Seagrass light requirements using an algorithm for spatially-resolved depth of colonization

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1 Introduction

Issues related to excessive nutrient pollution have motivated a substantial amount of research to understand and address impacts on coastal waters. Eutrophication, defined as an increase in the rate of supply of organic matter to an ecosystem (Nixon 1995), is primarily caused by anthropegenic inputs of limiting nutrients that exceed background concentrations of receiving waters. Adverse impacts on aquatic resources are well-documented and have included increased occurrence in the frequency and severity of harmfal algal blooms (Cloern 1996), reduction of dissolved oxygen necessary to support heterotrophic organisms (Justíc et al. 1987, Diaz and Rosenberg 2008), and loss of ecosystem functioning through food web simplification (Tewfik et al. 2007). Although management activities have been successful in mitigating or reversing eutrophication impacts (e.g., Greening and Janicki 2006), the evaluation of response endpoints remains an important topic given that ecosystem changes in relation to different nutrient regimes are not fully understood nor anticipated (Duarte et al. 2009). The most appropriate indicators of ecosystem response may be those that exhibit clear biological linkages with water quality changes, such that the potential effects of management actions can be unambiguously characterized through known cause and effect pathways. Critical management decisions may be forced by tentative assessments, political or societal pressures, or qualitative criteria in the absence of empirical methods to identify adequate indicators of ecosytem response (Duarte et al. 2009).

The ecosystem services provided by seagrasses as well as their sensitivity to water quality changes has contributed to their proliferation as biological response endpoints for eutrophication. Seagrasses are ecosystem engineers (Jones et al. 1994, Koch 2001) that serve a structural and functional role in altering aquatic habitat often through multiple feedback mechanisms with other ecosystem components. For example, seagrass beds create habitat for juvenile fish and crabs by reducing wave action and stabilizing sediment (Williams and Heck 2001, Hughes et al. 2009). Seagrasses also respond to changes in water clarity through direct physiological linkages with light availability. In short, increased nutrient loading contributes to reductions in water clarity through increased algal concentrations, inhibiting the growth of seagrass through light limitation (Duarte 1995). Empirical relationships between nutrient loading, water clarity, light requirements, and the maximum depth of seagrass colonization have been identified (Duarte 1991, Kenworthy and Fonseca 1996, Choice et al. 2014), such that quantitative standards can be developed to maintain light regimes sufficient for seagrass growth targets (Steward et al. 2005). Conversely, seagrass depth limits have formed the basis of quantititative criteria for nutrient load targets (Janicki and Wade 1996). Contrasted with numeric standards for nutrients and phytoplankon, seagrass-based criteria may be more practical for developing water quality standards given that seagrasses are integrative of system-wide conditions over time and less variable with changes in nutrient regimes (Duarte 1995).

The development of numeric criteria and standards for coastal waters has been a management priority within the United States (USEPA, 1998) and internationally (WFD 2000). Numerous agencies and management programs have developed a variety of techniques for estimating seagrass depth limits as a basis for establishing numeric criteria, either as restoration targets or for identifying critical load limits. Such efforts have been useful for site-specific approaches where the analysis needs are driven by a particular management or research context (e.g., Iverson and Bittaker 1986, Hale et al. 2004). However, a lack of standardization among methods has prevented broad-scale comparisons between regions and has even contributed to discrepancies between measures of depth limits based on the chosen technique. For example, seagrass depth limits based on in situ techniques can vary with the sampling device (Spears et al. 2009). Despite the availability of data, techniques for estimating seagrass depth of colonization using remotely sensed data have not been extensively developed. Such techniques have the potential to facilitate broad-scale comparisons between regions given the spatial coverage and annual availability of many products. For example, recent analyses by Hagy, In review have shown that standardized techniques using seagrass coverage maps and bathymetric data can be developed to compare growth patterns over time among different coastal regions of Florida. Such methods show promise, although further development to improve the spatial resolution of the analysis are needed. Specifically, methods for estimating seagrass depth limits should be reproducible for broad-scale comparisons, while also maintaining flexibility for site-specific estimates depending on management needs.

Reproducible and empirical approaches can be developed to provide more consistent estimates of seagrass depth limits for restoration targets or criteria development. We describe a method for estimating seagrass depth of colonization using information-rich datasets to create a spatially explicit and repeatable estimate. In particular, methods described in Hagy, In review are improved upon by creating a flexible and repeatable technique for estimating seagrass depth limits from coverage maps and bathymetric data. The specific objectives are to 1) describe the method for estimating seagrass depth limits within a relevant spatial context, 2) apply the technique to four distinct regions of Florida to illustrate improved clarity of description for seagrass growth patterns, and 3) develop a spatially coherent relationship between depth limits and water clarity for the case studies. Overall, these methods are expected to inform the development of water quality criteria based on empirical relationships of seagrass depth limits with water clarity over time. The method is applied to data from Florida although the technique is transferable to other regions with comparable data.

2 *Methods*

Development of a spatially-resolved approach to estimate seagrass depth of {acro:doc colonization (Z_c) relied extensively on data and partially on methods described in Hagy, In review. The following is a summary of data sources, methods, and rationale for improving spatial resolution in seagrass Z_c estimates, and evaluation of the approach including relationships with water clarity.

2.1 Data sources

2.1.1 Study sites

Four locations in Florida were chosen for the analysis: Choctawhatchee Bay (Panhandle), Big Bend region (northeast Gulf of Mexico), Tampa Bay (central Gulf Coast of Florida), and Indian River Lagoon (east coast) (Table 1 and Fig. 1). These locations represent different geographic regions in the state, in addition to having available data and observed gradients in water clarity that contribute to hetereogeneity in seagrass growth patterns. For example, the Big Bend region was chosen based on location near an outflow of the Steinhatchee River where higher concentrations of dissolved organic matter are observed. Seagrasses near the outflow were observed to grow at shallower depths as compared to locations far from the river source. Coastal regions and estuaries in Florida are partitioned as distinct spatial units based on a segmentation scheme developed by US Environmental Protection Agency (EPA) for the development of {acro:EPA numeric nutrient criteria. One segment from each geographic location was used to estimate seagrass Z_c and to evaluate variation in growth patterns. The segments included portions of

Choctawhatchee Bay (segment 303), the big bend region (820), Old Tampa Bay (902), and Indian River Lagoon (1502) (Fig. 1).

2.1.2 Seagrass coverage and bathymetry {sec:data_

Spatial data describing seagrass aerial coverage combined with co-located bathymetric depth information were used to estimate Z_c. These geospatial data products are pubically available in coastal regions of Florida through the US Geological Survey, Florida Department of Environmental Protection, Florida Fish and Wildlife Conservation Commission, and watershed management districts. Seagrass coverage maps were obtained for recent years in each of the study sites described above (Table 1). Coverage maps were produced using photo-interpretations of aerial images to categorize seagrass as absent, discontinuous (patchy), or continuous. For this analysis, we considered seagrass as only present (continuous and patchy) or absent since differences between continuous and patchy coverage were often inconsistent between data sources.

Seagrass coverage maps were combined with bathymetric depth layers to characterize location and depth of growth in each location. Bathymetric depth layers for each location were obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Geophysical Data Center (http://www.ngdc.noaa.gov/) as either Digital Elevation {acro:DEM} Models (DEMs) or raw sounding data from hydroacoustic surveys. Tampa Bay data provided by the Tampa Bay National Estuary Program are described in Tyler et al. (2007). Bathymetric data for the Indian River Lagoon were obtained from the St. John's Water Management District (Coastal Planning and Engineering 1997). NOAA products were referenced to mean lower low water, whereas Tampa Bay data were referenced to the North American Vertical Datum of {acro:NAVI 1988 (NAVD88) and the Indian River Lagoon data were referenced to mean sea level. Depth layers were combined with seagrass coverage layers using standard union techniques for raster and vector layers in ArcMap 10.1 (Environmental Systems Research Institute 2012). To reduce computation time, depth layers were first masked using a 1 km buffer of the seagrass coverage layer. The final layer used for analysis was a point layer with attributes describing location (latitude, longitude, segment), depth (m), and seagrass (present, absent). All spatial data were referenced to the North American Datum of 1983 as geographic coordinates. Depth values in each seagrass layer were further adjusted from the relevant vertical reference datum to local mean {acro:MSL sea level (MSL) using the NOAA VDatum tool (http://vdatum.noaa.gov/).

2.1.3 Water clarity

Seagrass light requirements can be estimated by evaluating spatial relationships between depth of colonization and water clarity. Secchi measurements provide a precise estimate of water clarity and have been obtained at numerous locations documented in the Florida Department of Environmental Protection's Impaired Impaired Waters Rule (IWR) database. {acro:IWR Secchi data for Florida coastal waters were obtained from update 40 of the IWR database for all of Tampa Bay (2010 coverage) and the Indian River Lagoon (2009 coverage) given the spatial extent of secchi observations for the two locations relative to the Big Bend and Choctawhatchee segments. Secchi data within the previous ten years of the seagrass coverage data were evaluated to capture water quality trends from the most recent decade (i.e., 1999–2009 for the Indian River Lagoon and 2000–2010 for Tampa Bay). Secchi data were screened to exclude observations that were flagged indicating that the value was lower than the maximum depth of the observation point. Secchi data were also compared with bathymetric data to verify unflagged values were not missed by initial screening. Secchi observations that were measured at the same geographic location were averaged across all dates. This approach was preferred given that seagrass depth patterns are more representative of long-term trends in water clarity as opposed to individual secchi measures that may be highly variable (Dennison 1987, Dennison et al. 1993).

2.2 Segment-based estimates of seagrass depth of colonization

Hagy, In review describe an approach to estimate seagrass Z_c as a segment-wide median. Seagrass depth data described above can be used to estimate maximum (Z_{cMax}) and median ($Z_{c50\%}$) seagrass Z_c, where the maximum depth is defined as the deepest depth at which a “significant” coverage of mappable seagrasses occured in a segment and the median depth is defined as the median depth occurring at the deep water edge. The seagrass depth points are grouped into bins and the proportion of points within each depth bin that contain seagrass are quantified. Both seagrass Z_c estimates are obtained from a plot of proportion of points occupied at each depth bin. In general, the plot is characterized by a decreasing trend such that the proportion of occupied points by depth bin decreases and eventually flattens with increasing depth. A regression is fit on this descending portion of the curve such that the intercept point on the x-axis is considered the maximum depth of colonization. The median portion of this curve is considered the median depth of the deepwater edge of seagrass.

A segment-wide average of seagrass Z_c, although unbiased, may potentially reduce the ability to relate patterns in Z_c to relevant water quality variables. Considerable spatial heterogeneity in the observed seagrass growth patterns suggests that a segment-wide estimate of seagrass Z_c may not fully describe variation at relevant spatial scales. Fig. 2a illustrates variation in seagrass distribution for a location in the Big Bend region of Florida. Using methods in Hagy, In review, the segment-wide estimate for maximum depth of seagrass colonization (shown as a red contour line) does not adequately describe within-segment variation in depth limits. Z_c is greatly over-estimated at the outflow of the Steinhatchee River where high concentrations of dissolved organic matter reduce water clarity and naturally limit seagrass growth. This example suggests that it may be useful to have improved spatial resolution in estimates of Z_c, particularly when site-specific characteristics may require a more detailed description of seagrass growth patterns. Although the current example is immediately relevant for the Big Bend region of Florida, the remaining examples discussed throughout also provide a justification for a more comprehensive assessment of seagrass growth patterns.

2.3 Estimating seagrass depth of colonization for finite areas

The approach used to estimate seagrass Z_c with improved spatial resolution has several key differences that make it distinct from the original method. As before, seagrass Z_c estimates are based on empirical measures of the frequency occurrence of seagrass with increasing depth. The first difference is that maximum Z_c is estimated using a logistic growth curve fit through the data, as compared to a simple linear regression in the previous example. Second, a third measure describing the minimum depth of colonization was defined, in addition to median and maximum depth of growth. The third and most important difference is that the estimates are assigned to discrete cartesian locations, using either a grid of points or as a single location of interest. Methods and implications of these differences are described below.

The spatially-resolved approach for estimating Z_c begins by creating a grid of points within the segment where the same process for estimating Z_c is used for each point. Alternatively, a single location of interest can be chosen rather than a grid-based design. Seagrass depth data (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the chosen locations are selected for estimating seagrass Z_c values (Fig. 2). The estimate for each location is quantified from a plot of the proportion of bathymetric soundings that contain seagrass at each depth bin (Fig. 3a). Although the chosen radius for selecting depth points is problem-specific, the minimum radius must sample a sufficient number of points for estimating Z_c. In general, an appropriate radius will produce a plot that indicates a decrease in the proportion of points that are occupied by seagrass with increasing depth. An appropriate radius is also one that creates a sample area around each point that has minimal overlap with the seagrass depth data sampled by adjacent points.

A curve is fit to the sampled depth points using non-linear regression to characterize the reduction in seagrass as a function of depth (Fig. 3b). Specifically, a decreasing logistic growth curve is used with the assumption that seagrass decline with increasing depth is monotonic and asymptotic at the maximum depth of colonization. The curve is fit by minimizing the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992) and user-supplied starting parameters that are an approximate estimate of the curve characteristics. The model has the following form:

$$Proportion = \frac{\alpha}{1 + \mathrm{e}^{(\beta - Depth)/\gamma}} \tag{1}$$

{eqn:prop}

where the proportion of points occupied by seagrass at each depth is defined by a logistic curve with an asymptote α, a midpoint inflection β, and a scale parameter γ. Starting values α, β, and γ were estimated empirically from the observed data.

Finally, a simple linear curve is fit through the inflection point (β) of the logistic curve to estimate the three measures of depth of colonization (Fig. 3c). The inflection point is considered the depth at which seagrass are decreasing at a maximum rate and is used as the slope of the linear curve. Three measures describing seagrass growth characteristics are obtained. The maximum depth of seagrass colonization, $Z_{c,\,max}$, is the x-axis intercept of the linear curve. The minimum depth of seagrass growth, $Z_{c,\,min}$, is the location where the linear curve intercepts the asymptote of the logistic growth curve. This depth can be considered the start of the decline in seagrass coverage with increasing depth. The median depth of seagrass colonization, $Z_{c,\,med}$, is the depth halfway between $Z_{c,\,min}$ and $Z_{c,\,max}$. $Z_{c,\,med}$ was typically the inflection point of the logistic growth curve. Functionally, each measure has specific ecological significance. The median and maximum depth estimates describe the growth limitations of seagrasses as a function of water clarity, whereas minimum depth of growth was often where the highest percentage of seagrass coverage was observed in the sample. Median and maximum depth estimates differ in that the former describes the median depth of the deep water edge, whereas the latter describes a nominal characterization of maximum depth independent of outliers.

Estimates for each of the three Z_c measures are obtained only if specific criteria are met. These criteria were implemented as a safety measure that ensures a sufficient amount and appropriate quality of data were used. First, estimates were provided only if a sufficient number of seagrass depth points were present within the radius of the grid point to estimate a logistic growth curve. This criteria applies to the sample size as well as the number of points with seagrass in the sample. The curve could not be estimated for small samples or if an insufficient number of points contained seagrass regardless of sample size. Second, estimates were provided only if an inflection point was present on the logistic curve within the range of the sampled depth data. This criteria applied under two scenarios where the curve was estimated but a trend was not adequately described by the sampled data. That is, a curve could be estimated that described only the initial decrease in points occupied as a function of depth but the observed points do not occur at depths deeper than the predicted inflection point. The opposite scenario occurred when a curve was estimated but only the deeper locations beyond the inflection point were present in the sample. Third, the estimate for $Z_{c,\,min}$ was set to zero depth if the linear curve through the inflection point intercepted the asymptote at x-axis values less than zero. The estimate for $Z_{c,\,med}$ was also shifted to the depth value halfway between $Z_{c,\,min}$ and $Z_{c,\,max}$ if $Z_{c,\,min}$ was fixed at zero. Finally, estimates were considered invalid if the 95% confidence interval for $Z_{c,\,max}$ included zero. Methods used to determine confidence bounds on Z_c estimates are described below.

All estimates were obtained using custom-made functions in program R that were based on the `nls` and `SSlogis` functions to fit nonlinear least squares using a self-starting logistic growth model (Bates and Chambers 1992, R Development Core Team 2014). All seagrass depth shapefiles were imported and processed in R using functions in the `rgeos` and `sp` packages (Bivand et al. 2008, Bivand and Rundel 2014).

2.4 Comparison with segment-based approach and sensitivity analysis

Spatially-resolved estimates for seagrass Z_c were obtained for each of the four segments described above. Segment-wide estimates obtained using methods in Hagy, In review were used as a basis of comparison such that departures from these values were evidence of spatial heterogeneity in seagrass growth patterns and improved clarity of description in depth estimates using the new approach. A sampling grid of locations for estimating each of the three depth values in Fig. 3 was created for each segment. The grid was masked by the segment boundaries, whereas seagrass depth points used to estimate Z_c extended beyond the segment boundariesto allow sampling by grid points that occurred near the edge of the segment. Initial spacing between sample points was chosen arbitrarily as 0.02 decimal degrees, which is approximately 2 km at 30 degrees N latitude. The sampling radius around each sampling location in the grid was also chosen as 0.02 decimal degrees to allow for complete coverage of seagrass within the segment while also minimizing redundancy of information described by each location. In other words, radii were chosen such that the seagrass depth points sampled by each grid location were only partially overlapped by those sampled by neighboring points.

The ability to characterize heterogeneity in seagrass growth patterns using the grid-based approach can be informed by evaluating the level of confidence associated with Z_c estimates. Confidence intervals for non-linear regression can be estimated using a Monte Carlo simulation approach that considers the variance and covariance between the model parameters and the depth measurements (Hilborn and Mangel 1997). For simplicity, we assume that the variability associated with parameter estimates is the dominant source of uncertainty. A 95% confidence interval for each Z_c estimate was constructed by repeated sampling of a multivariate normal distribution followed by prediction of the proportion of points occupied by seagrass as in eq. (1). The sampling distribution assumes:

$$x \sim N(\mu, \Sigma) \tag{2}$$

where x is a predictor variable used in eq. (1) (depth) that follows a multivariate normal distribution with mean μ, and variance-covariance matrix Σ. The mean values are set at the depth value corresponding to the inflection point on the logistic curve and the predicted model parameters (i.e., α, β, and γ), whereas Σ is the variance-covariance matrix of the model parameters. A large number of samples ($n = 10000$) were drawn from the distribution to characterize the uncertainty of the depth value at the inflection point. The 2.5$^{\text{th}}$ and 97.5$^{\text{th}}$ quantile values of the sample were considered bounds on the 95% confidence interval.

The uncertainty associated with the Z_c estimates were based on the upper and lower limits of the estimated inflection point on the logistic growth curve. This approach was used because uncertainty in the inflection point is directly related to uncertainty in each of the Z_c estimates that are based on the linear curve fit through the inflection point. Specifically, linear curves were fit through the upper and lower estimates of the depth value at the inflection point to identify upper and lower limits for the estimates of $Z_{c,\,min}$, $Z_{c,\,med}$, and $Z_{c,\,max}$. These values were compared with the initial estimates from the linear curve that was fit through the inflection point on the predicted logistic curve (i.e., Fig. 3c). This approach provided an indication of uncertainty for individual estimates for the chosen radius. Uncertainty estimates were obtained for each Z_c estimate for the grids in each segment.

2.5 Developing a spatially coherent relationship of water clarity with depth of colonization

The relationship between seagrass depth limits and secchi measurements were explored using established light requirements and attenuation equations. The traditional Lambert-Beer equation describes the exponential decrease of light availability with depth:

$$I_z = I_O \cdot \exp\left(-K_d \cdot Z\right) \tag{3}$$

{eqn:lambe

such that the irradiance of incident light at depth Z (I_Z) can be estimated from the irradiance at the surface (I_O) and a light extinction coefficient (K_d). Duarte (1991) indicate that minimum light requirements for seagrass are on average 11% of surface irradiance. Light requirements may also be species-specific and variable by latitude such that value may range from less than 5% to greater than 30% (Dennison et al. 1993). Light requirements of seagrass at a specific location can be estimated by rearranging eq. (3):

$$\%light = \exp\left(-K_d \cdot Z_{c,\,max}\right) \tag{4}$$ {eqn:percl

where the percent light requirements of seagrass at $Z_{c,\,max}$ are empirically related to light extinction. A conversion factor is often used to estimate the light extinction coefficient from secchi depth Z_d, such that such that $c = K_d \cdot Z_d$, where c has been estimated as 1.7 (Poole and Atkins 1929, Idso and Gilbert 1974). Thus, K_d can be replaced with the conversion factor and the equation is rearranged to describe $Z_{c,\,max}$ as a function of secchi depth Z_d:

$$Z_{c,\,max} = \frac{-\log\left(0.20\right)}{1.7} \cdot Z_d \tag{5}$$ {eqn:sgreg

A regression of seagrass depth estimates against secchi measurements is expected to have a slope corresponding to the constant in eq. (5). For the current analysis, 20% light requirements were assumed to be an approximate median requirement for seagrasses in Florida. Scatter in the regression through these points can be considered biologically meaningful, such that points below the curve are locations where seagrasses are observed at maximum depth with less irradiance than expected given eq. (5), whereas points above the curve are those where seagrasses are growing deeper than expected. The geographic coordinates for each secchi measurement in Tampa Bay and the Indian River Lagoon were used as locations for estimating $Z_{c,\,max}$. These estimates were compared with the averaged secchi estimates to identify light requirements at each location. However, the relationship is expected to vary depending on the specific radius around each sample point for estimating $Z_{c,\,max}$. An appropriate radius was chosen that minimized the difference between the empirically estimated slope and that in eq. (5). The estimated light requirements of each point were also plotted using the cartesian coordinates of each secchi observation to evaluate spatial variation in seagrass growth as a function of light-limitation. Light requirements were also summarized by individual segments in each bay to identify spatial trends for relevent management units.

3 Results

3.1 Segment characteristics and seagrass depth estimates

Each of the four segments varied by several key characteristics that potentially explain within-segment variation of seagrass growth patterns (Table 1). Mean surface area was 191.2 square kilometers, with area decreasing for the Big Bend (271.4 km), Indian River Lagooon (NA km), Old Tampa Bay (205.5 km), and Choctawhatchee Bay (59.4 km) segments. Seagrass coverage as a percentage of total surface area varied considerably by segment. Seagrasses covered a majority of the surface area for the Big Bend segment (74.8 %), whereas coverage was much less for Indian River Lagoon (NA %), Old Tampa Bay (11.9 %), and Choctawhatchee Bay (5.9 %). Visual examination of the seagrass coverage maps for the respective year of each segment suggested that seagrasses were not uniformly distributed (Fig. 1). Seagrasses in the Choctawhatchee Bay segments were generally sparse with the exception of a large patch located to the west of the inlet connection with the Gulf of Mexico. Seagrasses in the Big Bend segment were located throughout the segment with noticeable declines near the outflow of the Steinhatchee River, whereas seagrasses in Old Tampa Bay and the Indian River Lagoon segment were generally confined to shallow areas near the shore. Seagrass coverage showed a partial decline toward the northern ends of both Old Tampa Bay and the Indian River Lagoon segments.

Mean depth was less than 5 meters for each segment, excluding Choctawhatchee Bay which was slightly deeper than the other segments on average (5.3 m). Maximum depths were considerably deeper for Choctawhatchee Bay (11.9 m) and Old Tampa Bay (10.4 m), as compared to the Big Bend (3.6 m) and Indian River Lagoon (NA m) segments. Water clarity as indicated by average secchi depths was similar between the segments (1.5 m), although Choctawhatchee Bay had a slightly higher average (2.1 m).

Estimates of seagrass Z_c using a segment-wide approach that did not consider spatially explicit locations indicated that seagrasses generally did not grow deeper than three meters in any of the segments (Table 2). Maximum and median depth of colonization were deepest for the Big Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old Tampa Bay (1.1 and 0.9 m), whereas the minimum depth of colonization was deepest for Choctawhatchee Bay (1.8 m) and shallowest for Old Tampa Bay (0.6 m). Averages of all grid-based estimates for each segment were different than the segment wide estimates, which suggests potential bias associated with using a whole segment as a relevant spatial unit for estimating depth of colonization. In most cases, the averages of all grid-based estimates were less than the whole segment estimates, suggesting the latter provided an over-estimate of seagrass growth limits. For example, the average of all grid estimates for $Z_{c,\,max}$ in the Big Bend region suggested seagrasses grew to approximately 2 m, which was 1.6 m less than the whole segment estimate. This reduction is likely related to improved resolution of seagrass depth limits near the outflow of the Steinhatchee river. Although reductions were not as severe for the average grid estimates for the remaining segments, considerable within-segment variation was observed depending on grid location. For example, the deepest estimate for $Z_{c,\,min}$ (2 m) in the Indian River Lagoon exceeded the average of all grid locations for $Z_{c,\,max}$ (1.7 m). $Z_{c,\,min}$ also had minimum values of zero meters for the

Big Bend and Old Tampa Bay segments, suggesting that seagrasses declined continously from the surface for several locations.

Visual interpretations of seagrass depth estimates using the grid-based approach provided further information on the distribution of seagrasses in each segment (Fig. 4). Spatial heterogeneity in depth limits was particularly apparent for the Big Bend and Indian River Lagoon segments. As expected, depth estimates indicated that seagrasses grew deeper at locations far from the outflow of the SteinHatchee River in the Big Bend segment. Similarly, seagrasses were limited to shallower depths at the north end of the Indian River Lagoon segment near the Merrit Island National Wildlife Refuge. Seagrases were estimated to grow at maximum depths up to 2.1 m on the eastern portion of the Indian River Lagoon segment. Spatial heterogeneity was less distinct for the remaining segments. Seagrasses in Old Tampa Bay grew deeper in the northeast portion of the segment and declined to shallower depths near the inflow at the northern edge. Spatial variation in the Choctawhatchee Bay segment was not apparent, although the maximum Z_c estimate was observed in the northeast portion of the segment. Z_c values were not available for all grid locations givne the limitations imposed in the estimation method. Z_c could not be estimated in locations where seagrasses were sparse or absent, nor where seagrasses were present but the sampled points did not exhibit a sufficient decline with depth. The latter scenario was most common in Old Tampa Bay and Choctawhatchee Bay where seagrasses were unevenly distributed or confined to shallow areas near the shore. The former scenario was most common in the Big Bend segment where seagrasses were abundant but locations near the shore were inestimable given that seagrasses did not decline appreciably within the depths that were sampled.

Uncertainty for estimates of $Z_{c,\,max}$ indicated that confidence intervals were generally acceptable (i.e., greater than zero), although the ability to discriminate between the three depth estimates varied by segment (Fig. 5 and Table 3). Mean uncertainty for all estimates in each segment measured as the width of a 95% confidence interval was 0.2 m. Greater uncertainty was observed for Choctawhatchee Bay (mean width of all confidence intervals was 0.7 m) and Old Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Indian River Lagoon (0.1 m) segments. The largest confidence interval for each segment was 1 m for Old Tampa Bay, 2.5 m for Choctawhatchee Bay, 0.4 m for the Big Bend, and 0.3 m for the Indian River Lagoon segments. However, most confidence intervals for the remaining grid locations were much smaller than the maximum in each segment. A comparison of overlapping confidence intersals for $Z_{c,\,min}$, $Z_{c,\,med}$, and $Z_{c,\,max}$ at each grid location indicated that not every measure was unique. Specifically, only 12.5% of grid points in Choctawhatchee Bay and 38.9% in Old Tampa Bay had significantly different estimates, whereas 84% of grid points in the Indian River Lagoon and 94.1% of grid points in the Big Bend segments had estimates that were significantly different. By contrast, all grid estimates in Choctawhatchee Bay and Indian River Lagoon had $Z_{c,\,max}$ estimates that were significantly greater than zero, whereas all but 10% of grid points in Old Tampa Bay and 5.6% of grid points in the Big Bend segment had $Z_{c,\,max}$ estimates significantly greater than zero.

3.2 Evaluation of seagrass light requirements

Estimates of seagrass light requirements for all segments of Tampa Bay and the Indian River Lagoon indicated substantial variation, both between and within the different bays (Table 4 and Figs. 6 and 7). Seagrass Z_c estimates were obtained for 51 locations in Tampa Bay and 80 locations in the Indian River Lagoon where secchi observations were available in the Florida IWR database. Mean secchi depth for all recorded observations was 1.8 m ($n = 51$) for Tampa Bay and 1 m ($n = 80$) for Indian River Lagoon. Mean light requirements were significantly different between the bays (two-sided t-test, $t = 8.1$, $df = 104.1$, $p < 0.001$) with a mean requirement of 21.9% for Tampa Bay and 10.7% for Indian River Lagoon. Within each bay, light requirements were significantly different between segments (ANOVA, $F = 3.5$, $df = 3, 47$, $p = 0.02$ for Tampa Bay, $F = 4.0$, $df = 7, 72$, $p = 0.001$ for Indian River Lagoon). However, post-hoc evaluation of all pair-wise comparisons of mean light requirements indicated that significant differences were only observed between a few segments within each bay. Significant differences in Tampa Bay were observed between Old Tampa Bay and Hillsborough Bay (Tukey multiple comparisons, $p = 0.119$). Significant differences in the Indian River Lagoon were observed between the Upper Indian River Lagoon and Banana River ($p = 0.998$), the Upper Indian River Lagoon and Lower Indian River Lagoon ($p = 0.023$), and Upper Indian River Lagoon and Lower St. Lucie ($p = 0.018$) segments. In general, spatial variation of light requirements in Tampa Bay suggested that seagrasses were less light-limited (i.e., lower percent light requirements at $Z_{c,\,max}$) in Hillsborough Bay and western areas of Lower Tampa Bay near the Gulf of Mexico (Fig. 6). Seagrassess in the Indian River Lagoon were generally less light-limited towards the south and in the Banana River segment (Fig. 7).

4 Discussion

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Table 1: Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates (see Fig. 1 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 meters and square kilometers, respectively. Secchi measurements (m) were obtained from the Florida Department of Environmental Protection's Impaired Waters Rule (IWR), update number 40. Secchi mean and standard errors are based on all observations within the ten years preceding each seagrass survey. tab:seg_summ

	Big Bend	Choctawhatchee Bay	Old Tampa Bay	Upper Indian R. Lagoon
Year[a]	2006	2007	2010	2009
Latitude	29.61	30.43	27.94	28.61
Longitude	-83.48	-86.54	-82.62	-80.77
Surface area	271.37	59.41	205.50	228.52
Seagrass area	203.02	3.51	24.48	74.89
Depth (mean)	1.41	5.31	2.56	1.40
Depth (max)	3.60	11.90	10.40	3.70
Secchi (mean)	1.34	2.14	1.41	1.30
Secchi (se)	0.19	0.08	0.02	0.02

[a] Seagrass coverage data sources, see section 2.1.2 for bathymetry data sources:
Big Bend: http://atoll.floridamarine.org/Data/metadata/SDE_Current/seagrass_bigbend_2006_poly.htm
Choctawhatchee Bay: http://atoll.floridamarine.org/data/metadata/SDE_Current/seagrass_chotawhatchee_2007_poly.htm
Tampa Bay: http://www.swfwmd.state.fl.us/data/gis/layer_library/category/swim
Indian R. Lagoon: http://www.sjrwmd.com/gisdevelopment/docs/themes.html

Table 2: Summary of seagrass depth estimates (m) for each segment using all grid locations in Fig. 4. Whole segment estimates were obtained from all seagrass depth data for each segment. tab:est_summ

Segment[a]	Whole segment	Mean	St. Dev.	Min	Max
BB					
$Z_{c,\,min}$	1.25	1.33	0.82	0.00	2.64
$Z_{c,\,med}$	2.46	1.68	0.77	0.66	2.85
$Z_{c,\,max}$	3.66	2.03	0.80	0.86	3.31
CB					
$Z_{c,\,min}$	1.82	1.57	0.72	0.00	2.27
$Z_{c,\,med}$	2.16	1.98	0.46	1.19	2.48
$Z_{c,\,max}$	2.50	2.40	0.32	1.86	2.74
OTB					
$Z_{c,\,min}$	0.61	0.52	0.29	0.05	0.98
$Z_{c,\,med}$	0.88	0.85	0.27	0.30	1.24
$Z_{c,\,max}$	1.15	1.18	0.39	0.37	1.81
UIRL					
$Z_{c,\,min}$	1.25	1.32	0.23	1.00	2.02
$Z_{c,\,med}$	1.51	1.49	0.21	1.12	2.08
$Z_{c,\,max}$	1.77	1.66	0.21	1.23	2.14

[a]BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon.

Table 3: Summary of uncertainty for seagrass depth estimates (m) for each segment using all grid locations in Fig. 5. The uncertainty values are equally applicaable to each seagrass depth measure ($Z_{c,\,min}$, $Z_{c,\,med}$, $Z_{c,\,max}$). tab:sens_summ

Segment[a]	Mean	St. Dev	Min	Max
BB	0.11	0.10	0.01	0.35
CB	0.72	0.74	0.22	2.52
OTB	0.36	0.28	0.11	1.04
UIRL	0.09	0.06	0.01	0.30

[a]BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon.

Table 4: Summary of water clarity data and estimated light requirements for all bay segments of the Indian River Lagoon and Tampa Bay. Water clarity data were obtained from secchi observations in the Florida Impaired Waters Rule database for all available locations and dates within ten years of the seagrass survey in each bay. Values are minimum and maximum years of secchi data, sample size of secchi data (n_{Secchi}), sample size of seagrass depth estimates (n_Z) at each unique secchi location, mean values (m) of secchi data, mean $Z_{c,\,max}$, and estimated % light requirements for each segment. Summaries are based primarily on data in Figs. 6 and 7. tab:secc_summ

Segment[a]	Min year	Max year	n_{Secchi}	n_Z	Secchi	$Z_{c,\,max}$	% light
Indian River Lagoon							
BR	2000	2009	909	21	1.06	1.27	17.91
LCIRL	2000	2009	656	19	1.03	1.36	11.62
LIRL	2000	2005	111	6	0.93	1.88	3.68
LML	2000	2009	239	13	1.11	1.13	14.07
LSL	2000	2005	52	3	0.94	2.90	0.97
UCIRL	2000	2009	1165	35	1.13	1.21	9.33
UIRL	2000	2009	599	15	1.30	1.15	22.30
UML	2000	2009	258	11	1.03	1.42	14.96
Tampa Bay							
HB	2001	2003	412	10	1.25	1.25	16.24
LTB	2001	2009	807	26	2.47	2.06	19.18
MTB	2001	2009	571	16	2.18	1.76	25.27
OTB	2001	2003	671	15	1.44	1.18	23.78

[a]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, HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

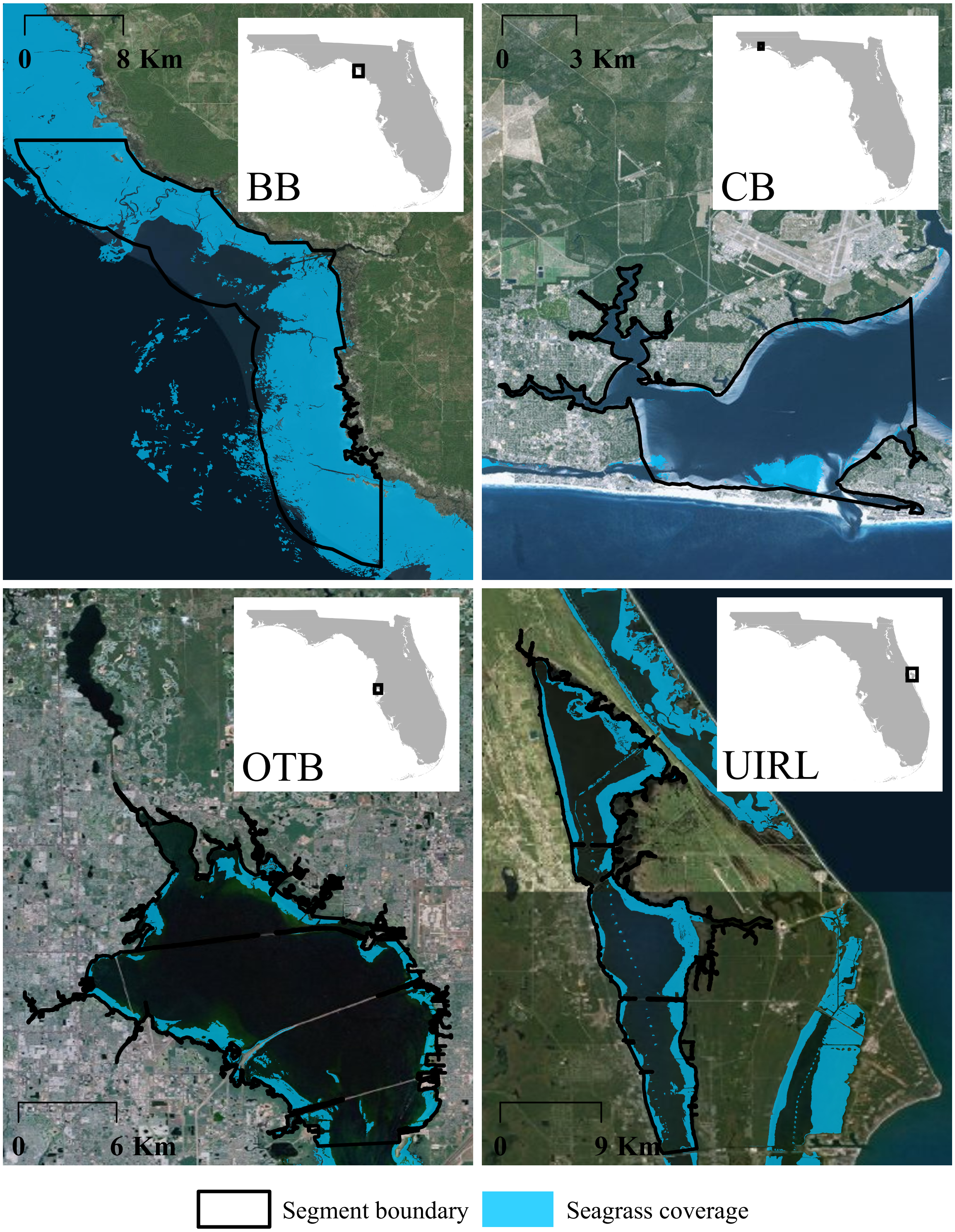

Fig. 1: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (CB: Choctawhatchee Bay), 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), and 2009 (UIRL: Upper Indian R. Lagoon).

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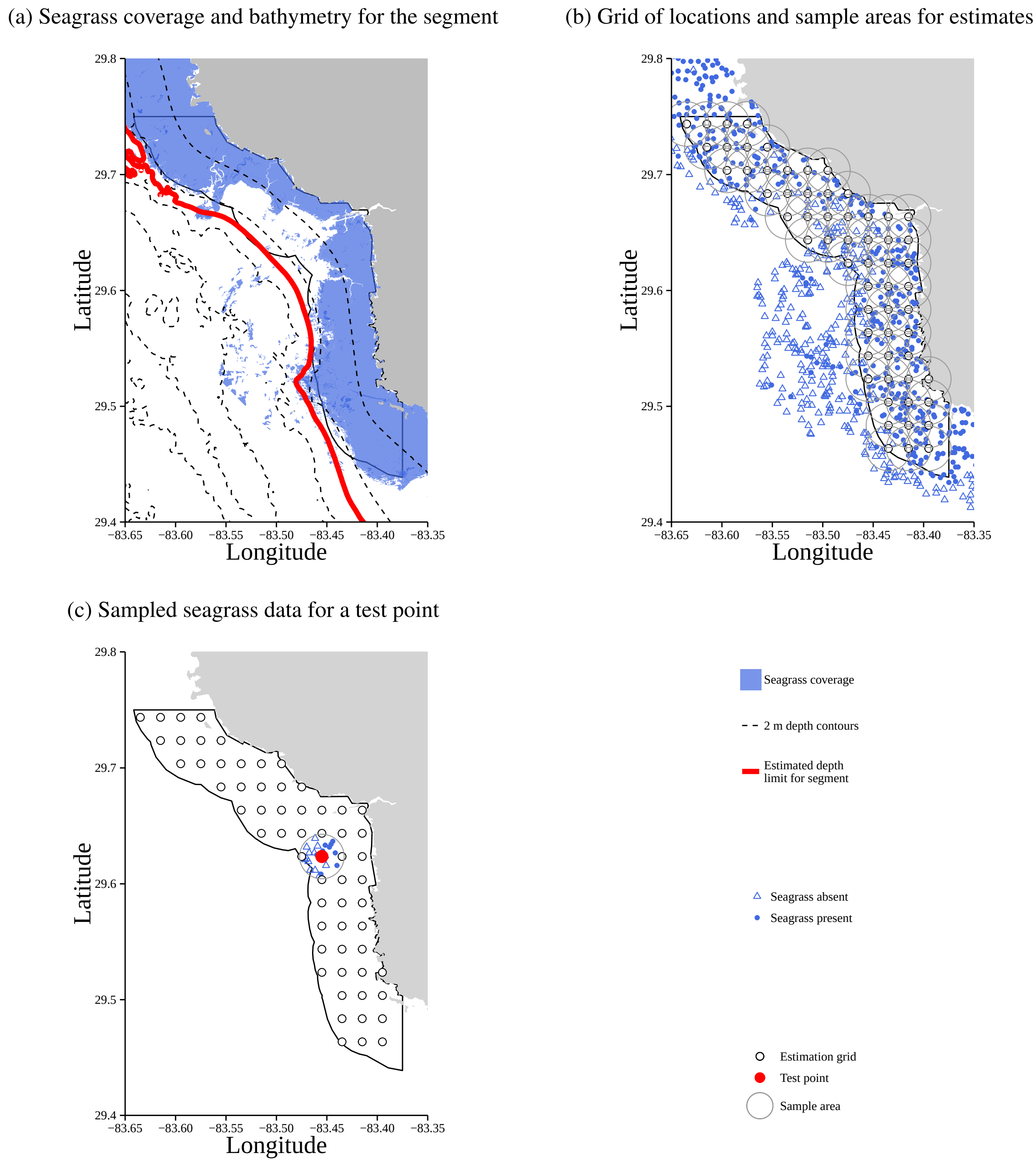

Fig. 2: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 2a shows the seagrass coverage and depth contours at 2 meter intervals, including the whole segment estimate for depth of colonization. Fig. 2b shows a grid of sampling locations with sampling radii for estimating Z_c and seagrass depth points derived from bathymetry and seagrass coverage layers. Fig. 2c shows an example of sampled seagrass depth points for a test location. Estimates in Fig. 3 were obtained from the test location in Fig. 2c. {fig:buff_

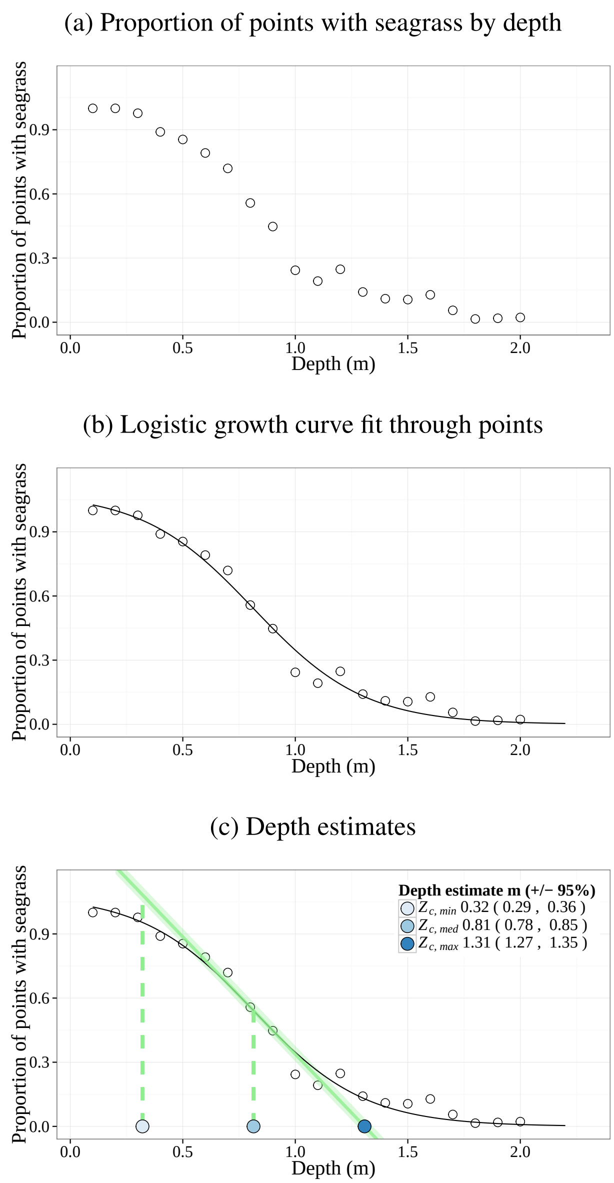

Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 2. Fig. 3b adds a decreasing logistic growth curve fit through the points. Fig. 3c shows three depth estimates based on a linear curve fit through the inflection point of logistic growth curve. {fig:est_e

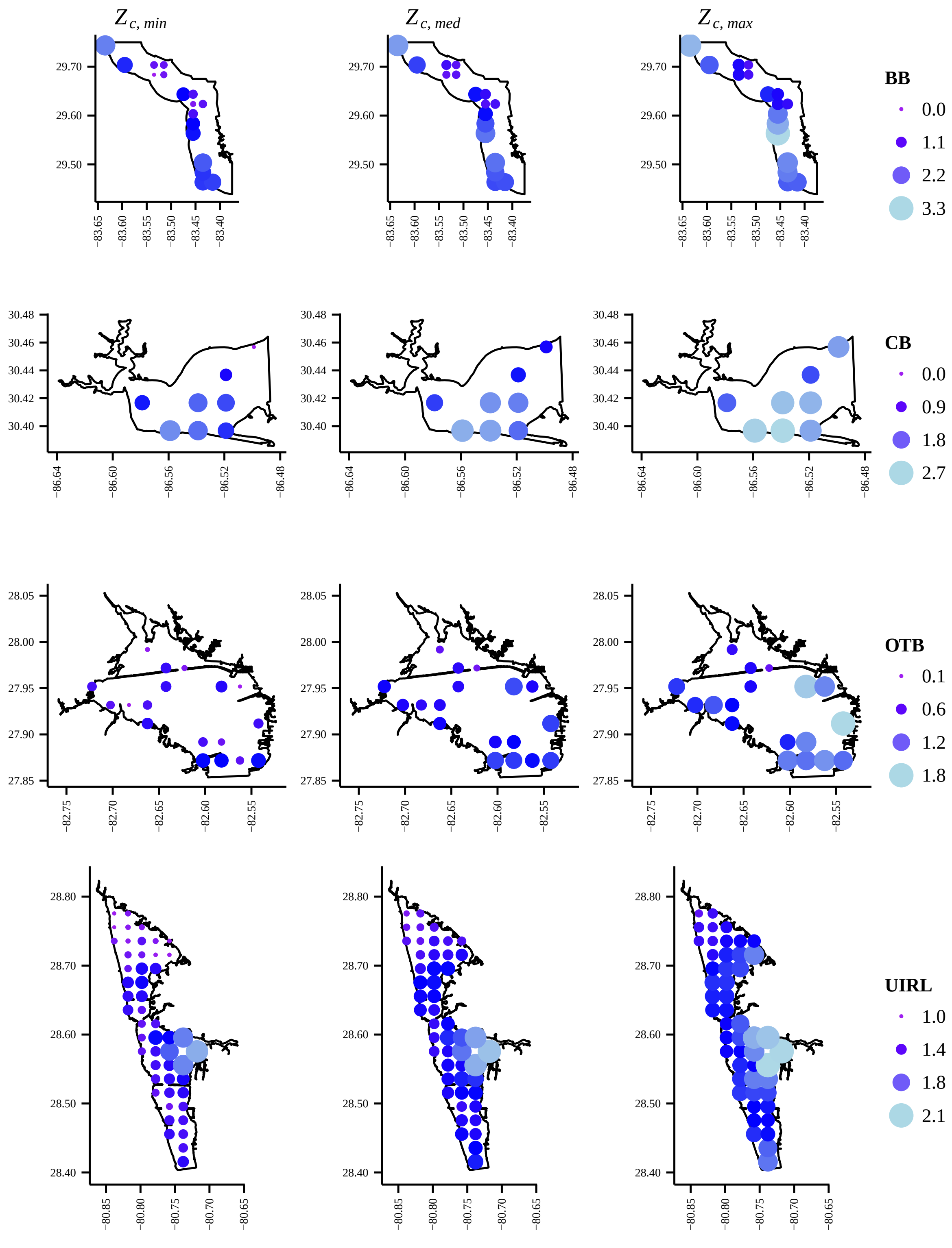

Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Estimates include minimum ($Z_{c,\,min}$), median ($Z_{c,\,med}$), and maximum depth of colonization ($Z_{c,\,max}$). Estimates are assigned to grid locations for each segment, where grid spacing was fixed at 0.02 decimal degrees. Radii for sampling seagrass bathymetric data around each grid location were fixed at 0.06 decimal degrees. BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon.

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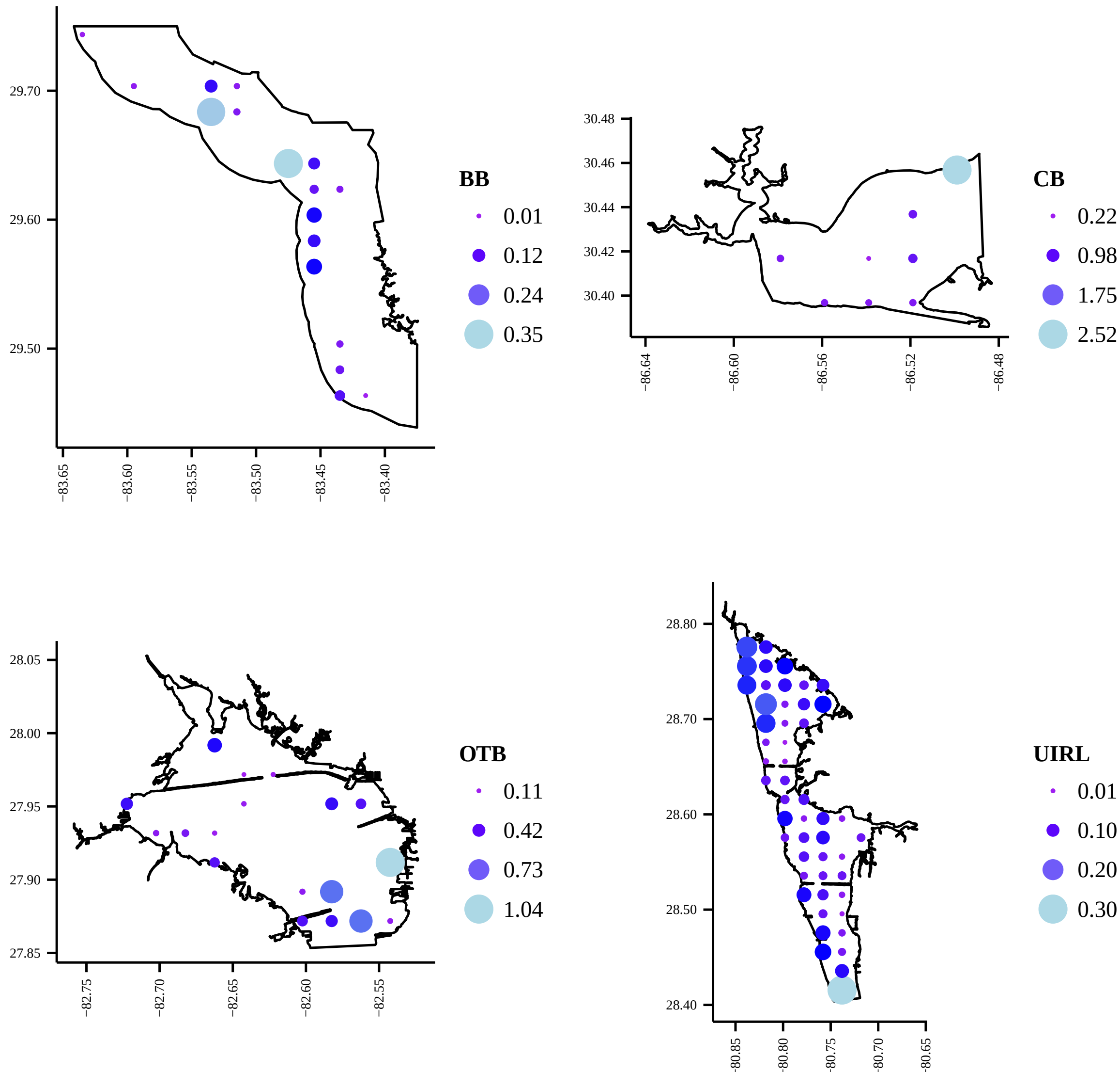

Fig. 5: Size of confidence intervals (m) for depth of colonization estimates in Fig. 4. Points are colored and sized based on the difference between the upper and lower bounds of a 95% confidence interval for all three Z_c estimates ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$). Bounds were obtained using Monte Carlo simulations to estimate uncertainty associated with the inflection point of the estimated logistic curve (Fig. 3) for each sample. BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon. {fig:all_

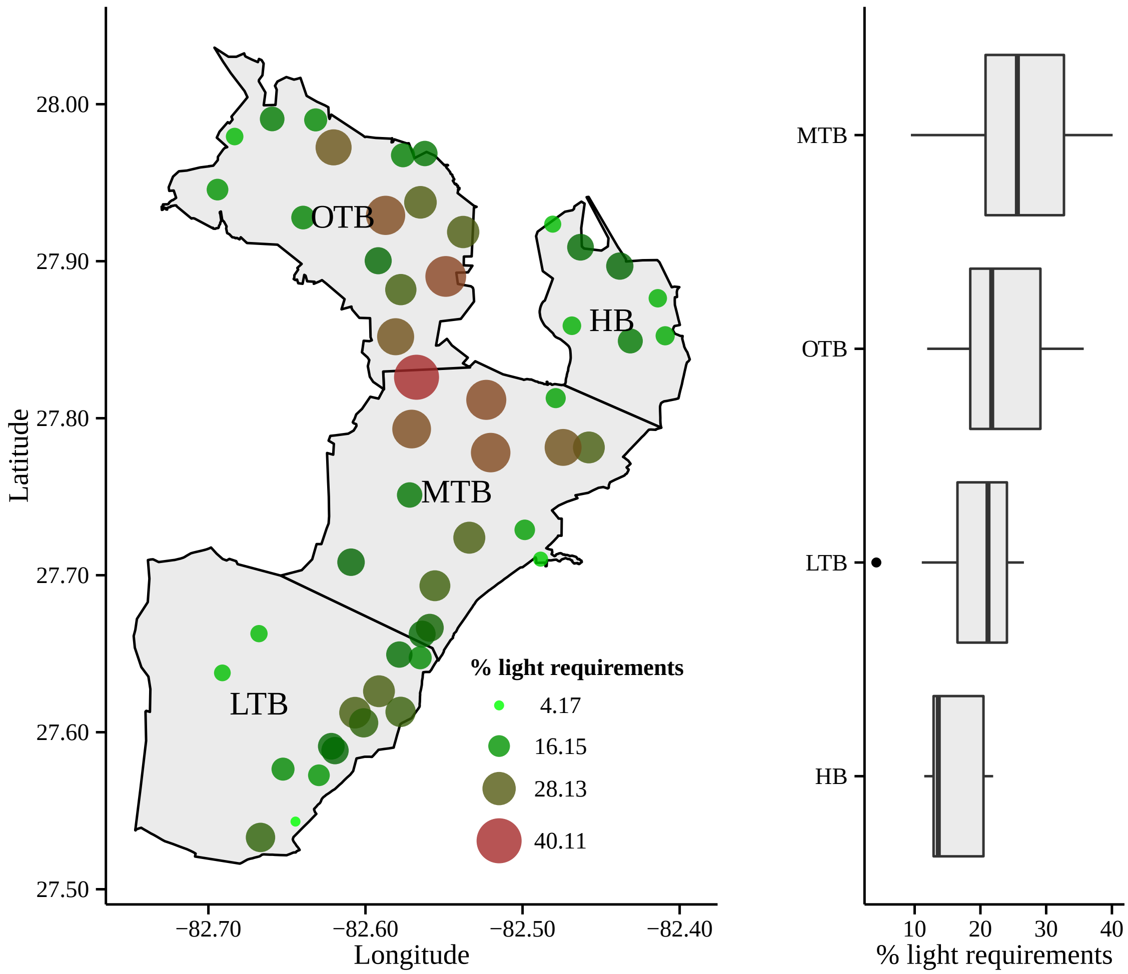

Fig. 6: Estimated light requirements of seagrass for multiple locations in Tampa Bay, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots where the dimensions are the 25$^{\mathrm{th}}$ percentile, median, and 75$^{\mathrm{th}}$ percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. Light requirements are based on daily average secchi values for each location using all observations for Tampa Bay, estimated maximum depth of colonization using a radius of 0.7 decimal degrees for each secchi location to sample seagrass depth points for 2010 coverage data, and empirical relationships described by eq. (3). HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

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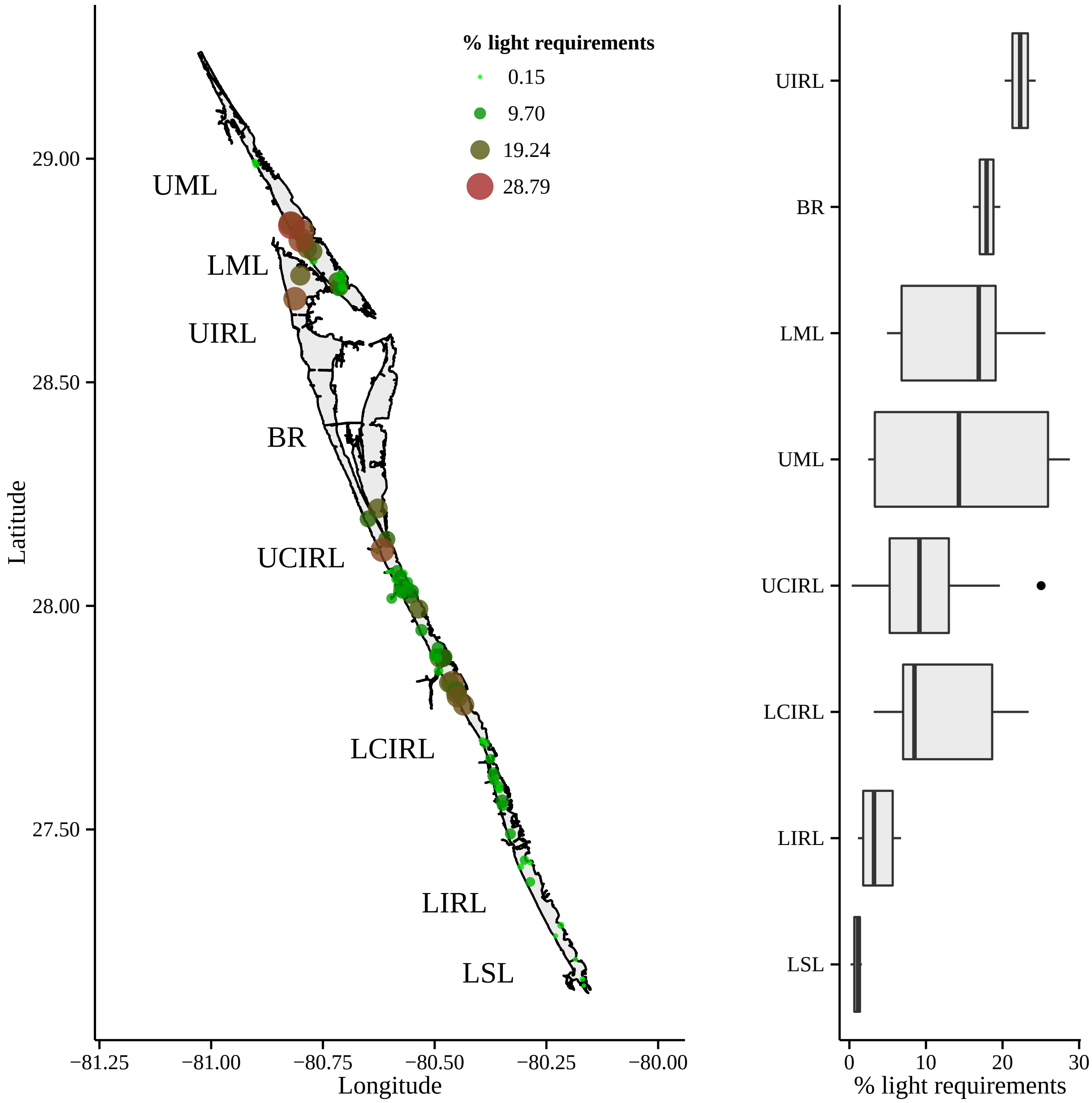

Fig. 7: Estimated light requirements of seagrass for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots as in Fig. 6. Light requirements are based on daily average secchi values for each location using all observations for Tampa Bay, estimated maximum depth of colonization using a radius of 0.02 decimal degrees for each secchi location to sample seagrass depth points for 2009 coverage data, and empirical relationships described by eq. (3). 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:light