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

Marcus W. Beck[1], James D. Hagy III[2], Chengfeng Le[3]

[1]*ORISE Research Participation Program*
USEPA National Health and Environmental Effects Research Laboratory
Gulf Ecology Division, 1 Sabine Island Drive, Gulf Breeze, FL 32561
Phone: 850-934-2480, Fax: 850-934-2401, Email: beck.marcus@epa.gov

[2]*USEPA National Health and Environmental Effects Research Laboratory*
Gulf Ecology Division, 1 Sabine Island Drive, Gulf Breeze, FL 32561
Phone: 850-934-2455, Fax: 850-934-2401, Email: hagy.jim@epa.gov

[3]*ORISE Research Participation Program*
USEPA National Health and Environmental Effects Research Laboratory
Gulf Ecology Division, 1 Sabine Island Drive, Gulf Breeze, FL 32561
Phone: 850-934-9308, Fax: 850-934-2401, Email: le.chengfeng@epa.gov

Abstract

Physiological relationships between water clarity and growth of submersed aquatic vegetation have been used to characterize nutrient limits in aquatic systems. Specifially, the maximum limit of depth of colonization (Z_c) is a useful measure of seagrass growth that describes response to light attenuation in the water column. However, lack of standardization among methods for estimating Z_c has limited the description of habitat requirements at relevant spatial scales. An algorithm is presented for estimating seagrass Z_c using geospatial datasets that are commonly available for coastal regions. A defining characteristic of the algorithm is the ability to estimate Z_c using a flexible spatial unit such that the quantified values can be appplied to a specific area of interest. These spatially-resolved estimates of Z_c can then be related to light attenuation to develop a characterization of factors that limit seagrass growth, such as minimum light requirements at depth. Four distinct coastal regions of Florida were evaluated to describe heterogeneity in seagrass growth patterns on relatively small spatial scales. The analysis was further extended to entire bay systems to quantify minimum light requirements using spatially-explicit Z_c values and satellite-derived light attenuation. Sensitivity analyses indicated that confidence intervals for Z_c were within reasonable limits for each case study, although the ability to quantify Z_c varied with characteristics of the sampled data. Z_c estimates also varied along water quality gradients such that seagrass growth was more limited near locations with reduced water clarity. Site-specific characteristics that contributed to variation in growth patterns were easily distinguished using the algorithm as compared to more coarse estimates of Z_c. Minimum light requirements for the Indian River Lagoon (13.4%) on the Atlantic Coast were substantially lower than those for Tampa Bay (30.4%) and Choctawhatchee Bay (47.1%) on the Gulf Coast. High light requirements for Choctawhatchee Bay may indicate regional differences in species requirements or additional factors, such as epiphyte growth, that further reduce light availability at the leaf surface in addition to water column attenuation. A spatially robust characterization of seagrass Z_c is possible for other regions because the algorithm is transferable with minimal effort to novel datasets.

Key words: depth of colonization, estuary, Florida, light requirements, seagrasses, water clarity

1 Introduction

Seagrasses are ecologically valuable components of aquatic systems 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, seagrass beds create habitat for juvenile fish and invertebrates by reducing wave action and stabilizing sediment (Williams and Heck 2001, Hughes et al. 2009). Seagrasses also respond to changes in water clarity through physiological linkages with light availability. Seagrass communities in productive aquatic systems may be light-limited as increased nutrient loading reduces water clarity through increased algal concentration (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) and are often used to characterize light regimes sufficient to maintain habitat (Steward et al. 2005). Seagrass depth limits have also been used to establish quantititative criteria for nutrient load targets for the maintenance of water quality (Janicki and Wade 1996). Seagrasses are integrative of system-wide conditions over time in relation to changes in nutrient regimes (Duarte 1995) and are often preferred biological endpoints to describe ecosytem response to perturbations relative to more variable taxa (e.g., phytoplankton). Quantifying the relationship of seagrasses with water clarity is a useful approach to understanding ecological characteristics of aquatic systems with potential insights into system response to disturbance (Greve and Krause-Jensen 2005).

Many techniques have been developed for estimating seagrass depth limits to better understand water quality dynamics. Such efforts have been useful for site-specific approaches where the analysis needs are driven by a particular question (e.g., Iverson and Bittaker 1986, Hale et al. 2004). However, lack of standardization among methods has prevented broad-scale comparisons between regions and has even contributed to discrepancies between measures based on the technique (Spears et al. 2009). The availability of geospatial data that describe areal seagrass and bathymetric coverage suggests standardized techniques can be developed that can be applied across broad areas. Conversely, site-specific approaches with such datasets typically quantify habitat requirements within predefined management units that may prevent generalizations outside of the study area. For example, Steward et al. (2005) describe use of a segmentation scheme for the Indian River Lagoon on the Atlantic coast of Florida to assign seagrass depth limits to 19 distinct geospatial units. Although useful for the specific study goals, substantial variation in growth patterns and water quality characteristics at different spatial scales may prevent more detailed analyses. Methods for estimating seagrass depth limits should also be reproducible for broad-scale comparisons, while also maintaining flexibility based on the objectives. Such techniques can facilitate comparisons between regions given the spatial coverage and annual availability of many geospatial data sources.

Estimating seagrass light requirements is a useful application of maximum depth limits and water clarity data. Although growth of submersed aquatic plants is generally most limited by light availability (Barko et al. 1982, Hall et al. 1990, Dennison et al. 1993), substantial variation in light requirements may suggest additional factors are limiting (Dennison et al. 1993, Choice et al. 2014). Minimum light requirements for seagrasses are on average 11% of surface irradiance (Duarte 1991), although values may range from less than 5% to greater than 30% depending on site conditions (Dennison et al. 1993). Substantial variation in light requirements has been observed between species or based on regional differences in community attributes. For example, significant variation in light requirements for the Gulf Coast of peninsular Florida were attributed to morphological and physiological differences between species and adaptations to regional light regimes (Choice et al. 2014). Additional factors may also contribute to high estimates of light requirements, such as excessive epiphytic algal growth that reduces light availability on the leaf surface (Kemp et al. 2004). Spatial heterogeneity in light requirements is, therefore, a useful diagnostic tool for identifying factors that affect seagrass growth.

In addition to accurate measures of depth of colonization, the availability of water clarity data that are evenly distributed through space in time has also limited estimates of seagrass light requirements. Secchi observations can provide reliable measures of water clarity (USEPA 2006), although secchi data can be biased by location. Monitoring programs may have unbalanced coverage of aquatic resources with greater perceived importance relative to those that may have more ecological significance (Wagner et al. 2008, Lottig et al. 2014). Morever, infrequent field measurements that are limited to discrete time periods are more descriptive of short-term variability rather than long-term trends in water clarity (Elsdon and Connell 2009). Seagrasses growth patterns are integrative of seasonal and inter-annual patterns in water clarity, such that estimates of light requirements may be limited if water clarity measurements inadequately describe temporal variation. Remote sensing products can provide reliable estimates of water clarity and could be used to develop a more coherent description of relevant ecosystem characteristics. Although algorithms have been developed for coastal waters to estimate surface reflectance from satellite data (Woodruff et al. 1999, Chen et al. 2007), this information has rarely been used to develop descriptions of seagrass light requirements at a spatial resolution consistent with most remote sensing products.

Quantitative and flexible methods for estimating seagrass depth limits and light requirements can improve descriptions of aquatic habitat, thus enabling potentially novel insights into ecological characteristics of aquatic systems. This article describes a method for estimating seagrass depth of colonization using geospatial datasets to create a spatially-resolved and flexible measure. In particular, an empirical algorthm is described that estimates seagrass depth limits from coverage maps and bathymetric data using an *a priori* defined area of influence. These estimates are combined with measures of water clarity to develop a spatial characterization of light requirements. The specific objectives are to 1) describe the method for estimating seagrass depth limits, 2) apply the technique to four distinct regions of Florida to illustrate improved clarity of description, and 3) develop a spatial description of depth limits, water clarity, and light requirements for the case studies. The method is first illustrated using four relatively small areas of larger coastal regions followed by extension to entire estuaries to characterize spatial variation in light requirements. Overall, these methods inform the description of seagrass growth patterns by developing a more spatially relevant characterization of aquatic habitat. The method is applied to data from Florida, although the technique is easily transferable to other regions with comparable data.

2 Methods

Estimates of seagrass depth of colonization (Z_c) that are derived from relatively broad spatial aggregations, such as predefined management areas, may not fully describe relevant variation depending on the question of interest. Fig. 1a shows variation in seagrass distribution for a management segment (thick polygon) in the Big Bend region of Florida. The maximum depth colonization, shown as a red countour line, is based on a segment-wide average of all seagrasses within the polygon. Although such an estimate is not necessarily inaccurate, substantial variation in seagrass growth patterns at smaller spatial scales is not adequately described. In particular, Z_c is greatly over-estimated at the outflow of the Steinhatchee River (northeast portion of the segment) where high concentrations of dissolved organic matter reduce water clarity and naturally limit seagrass growth (personal communication, Nijole Wellendorf, Florida Department of Environmental Protection). 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. The following is a summary of data sources, methods and rationale for developing a flexible algorithm that improves spatial resolution in seagrass Z_c estimates. Data and methods described in Hagy In review are used as a foundation for developing the approach.

2.1 Data sources

2.1.1 Study sites

Four locations in Florida were chosen for the analysis: the Big Bend region (northeast Gulf of Mexico), Choctawhatchee Bay (pandhandle), Tampa Bay (central Gulf Coast), and Indian River Lagoon (east coast) (Table 1 and Fig. 2). These locations represent different geographic regions in the state, in addition to having available data and observed gradients in water clarity that contribute to heterogeneity in seagrass growth patterns. Coastal regions and estuaries in Florida are partitioned into distinct spatial units based on a segmentation scheme developed by US Environmental Protection Agency (EPA) for the development of numeric nutrient criteria. Site-specific estimates of seagrass depth colonization and light requirements are the primary focus of the analysis, with emphasis on improved clarity of description with changes in spatial context. As such, estimates that use management segments as relevant spatial units are used as a basis of comparison to evaluate variation in growth patterns at difference scales. The analysis focuses on Choctawhatchee Bay (central pandhandle), the big bend region (northeast pandhandle), Tampa Bay (west coast), and Indian River Lagoon (east coast) . One segment within each region is first evaluated to illustrate use of the method and variation at relatively small spatial scales. The segments included a location near the outflow of the Steinhatchee River for the Big Bend (BB) region, Old Tampa Bay (OTB), Upper Indian River Lagoon (UIRL), and Western

Choctawhatchee Bay (WCB) Fig. 2). A second analysis focused on describing seagrass depth limits for the entire area of each bay (Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon) to develop a spatial description of light requirements.

2.1.2 Seagrass coverage and bathymetry

Spatial data describing seagrass aerial coverage combined with co-located bathymetric depth information were used to estimate Z_c. These geospatial data products are publically 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.

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 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 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. Raster bathymetric layers were converted to vector point layers to combine with seagrass coverage maps, described below. 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 sea level (MSL) using the NOAA VDatum tool (http://vdatum.noaa.gov/).

2.1.3 *Water clarity estimates*

Seagrass light requirements can be estimated by evaluating spatial relationships between depth of colonization and water clarity. These relationships were explored using Z_c and water clarity estimates for the entire areas of Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon. Limited data in the Big Bend region prohibited analysis in this location. Satellite images were used to create a gridded 1 km^2 map as estimated water clarity (m, Tampa Bay) or light extinction (K_d, m^{-1}, Choctawhatchee Bay). Secchi data were used directly to evaluate light requirements for the Indian River Lagoon because satellite data were inestimable.

Daily MODIS (Aqua level-2) satellite data for the preceding five years from the seagrass coverage layer were downloaded from the NASA website (http://oceancolor.gsfc.nasa.gov/) for Tampa and Choctawhatchee Bays. Images were reprocessed using the SeaWiFS Data Analysis System software (SeaDAS, Version 7.0). In Tampa Bay, water clarity was derived from daily MODIS images using a previously-developed algorithm (Chen et al. 2007). Monthly and annual mean water clarity was calculated from the daily images, which were then averaged to create a single layer. Similarly, K_d in Choctawhatchee bay was derived from MODIS using the QAA algorithm (Lee et al. 2005). Field measurements of K_d for 2010 obtained at ten locations in Choctawhatchee Bay at monthly intervals were used to correct the satellite K_d values. Annual mean field measurements of K_d were compared to the annual mean satellite estimates in 2010. An empirical correction equation was developed based on the difference between the cumulative distribution of the in situ K_d estimates and the satellite estimated K_d at the same locations. The 2010 correction was applied to all five years of annual mean satellite data prior to averaging to create a single layer for further analysis.

Satellite estimates of water clarity were unobtainable in the Indian River Lagoon because of significant light scattering from bottom reflectance and limited resolution for narrow segments along the north-south axis. Secchi data (meters, Z_{secchi}) within the previous ten years of the seagrass coverage data (i.e., 1999–2009) were obtained from update 40 of the Impaired Waters Rule (IWR) database for all of the Indian River Lagoon. More than five years of clarity data was used for Indian River Lagoon due to uneven temporal coverage relative to the satellite-based estimates described above. Stations with less than five observations and observations that were flagged indicating that the value was lower than the maximum depth of the observation point were removed. Secchi data were also compared with bathymetric data to verify unflagged values were not missed by initial screening.

2.2 Estimation of seagrass depth of colonization

The approach to estimating seagrass depth of colonization uses combined seagrass coverage maps and bathymetric depth data described above. The combined layer used for analysis was a point shapefile with attributes describing location (latitude, longitude, segment), depth (m), and seagrass (present, absent). Seagrass Z_c values are estimated from these data by quantifying the proportion of points with seagrass at each observed depth. Three unique measures describing seagrass depth limits obtained from these data are minimum ($Z_{c,\,min}$), median ($Z_{c,\,med}$), and maximum ($Z_{c,\,max}$) depth of colonization. Operationally, these terms describe characteristics of the seagrass coverage map with quantifiable significance. $Z_{c,\,max}$ is defined as the deepest depth at which a significant coverage of mappable seagrasses occured independent of outliers, whereas $Z_{c,\,med}$ is the median depth occurring at the deep water edge. $Z_{c,\,min}$ is the depth at which seagrass coverage begins to decline with increasing depth and may not be statistically distinguishable from zero depth, particularly in turbid waters. Specific methods for estimating each Z_c value using spatially-resolved information are described below.

The spatially-resolved approach for estimating Z_c begins by choosing an explicit location in cartesian coordinates within the general boundaries of the available data. Seagrass depth data (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the chosen location are selected for estimating seagrass Z_c values (Fig. 1). The estimate for each location is quantified from a plot of the proportion of sampled points that contain seagrass at decreasing 0.1 meter depth bins from the surface to the maximum observed depth in the sample (Fig. 3a). Although the chosen radius for selecting depth points is problem-specific, the minimum radius should be chosen to 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. If more than one location is used to estimate Z_c, appropriate radii for each point would have minimal overlap with the seagrass depth data sampled by neighboring 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 minimum and maximum depths of colonization. The curve is fit by minimizing the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992) with starting parameters estimated from the observed data that are initial approximations of the curve characteristics. The model has the following form:

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

where the proportion of points occupied by seagrass at each depth, Z, is defined by a logistic curve with an asymptote α, a midpoint inflection β, and a scale parameter γ. 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. 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 upper asymptote of the logistic growth curve. The median depth of seagrass colonization, $Z_{c,\,med}$, is the depth halfway between $Z_{c,\,min}$ and $Z_{c,\,max}$. $Z_{c,\,med}$ is typically the inflection point of the logistic growth curve.

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 sampled within the chosen radius. First, estimates were provided only if a sufficient number of seagrass depth points were present in the sampled data 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. 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, estimates were unavailabled if hte logistic curve 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.

2.3 Estimating uncertainty in depth of colonization estimates

Confidence intervals for the Z_c values were estimated using a Monte Carlo simulation approach that considered the variance and covariance between the model parameters (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 was 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.

The algorithm for estimating Z_c was implemented custom-made and pre-existing functions in program R. Nonlinear least squares models were based on the `nls` and `SSlogis` functions that used a self-starting logistic growth model (Bates and Chambers 1992, R Development Core Team 2014). Multivariate normal distributions used to evaluate uncertainty were simulated using functions in the MASS package (Venables and Ripley 2002). Geospatial data were imported and processed using functions in the rgeos and sp packages (Bivand et al. 2008, Bivand and Rundel 2014).

2.4 Evaluation of spatial heterogeneity of seagrass depth limits

Spatially-resolved estimates for seagrass Z_c were obtained for each of the four coastal segments described above: BB, OTB, UIRL, and WCB. Segment-wide estimates obtained using all data were used as a basis of comparison such that departures from these values at smaller scales were evidence of spatial heterogeneity in seagrass growth patterns and improved clarity of description in depth estimates. 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 boundaries to allow sampling by grid points that occurred near the edge of the segment. Initial spacing between sample points was chosen arbitrarily as 0.01 decimal degrees, which is approximately 1 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, while also ensuring an adequate number of locations were sampled that included seagrass.

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

Relationships between seagrass depth limits and water clarity were explored by estimating light requirements for the entire areas of Choctawhatchee Bay, Tampa Bay, and Indian River Lagoon. Seagrass depth limits that were co-located with estimates of water clarity, either as satellite-based estimates or in situ secchi observations, were related using empirical light attentuation equations. The Lambert-Beer equation describes the exponential decrease of light availability with depth:

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

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). Light requirements of seagrass at a specific location can be estimated by rearranging eq. (3):

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

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_{secchi}, such that $c = K_d \cdot Z_{secchi}$, where c has been estimated as 1.7 (Poole and Atkins 1929, Idso and Gilbert 1974):

$$\%\, light = \exp\left(-\left(\frac{1.7}{Z_{secchi}}\right) \cdot Z_{c,\, max}\right) \tag{5}$$

such that K_d in eq. (4) is replaced by the ratio of the conversion factor and Z_{secchi}.

Two different approaches were used to estimate light requirements based on the availability of satellite-based estimates or in situ observations of water clarity. For Choctawhatchee and Tampa Bay, an evenly-spaced grid of sampling points was created that covered each bay to estimate $Z_{c,\, max}$ and sample the raster grid of satellite-derived water clarity. Grid spacing was different in each bay (0.005 for Choctawhatchee Bay, 0.01 for Tampa Bay) to account for variation in spatial scales of seagrass coverage. Equation (4) was used to estimate light requirements at each point for Choctawhatchee Bay and eq. (5) was used for Tampa Bay. Similarly, the geographic coordinates for each in situ secchi measurement in the Indian River Lagoon were used as locations for estimating $Z_{c,\, max}$ and light requirements using eq. (5). Excessively small estimates for light requirements were removed for Indian River Lagoon which were likely caused by shallow secchi observations that were not screened during initial data processing. Sampling radii for locations in each bay were chosen to maximize the number of points with estimable values for $Z_{c,\,max}$ (as described in section 2.2), while limiting the upper radius to adequately describe variation in seagrass growth patterns for emphasizing gradients in light requirements. Radii were fixed at 0.04 decimal degrees for Choctawhatchee Bay, 0.1 decimal degrees for Tampa Bay, and 0.15 decimal degrees for Indian River Lagoon. The estimated maximum depth values and light requirements of each point were plotted by location to evaluate spatial variation in seagrass growth as a function of light-limitation.

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), Upper Indian River Lagoon (228.5 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 Upper Indian River Lagoon (32.8 %), Old Tampa Bay (11.9 %), and Western 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. 2). 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 Upper Indian River Lagoon 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 Upper Indian River Lagoon segments. Mean depth was less than 5 meters for each segment, excluding Western Choctawhatchee Bay which was slightly deeper than the other segments (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 (1.4 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 that did not consider spatially explicit locations (i.e., segment-wide) 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 Western Choctawhatchee Bay (1.8 m) and shallowest for Old Tampa Bay (0.6 m). In most cases, the averages of all grid-based estimates were less than the whole segment estimates, indicating 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 indicated seagrasses grew to approximately 2.1 m, which was 1.6 m less than the whole segment estimate. 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 Upper 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 Upper 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 Upper Indian River Lagoon segment near the Merrit Island National Wildlife Refuge. Seagrasses were estimated to grow at maximum depths up to 2.2 m on the eastern portion of the Upper Indian River Lagoon segment. Spatial heterogeneity was less distinct for the remaining segments although some patterns were apparent. 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 Western Choctawhatchee Bay segment was minimal, 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 given 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 Western 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. 4 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 Western Choctawhatchee Bay (mean width of all confidence intervals was 0.5 m) and Old Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Upper Indian River Lagoon (0.1 m) segments. The largest confidence interval for each segment was 1.4 m for Old Tampa Bay, 1.6 m for Western Choctawhatchee Bay, 0.5 m for the Big Bend, and 0.8 m for the Upper Indian River Lagoon segments. Most confidence intervals for the remaining grid locations were much smaller than the maximum in each segment (e.g., central location of the Upper Indian River Lagoon, Fig. 4). A comparison of overlapping confidence intervals for $Z_{c,\,min}$, $Z_{c,\,med}$, and $Z_{c,\,max}$ at each grid location indicated that not every measure was unique. Specifically, only 11.1% of grid points in Choctawhatchee Bay and 28.2% in Old Tampa Bay had significantly different estimates, whereas 82.4% of grid points in the Indian River Lagoon and 96.2% 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 12.4% of grid points in Old Tampa Bay and 8% 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 water clarity, seagrass depth limits and corresponding light requirements for all segments of Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon indicated substantial variation, both between and within the different bays. Satellite-derived estimates of light attenuation for Choctawhatchee Bay (as K_d, Fig. 5) and Tampa Bay (as clarity, Fig. 6) indicated variation between years and along major longitudinal and lateral axes. For Choctawhatchee Bay, K_d estimates for western and central segments were substantially lower than those for the more shallow, eastern segment. Maximum K_d values were also observed in earlier years (e.g., 2003, 2004). Clarity estimates for Tampa Bay also showed an increase towards more seaward segments, with particularly higher clarity along the mainstem. Clarity in 2006 was relatively lower than other years, with noticeable increases in 2007 and 2008. In situ secchi observations for the Indian River Lagoon followed a clear latitudinal gradient with higher values in more southern segments (Fig. 9). Very few measurements were available for the Upper Indian River Lagoon and Banana River segments, likely due to water clarity exceeding the maximum depth in shallow areas.

Seagrass Z_c estimates were obtained for 259 locations in Choctawhatchee Bay, 566 locations in Tampa Bay, and 37 locations in the Indian River Lagoon (Table 4 and Figs. 7 to 9). Mean $Z_{c,\,max}$ for each bay was 2.5, 1.7, and 1.3 m for Choctawhatchee Bay, Tampa Bay, and Indian River Lagoon, respectively, with all values being significantly different beetween bays (ANOVA, $F = 326.9$, $df = 2, 859$, $p < 0.001$, followed by Tukey multiple comparison, $p < 0.001$ for all). Generally, spatial variation in $Z_{c,\,max}$ followed variation in light requirements for broad spatial scales with more seaward segments or areas near inlets having lower light requirements. Mean light requirements were significantly different between all bays (ANOVA, $F = 463.7$, $df = 2, 859$, $p < 0.001$, Tukey $p < 0.001$ for all), with a mean requirement of 47.1% for Choctawhatchee Bay, 30.4% for Tampa Bay, and 13.4% for Indian River Lagoon. Significant differences in light requirements between segments within each bay were also observed (ANOVA, $F = 12.1$, $df = 2, 256$, $p < 0.001$ for Choctawhatchee Bay, $F = 84.6$, $df = 3, 562$, $p < 0.001$ for Tampa Bay, $F = 7.6$, $df = 6, 30$, $p < 0.001$ for Indian River Lagoon). Post-hoc evaluation of all pair-wise comparisons of mean light requirements between segments within each bay indicated that significant differences varied. Significant differences were observed between all segments in Choctawhatchee Bay ($p < 0.001$ for all), except the central and western segments (Fig. 7). Similarly, significant differences in Tampa Bay were observed between all segments ($p < 0.05$ for all), except Middle Tampa Bay and Old Tampa Bay (Fig. 8). Finally, for the Indian River Lagoon, significant differences were observed only between the Lower Central Indian River Lagoon and the Upper ($p < 0.001$) and Lower Mosquito Lagoons ($p = 0.023$), the Lower Indian River Lagoon and the Upper ($p < 0.001$) and Lower Mosquito Lagoons ($p = 0.013$), and the Upper Central Indian River and the Upper Mosquito Lagoon ($p = 0.018$) (Fig. 9).

4 *Discussion*

Seagrass depth of colonization is tightly coupled to variation in water quality such that an accurate and reproducible method for estimating $Z_{c,\,max}$ provides biologically relevant information describing the condition of aquatic habitat. Accordingly, the ability to estimate seagrass depth of colonization and associated light requirements from relatively inexpensive sources of information has great value for developing an understanding of potentially limiting factors that affect ecosystem condition. To these ends, this study presented an approach for estimating seagrass depth of colonization from existing geospatial datasets that has the potential to greatly improve clarity of description within multiple spatial contexts. We evaluated four distinct coastal regions of Florida to illustrate utility of the method for describing seagrass depth limits at relatively small spatial scales and extended the analysis to entire bay systems by combined estimates with satellite-derived observations of water clarity to characterize spatial variation in light requirements. The results indicated that substantial variation in seagrass depth limits were observed, even within relatively small areas of interest. Estimated light requirements also indicated substantial heterogeneity within individual bays, suggesting uneven distribution of factors that limit seagrass growth patterns. To our knowledge, such an approach has yet to be implemented in widespread descriptions of aquatic habitat and there is great potential to expand the method beyond the current case studies. The reproducible nature of the algorithm also enables a context-dependent approach given the high level of flexibility.

4.1 Evaluation of the algorithm

The algorithm for estimating seagrass depth of colonization has three primary advantages that facilitated a description of aquatic habitat in each of the case studies. First, the method incorporated an empirical model fitting approach using non-linear least squares regression to characterize the reduction of seagrass coverage with increasing depth. This approach was necessary for estimating each of the three depth limits ($Z_{c,\,min}$, $Z_{c,\,med}$, $Z_{c,\,max}$) using the maximum slope of the curve. This maximum rate of decline with depth described a direct and estimable physiological response of seagrass to decreasing light availability such that each measure provided an operational characterization of growth patterns (see section 2.2). The regression approach also allowed an estimation of confidence in Z_c values by accounting for uncertainty in each of the three parameters of the logistic growth curve (α, β, γ). Indications of uncertainty are required components of any esimation technique that provide an implicit indication of the quality of data used to estimate the model fit. By default, estimates with confidence intervals for $Z_{c,\,max}$ that included zero were discarded to remove highly imprecise estimates. Despite this restriction, some examples had exceptionally large confidence intervals relative to neighboring estimates (e.g., center of Upper Indian River Lagoon, Fig. 4), which suggests not all locations are suitable for applying the algorithm. The ability to estimate Z_c and to discriminate between the three measures depended on several factors, the most important of which is the extent to which the sampled seagrass points described a true reduction of seagrass coverage with depth. Sampling method (e.g., chosen radius) as well as site-specific characteristics (e.g., bottom-slope, actual occurrence of seagrass) are critical factors that directly influence confidence in Z_c estimates. A pragmatic approach should be used when applying the algorithm to novel data such that the location and chosen sample radius should be suitable for characterizing growth conditions within the limits of the analysis objectives.

A second advantage is that the algorithm is highly flexible depending on the desired spatial context. Although this attribute directly affects confidence intervals, the ability to arbitrarily choose a sampling radius that is specific to a problem of interest can greatly improve the characterization of aquatic habitat given site-level characteristics. The previous example described for the Big Bend region highlights this flexibility, such that a segment-wide estimate was inadequate for characterizing $Z_{c,\,max}$ that was limited near the outflow of the Steinhatchee river. The ability to choose a smaller sampling radius more appropriate for the location produced stimates of $Z_{c,\,max}$ that reflected known differences in water clarity near the outflow relative to other locations in the segment. However, an important point is that a segment-wide estimate is not necesarily biased such that a sampling radius that covers a broad spatial area could be appropriate depending on the question of interest. If in fact the effect of water clarity near the outflow of the Steinhatchee River was not a concern, the segment-wide estimate could describe seagrass growth patterns for the larger area without inducing descriptive bias. However, water quality standards as employed by management agencies are commonly based on predefined management units, which may not be appropriate for all locations. The flexibility of the algorithm could facilitate the development of point-based, site-specific standards that eliminates the need to develop or use a pre-defined classification scheme. In essence, the relevant management area can be defined a priori based on known site characteristics.

The ability to use existing geospatial datasets is a third advantage of the algorithm. At the most generic level, the algorithm requires only georeferenced bathymetry data and seagrass coverage for a particular year to develop a spatial description of annual growth patterns. These datasets are routinely collected by various agencies at annual or semi-annual cycles for numerous coastal regions. Accordingly, data availability and the relatively simple method for estimating Z_c suggests that spatial descriptions of seagrass coverage could be developed for much larger regions with minimal effort. The availability of satellite-based products with resolutions appropriate for the scale of assessment of large coastal regions could also facilitate a broader understanding of seagrass light requirements when combined with Z_c estimates. However, data quality is always a relevant issue when using secondary information as a means of decision-making or addressing specific research questions. Methods for acquiring bathymetric or seagrass coverage data are generally similar between agencies such that the validity of data comparisons from multiple sources is typically not a major concern. However, the ability of seagrass coverage maps to adequately characterize growth patterns is a valid issue. The minimum mapping unit for each coverage layer is limited by the resolution of the original aerial photos, and to a lesser extent, the comparability of photo-interpreted products created by different analysts. Seagrass maps routinely classify coverage as absent, patchy, or continuous. Discrepancies between the latter two categories between regions limited the analysis to a simple binary categorization of seagrass as present or absent. An additional evaluation of comparability between categories for different coverage maps could improve the power of the analysis by increasing the descriptive capabilities of Z_c estimates. A final point of concern is applicability of the water clarity algorithm developed for Tampa Bay as applied to Choctawhatchee Bay imagery. Although we validated and corrected the light attenuation estimates with in situ data, further validation may be needed to include field observations with greater temporal and spatial coverage.

4.2 Heterogeneity in growth patterns and light requirements

Variation in seagrass depth of colonization for each of the case studies was typically most pronounced along mainstem axes of each estuary or as distance from an inlet. Greater depth of colonization was observed near seaward locations and was also most limited near river inflows.

Although an obvious conclusion would be that depth of colonization is correlated with bottom depth, i.e., seagrasses grow deeper because they can, a more biologically-relevant conclusion is that seagrass depth of colonization follows expected spatial variation in water clarity. Shallow areas within an estuary are often near river outflows where discharge is characterized by high sediment or nutrient loads that contribute to light scattering and increased attenuation. Variation in Z_c along mainstem axes was not unexpected, although the ability to characterize within-segment variation for each of the case studies was greatly improved. Seagrasses may also be limited in shallow areas by tidal stress such that a minimum depth can be defined that describes the upper limit related to dessication stress from exposure at low tide. Coastal regions of Florida, particularly the Gulf Coast, are microtidal with amplitudes generally not exceeding 0.5 meters. Accordingly, the effects of tidal stress on limiting the minimum depth of colonization were not apparent for many locations in the case studies such that $Z_{c,\,min}$ estimates were routinely observed at zero depth. Although this measure operationally defines the depth at which seagrasses begin to decline with decreasing light availability, $Z_{c,\,min}$ could also be used to describe the presence or absence of tidal stress.

The use of light attenuation data, either as satellite-derived estimates or field-based secchi observations, combined with Z_c estimates provided detailed characterizations of light requirements within the three estuaries. Light requirements varied substantially both within bays and between different coastal regions of Florida. In general, light requirements were lowest for the Indian River Lagoon, whereas estimates were higher for Tampa Bay and highest for Choctawhatchee Bay. Minimum light requirements for the Indian River Lagoon were generally in agreement with other Atlantic coastal systems (Dennison et al. 1993, Kemp et al. 2004), such that estimates typically did not exceed 25% with mean requirements of 13.4%. However, light requirements for Indian River Lagoon were based on secchi observations with uneven spatial and temporal coverage, which potentially led to an incomplete description of true variation in light attenuation. Alternative measures to estimate K_d (e.g., vertically-distributed PAR sensors) could be used when bottom depth is shallower than maximum water clarity, which is common for the Indian River Lagoon. Conversely, satellite-derived estimates of light attenuation were possible for Tampa and Choctawhatchee Bays where water column depth was sufficient to produce reasonable values. Mean light requirements for the whole of Tampa Bay were 30.4% of surface irradiance, which was in agreement with previously reported values, particularly for Lower Tampa Bay (Dixon and Leverone 1995). Estimates for Choctawhatchee Bay were substantially higher with a bay-wide average of 47.1%. The relatively higher light requirements for Gulf Coast esuaries, particularly Choctawhatchee Bay, may reflect the need for additional validation data for the conversion of satellite reflectance values to light attenuation. However, estuaries in the northern Gulf of Mexico are typically shallow and highly productive (Caffrey et al. 2014), such that high light requirements may in fact be related to the effects of high nutrient loads on water clarity. Further evaluation of seagrass light requirements in the northern Gulf of Mexico could clarify the extent to which our results reflect true differences relative to other coastal regions.

Substantial within-bay variation in light requirements was also observed such that higher light requirements were generally more common towards upper bay segments. As previously noted, variation in seagrass light requirements can be attributed to differences in physiological requirements between species or regional effects of different light regimes (Choice et al. 2014). For example, *Halodule wrightii* is the most abundant seagrass in Choctawhatchee Bay and occurs in the western polyhaline portion near the outflow with the Gulf of Mexico. Isolated patches of *Ruppia maritima* are also observed in the oligohaline eastern regions of the bay. Although $Z_{c,\,max}$ was only estimable for a few points in eastern Choctawhatchee Bay, differences in species assemblages along a salinity gradient likely explain the differences in light requirements. The decline of *R. maritima* in eastern Choctawhatchee Bay has been attributed to species sensitivity to turbidity from high rainfall events, whereas losses of *H. wrightii* have primarily been attributed to physical stress during storm overwash and high wave energy (FLDEP 2012). The relatively high light requirements of eastern Choctawhatchee Bay likely reflect differing species sensitivity to turbidity, either through sediment resuspension from rainfall events or light attenuation from nutrient-induced phytoplankton production. Similarly, high light requirements may be related to epiphyte production at the leaf surface (Kemp et al. 2004). Estimated light requirements based solely on water column light attenuation, as for secchi or satellite-derived values, may indicate unusually large light requirements if seagrasses are further limited by epiphytic growth. Although the true light requirements would be less than indicated, the estimated values provide a potentially diagnostic measure to evaluate limiting factors for seagrass growth. Epiphyte limitation may be common for upper bay segments where nutrient inputs from freshwater inflows enhance algal production (Kemp et al. 2004). For example, lower light requirements for Hillsborough Bay relative to Old Tampa Bay may reflect a reduction in epiphyte load from long-term decreases in nitrogen inputs to northeast Tampa Bay (Dawes and Avery 2010).

4.3 Conclusions

Spatially-resolved estimates of Z_c combined with high-resolution measures of light attenuation provided an effective means of evaluating variation in light requirements. In the context of seagrass management, an important realization is that light requirements, although important, may only partially describe ecosystem characteristics that influence growth patterns. Seagrasses may be limited by additional physical, geological, or geochemical factors, including effects of current velocity, wave action, sediment grain size distribution, and sediment organic content (Koch 2001). Accordingly, spatially-resolved estimates of Z_c and associated light requirements must be evaluated in the context of multiple ecosystem characteristics that may act individually or interactively with light attenuation. Extreme estimates of light requirements may suggest light attenuation is not the primary determining factor for seagrass growth. An additional constraint is the quality of data that describe water clarity to estimate light requirements. Although the analysis used satellite-derived clarity to create a more complete description relative to in situ data, the conversion of reflectance data from remote sensing products to attenuation estimates is not trivial. Further evaluation of satellite-derived data is needed to create a broader characterization of light requirements. However, the algorithm was primarily developed to describe maximum depth of colonization and the estimation of light requirements was a secondary product that illustrated an application of the method. Spatially-resolved Z_c estimates are a primary source of information for developing a more detailed characterization of seagrass habitat requirements and the potential to develop broad-scale descriptions has been facilitated as a result. Specifically, Hagy In review developed a more generalized approach for estimating Z_c for each coastal segment of Florida such that data are available to apply the current method on a much broader scale. Applications outside of Florida are also possible given the minimal requirements for geospatial data products to estimate depth of colonization.

References

Barko JW, Hardin DG, Matthews MS. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Canadian Journal of Botany, 60(6):877–887.

Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors, Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.

Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-8.

Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer, New York, New York.

Caffrey JM, Murrell MC, Amacker KS, Harper J, Phipps S, Woodrey M. 2014. Seasonal and inter-annual patterns in primary production, respiration and net ecosystem metabolism in 3 estuaries in the northeast Gulf of Mexico. Estuaries and Coasts, 37(1):222–241.

Chen Z, Muller-Karger FE, Hu C. 2007. Remote sensing of water clarity in Tampa Bay. Remote Sensing of Environment, 109(2):249–259.

Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from historical records of light attenuation along the Gulf coast of peninsular Florida. Marine Pollution Bulletin, 81(1):94–102.

Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report to St. John's River Water Management District. Technical Report Contract 95W142, Coastal Planning and Engineering, Palatka, Florida.

Dawes C, Avery W. 2010. Epiphytes of the seagrass *halodule wrightii* in Hillsborough Bay, Florida, a 14 year study in an estuary recovering from eutrophication. Florida Scientist, 73(3-4):185–195.

Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA. 1993. Assessing water quality with submersed aquatic vegetation. BioScience, 43(2):86–94.

Dixon LK, Leverone JR. 1995. Light requirements of *Thalassia testudinum* in Tampa Bay, Florida. Technical report, Number 425, Mote Marine Lab, Sarasota, Florida.

Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.

Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia, 41:87–112.

Elsdon TS, Connell SD. 2009. Spatial and temporal monitoring of coastal water quality: refeining the way we consider, gather, and interpret patterns. Aquatic Biology, 5(2):157–166.

Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.

Florida Department of Environmental Protection (FLDEP). 2012. Site-specific information in support of establishing numeric nutrient criteria for Choctawhatchee Bay. Technical report, Florida Department of Environmental Protection, Tallahassee, Florida.

Greve T, Krause-Jensen D. 2005. Stability of of eelgrass (*Zostera marine L.*) depth limits: influence of habitat type. Marine Biology, 147(3):803–812.

Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.

Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species along Florida's central gulf coast: Iverson and Bittaker revisited. Estuaries, 27(1):36–43.

Hall MO, Durako MJ, Fourqurean JW, Zieman JC. 1990. Decadal changes in seagrass distribution and abundance in Florida Bay. Estuaries, 22(2B):445–459.

Hilborn R, Mangel M. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern: declining seagrasses and threatened dependent species. Frontiers in Ecology and the Environment, 7(5):242–246.

Idso SB, Gilbert RG. 1974. On the universality of the Poole and Atkins secchi disk-light extinction equation. Journal of Applied Ecology, 11(1):399–401.

Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico coastal waters. Estuarine, Coastal and Shelf Science, 22(5):577–602.

Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary: An empically based approach to setting management targets. Technical Report 06-96, Tampa Bay National Estuary Program, St. Petersburg, Florida.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. OIKOS, 69(3):373–386.

Kemp WC, Batiuk R, Bartleson R, Bergstrom P, Carter V, Gallegos CL, Hunley W, Karrh L, Koch EW, Landwehr JM, Moore KA, Murray L, Naylor M, Rybicki NB, Stevenson JC, Wilcox DJ. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. Estuaries, 27(3):363–377.

Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and *Syringodium filiforme* derived from the relationship between diffuse light attenuation and maximum depth distribution. Estuaries, 19(3):740–750.

Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries, 24(1):1–17.

Lee ZP, Due KP, Arnone R. 2005. A model for the diffuse attenuation of downwelling irradiance. Journal of Geophysical Research, 110(C2):10.

Lottig NR, Wagner T, Henry EN, Cheruvelil KS, Webster KE, Downing JA, Stow CA. 2014. Long-term citizen-collected data reveal geographical patterns and temporal trends in water clarity. PLoS ONE, 9(4):e95769.

Poole HH, Atkins WRG. 1929. Photo-electric measurements of submarine illumination throughout the year. Journal of the Marine Biological Association of the United Kingdom, 16:297–324.

R Development Core Team. 2014. R: A language and environment for statistical computing, v3.1.2. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Spears BM, Gunn IDM, Carvalho L, Winfield IJ, Dudley B, Murphy K, May L. 2009. An evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven, Scotland. Aquatic Botany, 91(2):75–81.

Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon system, Florida. Estuaries, 28(6):923–935.

Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007. Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.

USEPA (US Environmental Protection Agency). 2006. Volunteer estuary monitoring: A methods manual, second edition. Technical Report EPA-842-B-06-003, Washington, DC.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Springer, New York, New York, fourth edition.

Wagner T, Soranno PA, Cheruvelil KS, Renwick WH, Webster KE, Vaux P, Abbitt RJ. 2008. Quantifying sample biases of inland lake sampling programs in relation to lake surface area and land use/cover. Environmental Monitoring and Assessment, 141(1-3):131–147.

Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay ME, editors, Marine Community Ecology. Sinauer Associates, Sunderland, Massachusetts.

Woodruff DL, Stumpf RP, Scope JA, Paerl HW. 1999. Remote estimation of water clarity in optically complex estuarine waters. Remote Sensing of Environment, 68(1):41–52.

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 meters and square kilometers, 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	205.50	228.52	59.41
Seagrass area	203.02	24.48	74.89	3.51
Depth (mean)	1.41	2.56	1.40	5.31
Depth (max)	3.60	10.40	3.70	11.90
Secchi (mean)	1.34	1.41	1.30	2.14
Secchi (se)	0.19	0.02	0.02	0.08

[a] BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon, WCB: Western Choctawhatchee Bay
[b] 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
W. 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
Upper 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.

Segment[a]	Whole segment	Mean	St. Dev.	Min	Max
BB					
$Z_{c,\,min}$	1.25	1.39	0.77	0.00	2.68
$Z_{c,\,med}$	2.46	1.74	0.76	0.47	2.90
$Z_{c,\,max}$	3.66	2.09	0.80	0.74	3.33
OTB					
$Z_{c,\,min}$	0.61	0.60	0.29	0.00	1.23
$Z_{c,\,med}$	0.88	0.90	0.29	0.30	1.64
$Z_{c,\,max}$	1.15	1.19	0.38	0.37	2.16
UIRL					
$Z_{c,\,min}$	1.25	1.35	0.25	0.81	2.01
$Z_{c,\,med}$	1.51	1.52	0.23	0.97	2.08
$Z_{c,\,max}$	1.77	1.69	0.23	1.06	2.22
WCB					
$Z_{c,\,min}$	1.82	1.56	0.50	0.44	2.23
$Z_{c,\,med}$	2.16	1.93	0.37	1.26	2.49
$Z_{c,\,max}$	2.50	2.30	0.39	1.63	2.99

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

Table 3: Summary of uncertainty for seagrass depth estimates (m) for each segment using all grid locations in Fig. 4. The uncertainty values are equally applicable to each seagrass depth measure ($Z_{c,\,min}$, $Z_{c,\,med}$, $Z_{c,\,max}$).

Segment[a]	Mean	St. Dev	Min	Max
BB	0.10	0.09	0.01	0.49
OTB	0.38	0.26	0.06	1.40
UIRL	0.10	0.10	0.00	0.81
WCB	0.53	0.37	0.12	1.57

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

Table 4: Summary of maximum depth of colonization ($Z_{c,\,max}$, m) and light requirements (%) for all bay segments of Choctawhatchee Bay, Indian River Lagoon, and Tampa Bay. See Figs. 7 to 9 for spatial distribution of the results.

Segment[a]		$Z_{c,\,max}$				**% light**			
	n	Mean	St. Dev.	Min	Max	Mean	St. Dev.	Min	Max
Choctawhatchee Bay									
CCB	121	2.4	0.4	0.9	3.2	48.2	10.2	15.6	78.3
ECB	3	0.9	0.0	0.8	0.9	67.8	2.7	64.8	69.9
WCB	135	2.6	0.2	2.1	2.9	45.6	6.6	24.2	70.9
Indian River Lagoon									
BR	2	1.4	0.0	1.4	1.4	12.0	1.1	11.2	12.8
LCIRL	11	1.4	0.3	1.1	1.7	9.7	4.7	4.5	18.0
LIRL	3	1.8	0.0	1.8	1.8	6.5	2.0	4.2	7.9
LML	4	1.1	0.0	1.1	1.2	17.8	2.3	14.9	19.9
UCIRL	13	1.2	0.1	1.1	1.4	14.1	4.2	7.6	19.9
UIRL	1	1.2		1.2	1.2	20.3	NaN	20.3	20.3
UML	3	0.9	0.1	0.8	1.0	23.3	2.8	20.9	26.4
Tampa Bay									
HB	43	1.3	0.1	1.2	1.4	32.7	7.4	14.3	45.1
LTB	158	2.2	0.4	1.7	3.5	24.3	6.7	4.8	40.0
MTB	215	1.7	0.4	1.2	2.4	29.8	8.0	12.3	50.0
OTB	150	1.2	0.1	1.0	1.3	37.0	5.8	17.3	49.8

[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.

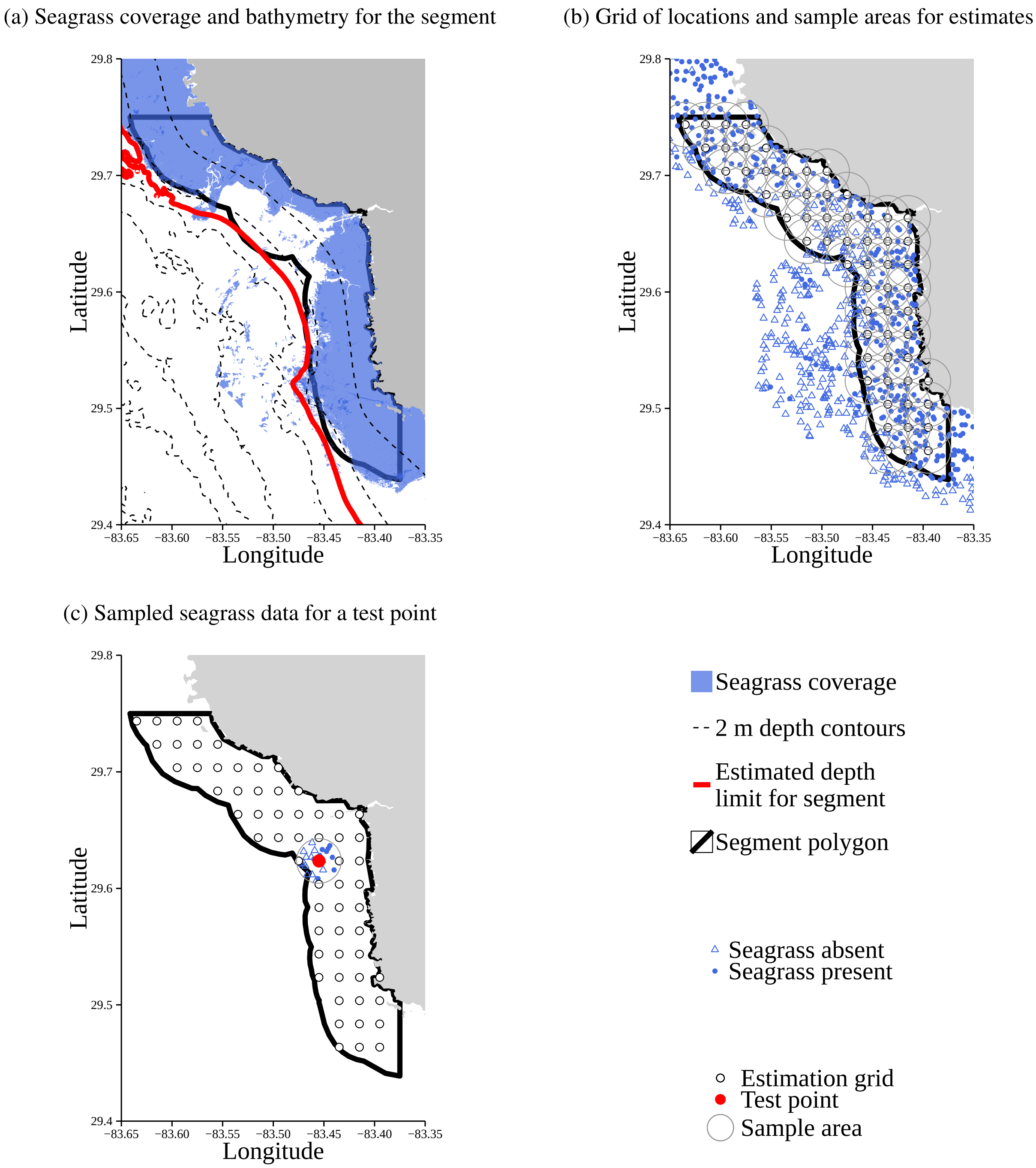

Fig. 1: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 1a shows the seagrass coverage and depth contours at 2 meter intervals, including the whole segment estimate for depth of colonization. Fig. 1b shows a grid of sampling locations with sampling radii for estimating Z_c and seagrass depth points derived from bathymetry and seagrass coverage layers. Fig. 1c shows an example of sampled seagrass depth points for a test location. Estimates in Fig. 3 were obtained from the test location in Fig. 1c.

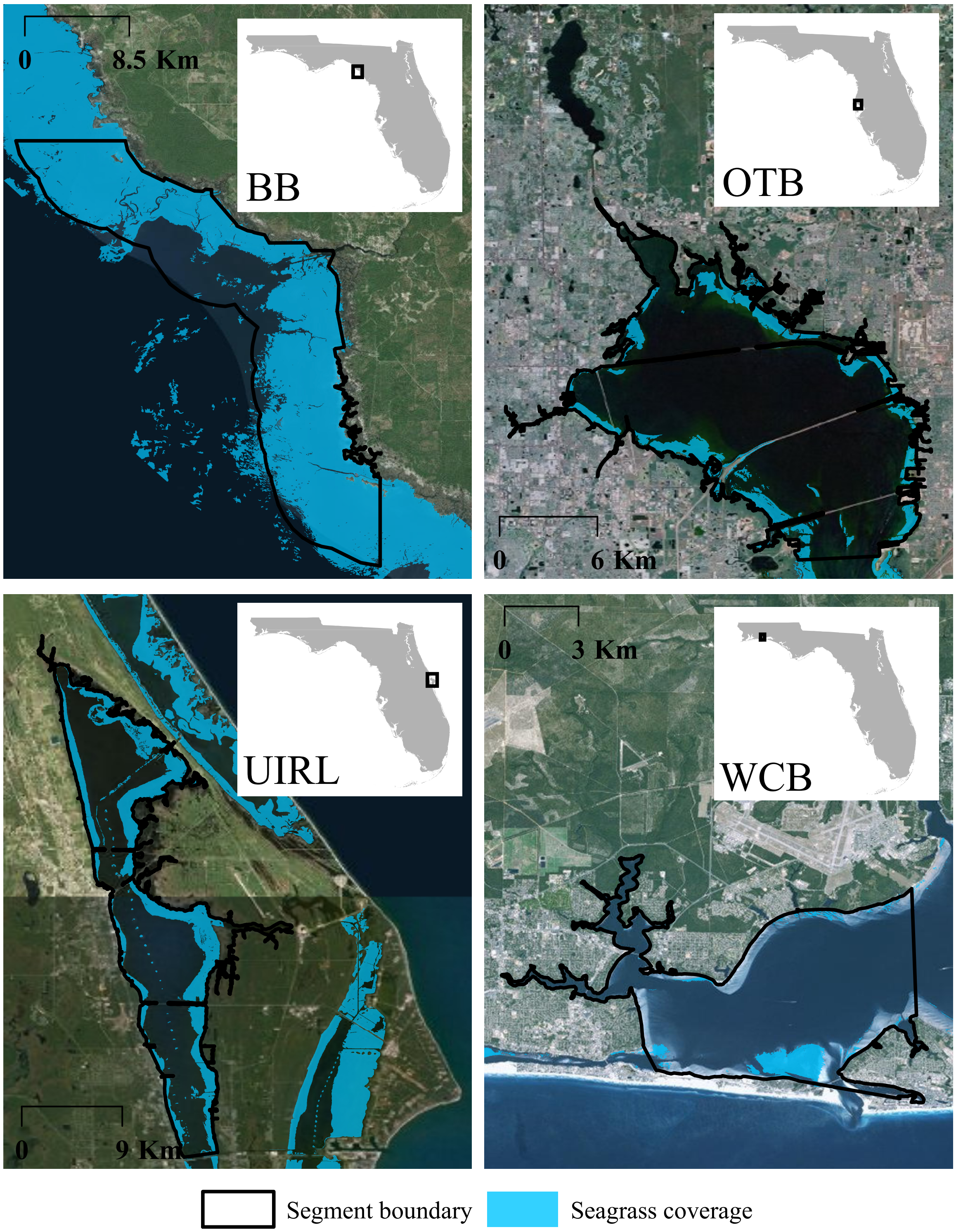

Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

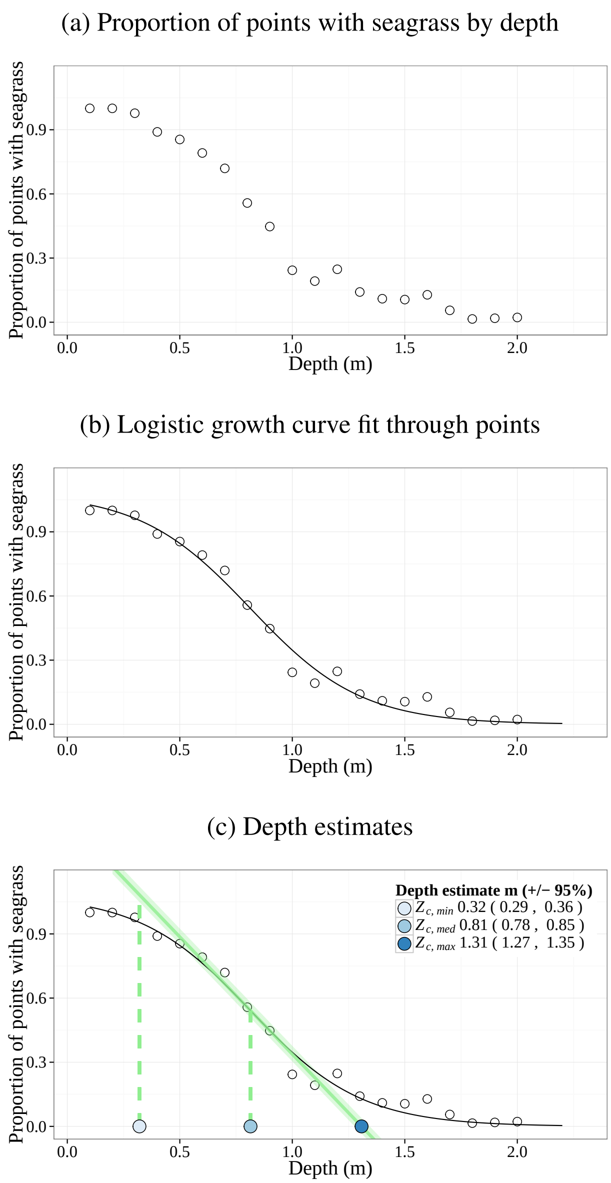

Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit through the points. Fig. 3c shows three depth estimates based on a linear curve fit through the inflection point of logistic growth curve.

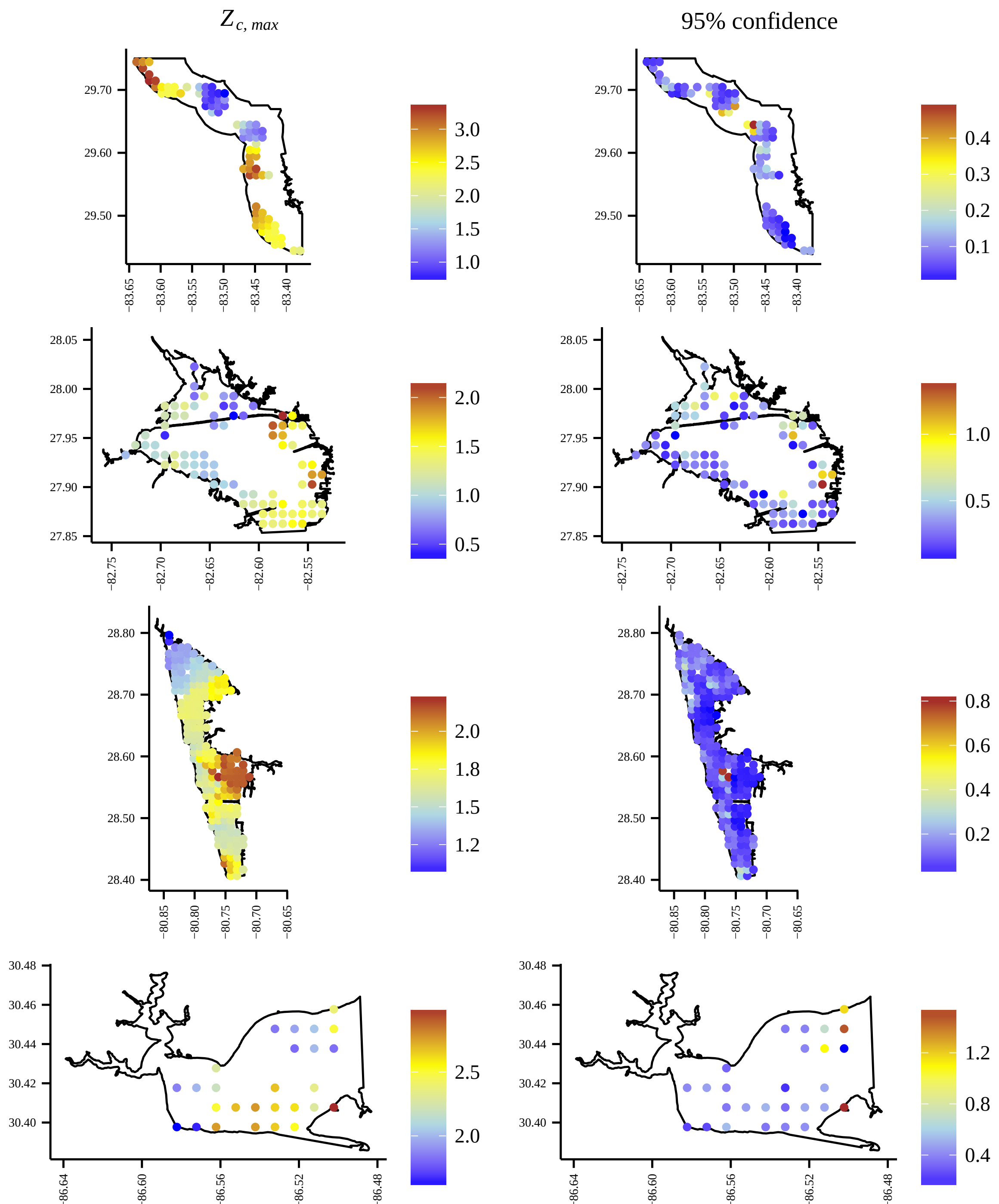

Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ($Z_{c,\,max}$) estimates are on the left and correspondings widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each 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. From top to bottom: Big Bend, Old Tampa Bay, Upper Indian R. Lagoon, Western Choctawhatchee Bay.

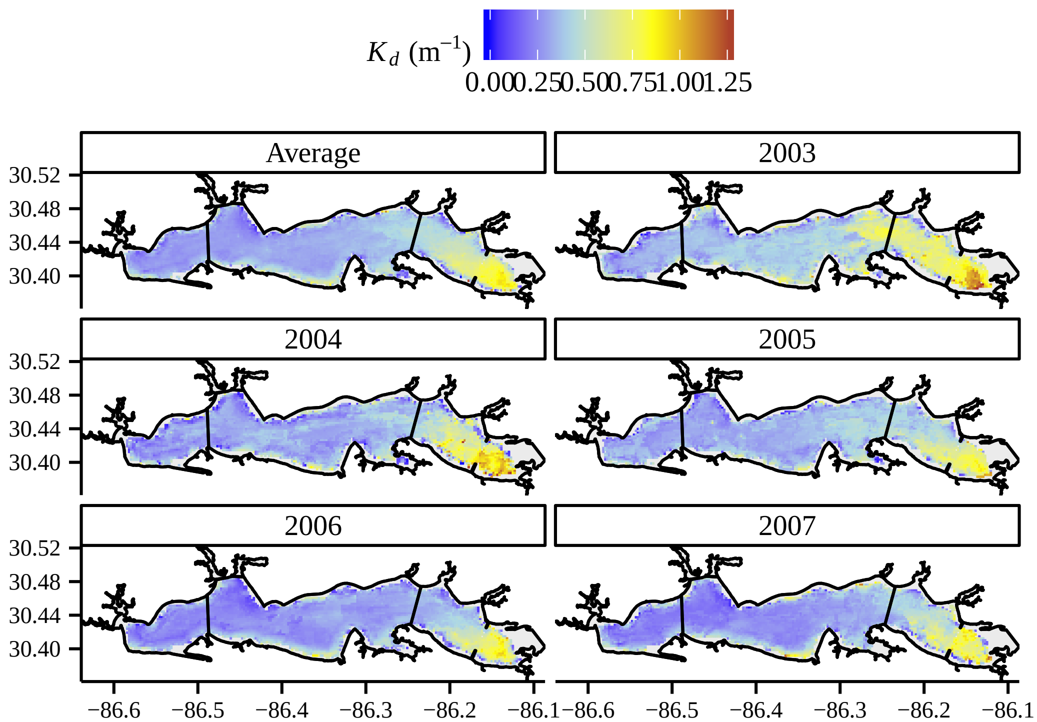

Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment identification.

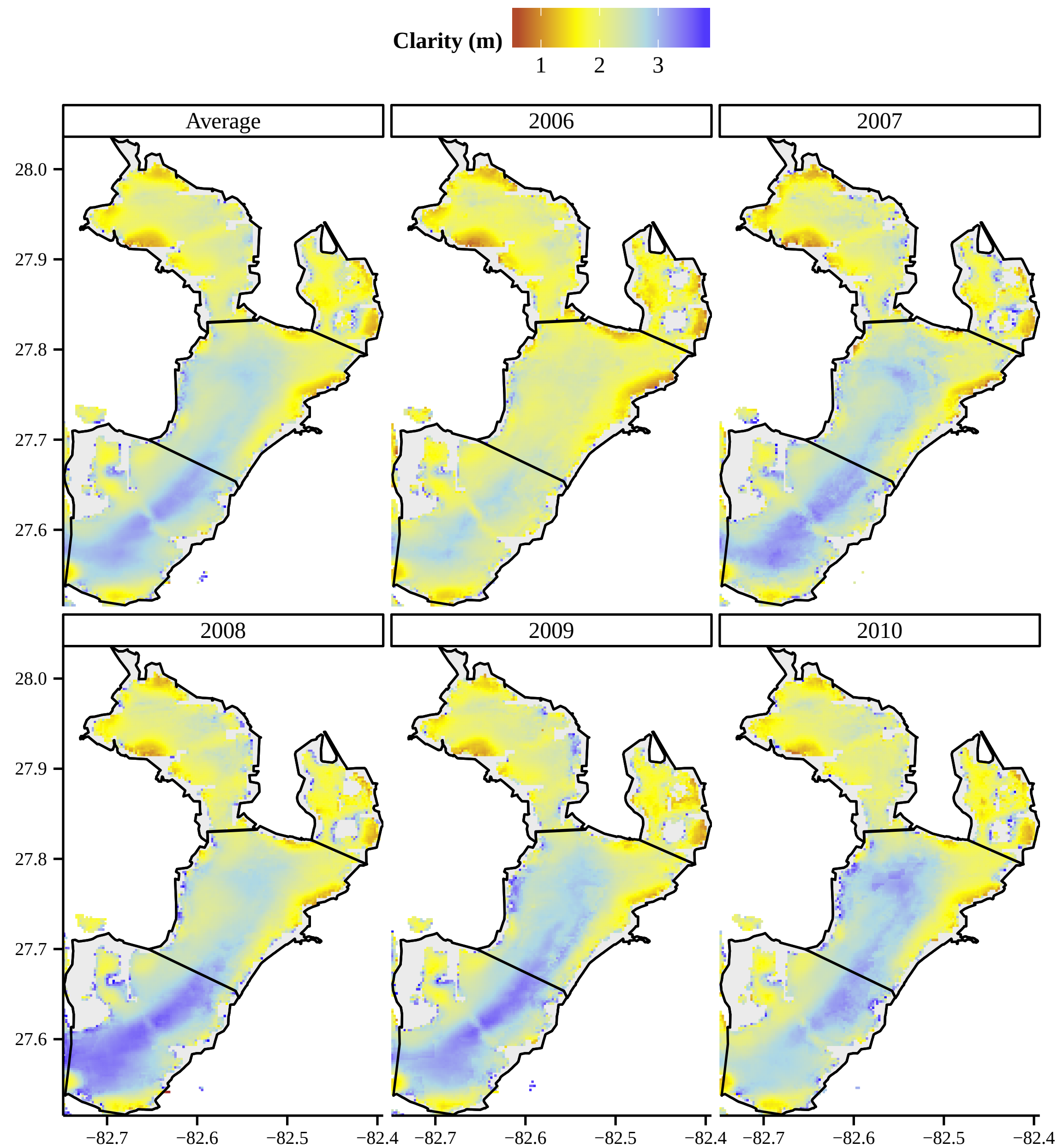

Fig. 6: Satellite estimated water clarity for Tampa Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

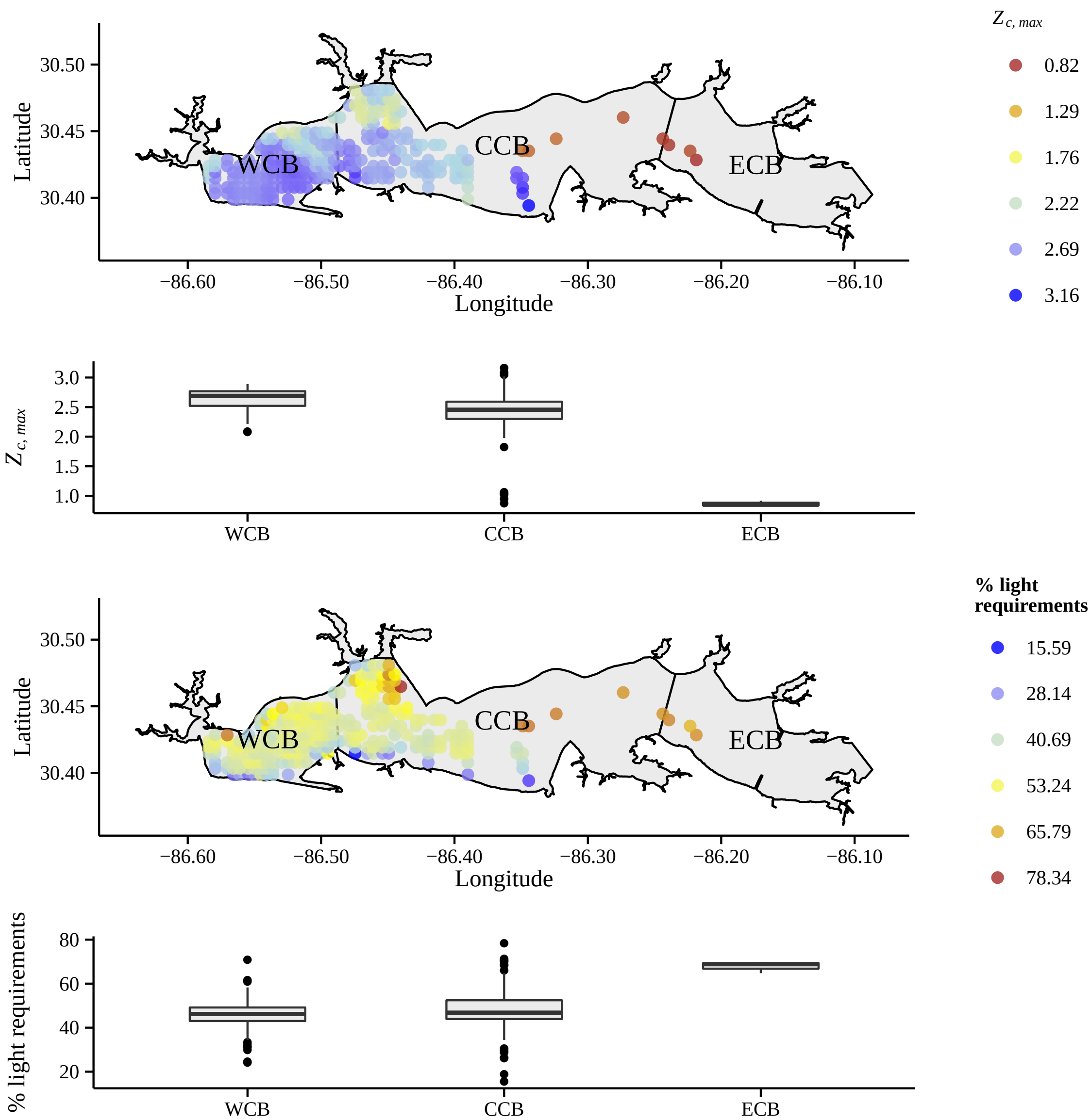

Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. CCB: Central Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay.

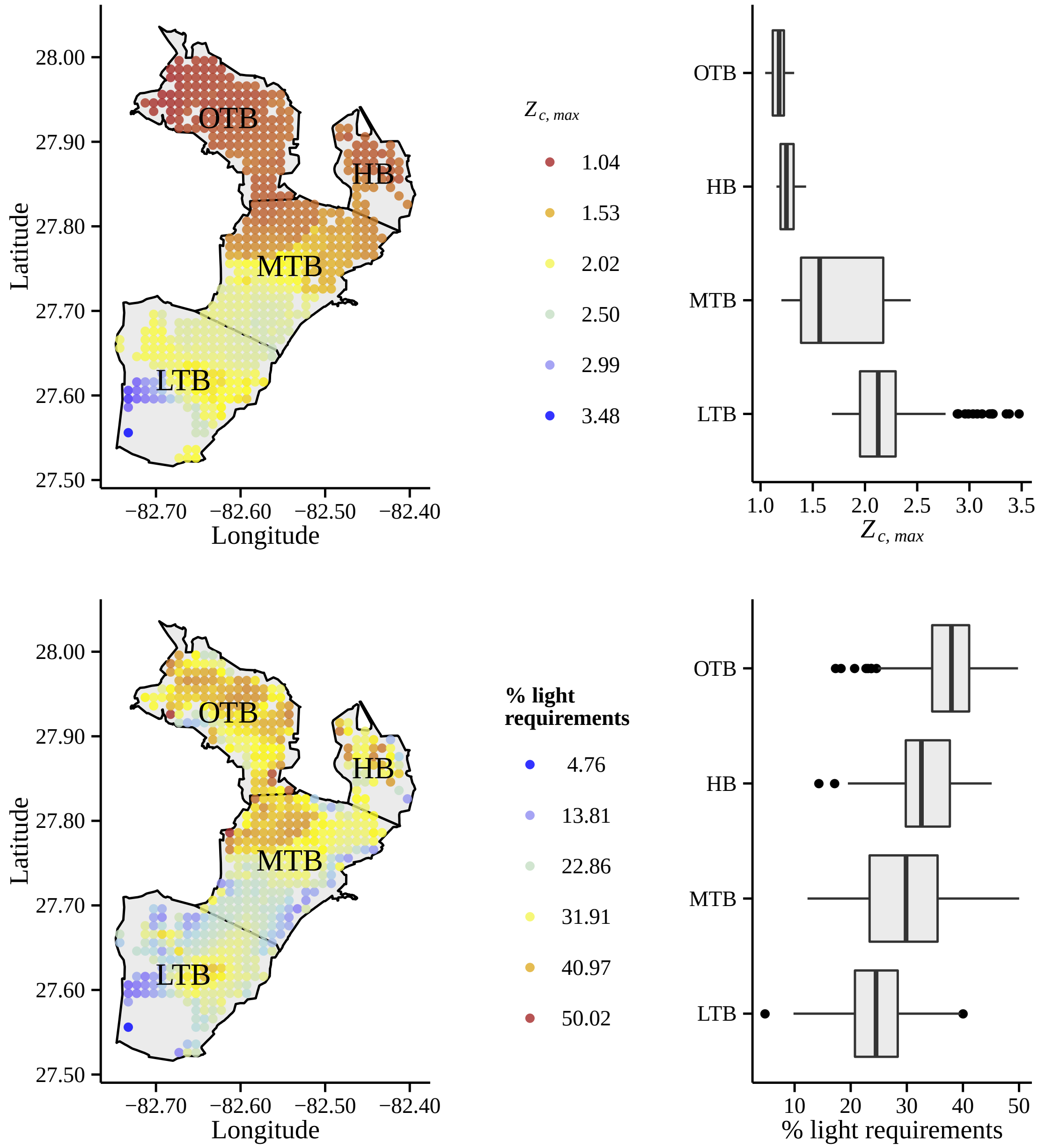

Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

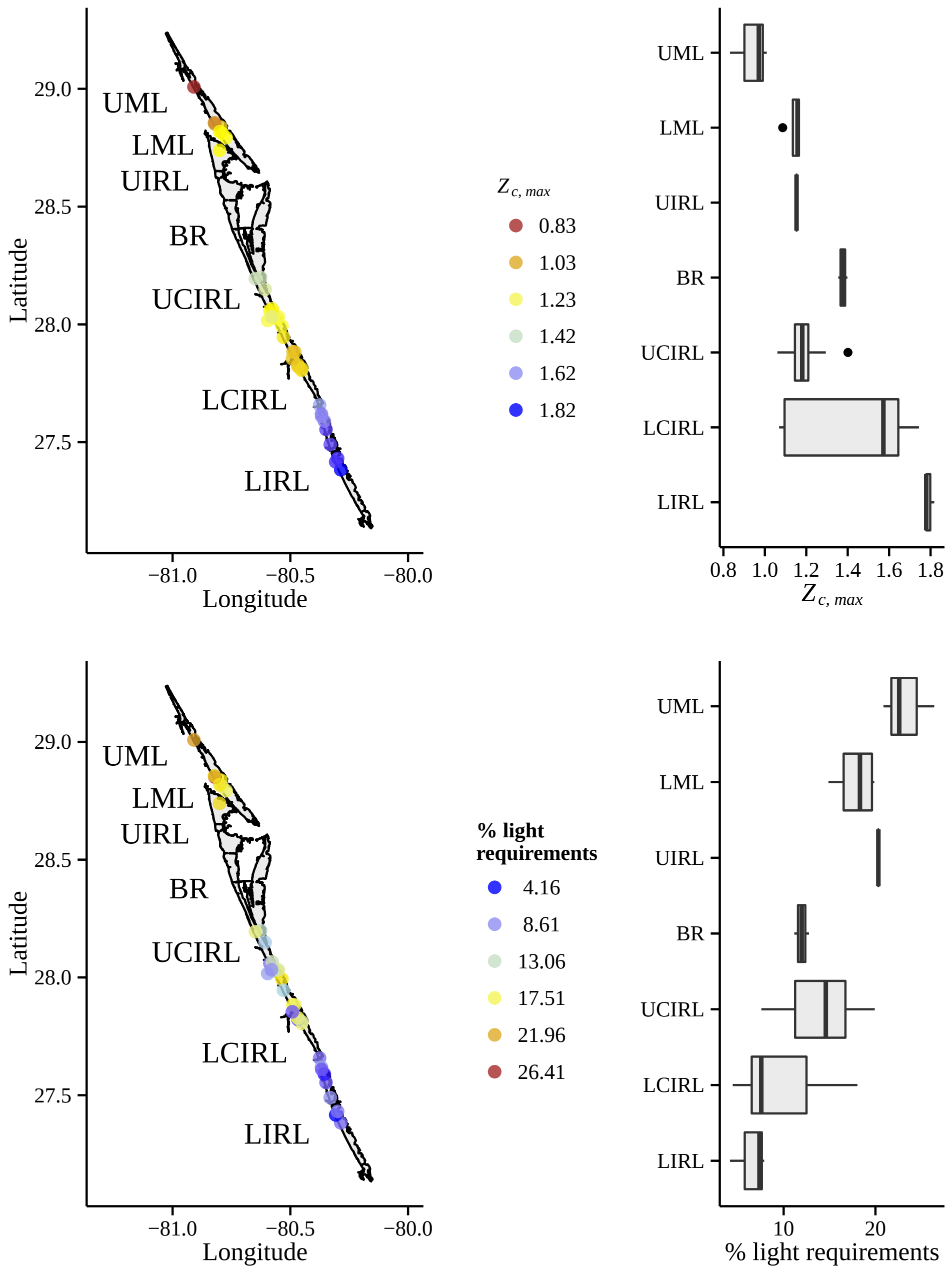

Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment as boxplots as in Fig. 8. Light requirements are based on averaged secchi values within ten years of the seagrass coverage data and estimated maximum depth of colonization using a radius of 0.02 decimal degrees for each secchi location to sample seagrass depth points. 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.