 1.0 | 1.0 |  | 22.1 | 6.9 | 19.3 | 24.3 |
| UCIRL | 17 | 1.0c | 0.3 | 0.8 | 1.1 |  | 20.0 | 6.4 | 7.5 | 30.7 |
| UIRL | 1 | 1.0c | 0.4 | 1.0 | 1.0 |  | 24.1 | 8.6 | 24.1 | 24.1 |
| UML | 6 | 1.0c | 0.3 | 0.8 | 1.0 |  | 24.0 | 6.7 | 15.2 | 30.9 |
| **Tampa Bay** |  |  |  |  |  |  |  |  |  |  |
| HB | 22 | 1.0de | 0.2 | 0.6 | 1.3 |  | 41.1 | 6.0 | 17.7 | 50.8 |
| LTB | 70 | 1.3de | 0.1 | 0.8 | 1.5 |  | 39.1 | 4.8 | 21.0 | 58.7 |
| MTB | 73 | 1.4e | 0.1 | 1.1 | 1.6 |  | 36.4 | 4.7 | 11.8 | 50.2 |
| OTB | 87 | 0.8d | 0.1 | 0.5 | 1.1 |  | 48.7 | 4.9 | 31.5 | 77.4 |
| *a*CCB: Central Choctawhatchee Bay, ECB: Eastern Choctawhatchee Bay, WCB: Western Choctawhatchee Bay, BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon, HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay. | | | | | | | | | | |