

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

3    **Marcus W. Beck<sup>1</sup>, James D. Hagy III<sup>2</sup>**

<sup>1</sup> *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](mailto:beck.marcus@epa.gov)*

<sup>2</sup> *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](mailto:hagy.jim@epa.gov)*

## **1 Introduction**

Seagrasses are ecologically valuable components of aquatic systems that serve a structural and functional role in shaping aquatic habitat. These ‘ecosystem engineers’ often govern multiple characteristics of aquatic systems through direct and indirect interactions with additional components (Jones et al. 1994, Koch 2001). For example, seagrass beds create desirable 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 direct physiological linkages with light availability. Seagrass communities in highly productive aquatic systems may be light-limited as increased nutrient loading may contribute to reductions in 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 through increased seagrass coverage (Steward et al. 2005). Seagrass depth limits have also been used to establish quantitative 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 ecosystem response to perturbations relative to more variable taxa (e.g., phytoplankton). Quantifying the relationship of seagrasses with water clarity is a viable means of understanding ecological characteristics of aquatic systems with potential insights into resilience and stability of system response to disturbance (Greve and Krause-Jensen 2005).

A variety of techniques have been developed for estimating seagrass depth limits as a basis for understanding water quality dynamics and developing a more robust description of aquatic habitat. Such efforts have been useful for site-specific approaches where the analysis needs are driven by a particular management or research question (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). Seagrass depth limits

33 can also be estimated from geospatial data that describe aerial coverage and bathymetric depth  
34 distribution. Despite the availability of such data, flexible techniques for estimating seagrass  
35 depth of colonization have not been extensively developed nor have standardized techniques been  
36 implemented across broad areas. Site-specific approaches typically involve the quantification of  
37 depth limits within a predefined management unit as a relevant spatial context. For example,  
38 Steward et al. (2005) describe use of a segmentation scheme for the Indian River Lagoon on the  
39 Atlantic coast of Florida to assign seagrass depth limits to 19 distinct geospatial units. Although  
40 useful within a limited scope, substantial variation in growth patterns and water quality  
41 characteristics at different spatial scales may prevent more detailed analyses, thus leading to  
42 limited descriptions of aquatic habitat. Methods for estimating seagrass depth limits should be  
43 reproducible for broad-scale comparisons, while also maintaining flexibility of estimates  
44 depending on research or management objectives. Such techniques have the potential to facilitate  
45 comparisons between regions given the spatial coverage and annual availability of many  
46 geospatial data sources.

47 A useful application comparing depth limit measures and water clarity is the estimation of  
48 light requirements to evaluate ecologically relevant characteristics of seagrass communities.  
49 Although growth of submersed aquatic plants is generally most limited by light availability  
50 (Barko et al. 1982, Hall et al. 1990, Dennison et al. 1993), substantial variation for a given level of  
51 light may be observed in the maximum depth of growth based on differences in light requirements  
52 (Dennison et al. 1993, Choice et al. 2014). In general, seagrasses with low light requirements are  
53 expected to grow deeper than seagrasses with high requirements as related to species or regional  
54 differences in community attributes. Significant variation in light requirements in seagrasses  
55 along the Gulf Coast of peninsular Florida were attributed to morphological and physiological  
56 differences between species and adaptations to regional light regimes (Choice et al. 2014).  
57 Minimum light requirements for seagrasses are on average 11% of surface irradiance (Duarte  
58 1991), although values may range from less than 5% to greater than 30% at depth (Dennison et al.  
59 1993). High light requirements estimated from maximum depth of colonization and water clarity  
60 may suggest seagrass growth is limited by additional factors, such as high biomass of epiphytic  
61 algal growth that reduces light availability on the leaf surface (Kemp et al. 2004). Spatial  
62 heterogeneity in light requirements is, therefore, a useful diagnostic tool for evaluating potential

63 factors that limit seagrass growth.

64 A potentially limiting factor for estimating seagrass light requirements is the availability  
65 of water clarity data that are evenly distributed through space in time, in addition to accurate  
66 measures of depth of colonization. Secchi observations are routine measurements that can provide  
67 consistent measures of water clarity ([USEPA, 2006](#)), although the distribution of available data  
68 may limit the certainty within which light requirements can be estimated. Secchi data can be  
69 biased by location such that monitoring programs may have unbalanced coverage towards aquatic  
70 resources with greater perceived importance relative to those that may have more ecological  
71 significance ([Wagner et al. 2008, Lottig et al. 2014](#)). Moreover, infrequent field measurements that  
72 are limited to discrete time periods are often more descriptive of short-term variability rather than  
73 long-term trends in water clarity ([Elsdon and Connell 2009](#)). Seagrasses growth patterns are  
74 integrative of seasonal and inter-annual patterns in water clarity, among other factors, such that  
75 estimates of light requirements may be limited if water clarity measurements inadequately  
76 describe temporal variation. Remote sensing products can provide a reasonable estimate of water  
77 clarity and could be used to develop a more spatially and temporally coherent description of  
78 relevant ecosystem characteristics. Although algorithms have been developed for coastal waters  
79 that relate surface reflectance to *in situ* data ([Woodruff et al. 1999, Chen et al. 2007](#)), this  
80 information has rarely been used to develop a description of seagrass light requirements at a  
81 spatial resolution consistent with most remote sensing products.

82 Quantitative and flexible methods for estimating seagrass depth limits and light  
83 requirements have the potential to greatly improve descriptions of aquatic habitat, thus enabling  
84 potentially novel insights into ecological characteristics that limit aquatic systems. This article  
85 describes a method for estimating seagrass depth of colonization using geospatial datasets to  
86 create a spatially-resolved and flexible measure. In particular, an empirical algorithm is described  
87 that estimates seagrass depth limits from aerial coverage maps and bathymetric data using an *a*  
88 *priori* defined area of influence. These estimates are combined with measures of water clarity to  
89 provide a spatial characterization of light requirements to better understand factors that limit  
90 seagrass growth. The specific objectives are to 1) describe the method for estimating seagrass  
91 depth limits within a relevant spatial context, 2) apply the technique to four distinct regions of  
92 Florida to illustrate improved clarity of description for seagrass growth patterns, and 3) develop a

93 spatial description of depth limits, water clarity, and light requirements for the case studies.  
94 Overall, these methods are expected to inform the description of seagrass growth patterns to  
95 develop a more ecologically relevant characterization of aquatic habitat. The method is applied to  
96 data from Florida although the technique is easily transferable to other regions with comparable  
97 data.

## 98 **2 Methods**

99 Estimates of seagrass depth of colonization ( $Z_c$ ) that are derived from relatively broad  
100 spatial aggregations, such as predefined management areas, may not fully describe relevant  
101 variation depending on the question of interest. Fig. 1a shows variation in seagrass distribution  
102 for a management segment (thick polygon) in the Big Bend region of Florida. The maximum  
103 depth colonization, shown as a red countour line, is based on a segment-wide average of all  
104 seagrasses within the polygon. Although such an estimate is not necessarily inaccurate,  
105 substantial variation in seagrass growth patterns at smaller spatial scales is not adequately  
106 described. In particular,  $Z_c$  is greatly over-estimated at the outflow of the Steinhatchee River  
107 (northeast portion of the segment) where high concentrations of dissolved organic matter reduce  
108 water clarity and naturally limit seagrass growth (personal communication, Nijole Wellendorf,  
109 Florida Department of Environmental Protection). This example suggests that it may be useful to  
110 have improved spatial resolution in estimates of  $Z_c$ , particularly when site-specific characteristics  
111 may require a more detailed description of seagrass growth patterns. The following is a summary  
112 of data sources, methods and rationale for developing a flexible algorithm that improves spatial  
113 resolution in seagrass  $Z_c$  estimates. Data and methods described in [Hagy, In review](#) are used as a  
114 foundation for developing the approach.

### 115 **2.1 Data sources**

#### 116 **2.1.1 Study sites**

117 Four locations in Florida were chosen for the analysis: the Big Bend region (northeast  
118 Gulf of Mexico), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf Coast), and Indian  
119 River Lagoon (east coast) (Table 1 and Fig. 2). These locations represent different geographic  
120 regions in the state, in addition to having available data and observed gradients in water clarity  
121 that contribute to heterogeneity in seagrass growth patterns. Coastal regions and estuaries in

122 Florida are partitioned as distinct spatial units based on a segmentation scheme developed by US  
123 Environmental Protection Agency (EPA) for the development of numeric nutrient criteria.  
124 Site-specific estimates of seagrass depth colonization and light requirements are the primary focus  
125 of the analysis, with emphasis on improved clarity of description with changes in spatial context.  
126 As such, estimates that use management segments as relevant spatial units are used as a basis of  
127 comparison to evaluate variation in growth patterns at difference scales. The segments included  
128 the big bend region (820), Old Tampa Bay (902), and Indian River Lagoon (1502) (Fig. 2).

### 129 **2.1.2 Seagrass coverage and bathymetry**

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

140 Bathymetric depth layers for each location were obtained from the National Oceanic and  
141 Atmospheric Administration's (NOAA) National Geophysical Data Center  
142 (<http://www.ngdc.noaa.gov/>) as either Digital Elevation Models (DEMs) or raw sounding data  
143 from hydroacoustic surveys. Tampa Bay data provided by the Tampa Bay National Estuary  
144 Program are described in Tyler et al. (2007). Bathymetric data for the Indian River Lagoon were  
145 obtained from the St. John's Water Management District (Coastal Planning and Engineering  
146 1997). NOAA products were referenced to mean lower low water, whereas Tampa Bay data were  
147 referenced to the North American Vertical Datum of 1988 (NAVD88) and the Indian River  
148 Lagoon data were referenced to mean sea level. Depth layers were combined with seagrass  
149 coverage layers using standard union techniques for raster and vector layers in ArcMap 10.1  
150 (Environmental Systems Research Institute 2012). To reduce computation time, depth layers were  
151 first masked using a 1 km buffer of the seagrass coverage layer. Raster bathymetric layers were

{acro:EPA}

{sec:data}

{acro:DEM}

{acro:NAV}

152 converted to vector point layers to combine with seagrass coverage maps, described below. All  
153 spatial data were referenced to the North American Datum of 1983 as geographic coordinates.  
154 Depth values in each seagrass layer were further adjusted from the relevant vertical reference  
155 datum to local mean sea level (MSL) using the NOAA VDatum tool (<http://vdatum.noaa.gov>).  
156 {acro:MSL}

### 156 **2.1.3 Water clarity and light attenuation**

157 Seagrass light requirements can be estimated by evaluating spatial relationships between  
158 depth of colonization and water clarity. These relationships were explored using  $Z_c$  estimates for  
159 the whole of Tampa Bay and the Indian River Lagoon based on large gradients in water clarity  
160 along longitudinal axes in each bay (cites). Satellite images were used to create a gridded map of  
161 water clarity based on a previously-developed algorithm to derive light attenuation (or light  
162 extinction coefficient  $K_Z$ ) from surface reflectance (Chen et al. 2007). This approach was  
163 preferred for Tampa Bay given the annual availability and the extent of coverage of remote  
164 sensing data. Daily MODIS (Aqua level-2) data from January 2003 to December 2010 that  
165 covered the spatial extent of Tampa Bay were downloaded from the NASA website  
166 (<http://oceancolor.gsfc.nasa.gov>). These images were reprocessed using the SeaWiFS Data  
167 Analysis System software (SeaDAS, Version 7.0). We used the clarity algorithm proposed by  
168 Chen et al. (2007) to derive monthly mean and annual mean light attenuation coefficients for  
169 Tampa Bay. Secchi data (meters,  $Z_{secchi}$ ) were also obtained from update 40 of the Impaired  
170 Waters Rule (IWR) database for all of the Indian River Lagoon (2009 coverage). Satellite  
171 estimates of water clarity were unobtainable in the Indian River Lagoon because of significant  
172 light scattering from bottom reflectance and limited resolution for extended narrow segments  
173 along the north-south axis. Secchi data within the previous ten years of the seagrass coverage data  
174 were evaluated to capture water quality trends from the most recent decade (i.e., 1999–2009 for  
175 the Indian River Lagoon). Stations with less than five observations and observations that were  
176 flagged indicating that the value was lower than the maximum depth of the observation point were  
177 removed. Secchi data were also compared with bathymetric data to verify unflagged values were  
178 not missed by initial screening.

## 179 **2.2 Flexible estimation of seagrass depth of colonization for finite areas**

180 The general approach to estimating seagrass depth of colonization uses combined seagrass  
181 coverage maps and bathymetric depth data described above. The combined layer used for analysis

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

193 The spatially-resolved approach for estimating  $Z_c$  begins by choosing an explicit location  
194 in cartesian coordinates within the general boundaries of the available data. Seagrass depth data  
195 (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the  
196 chosen location are selected for estimating seagrass  $Z_c$  values (Fig. 1). The estimate for each  
197 location is quantified from a plot of the proportion of sampled points that contain seagrass at  
198 decreasing 0.1 meter depth bins from the surface to the maximum observed depth in the sample  
199 (Fig. 3a). Although the chosen radius for selecting depth points is problem-specific, the minimum  
200 radius should be chosen to sample a sufficient number of points for estimating  $Z_c$ . In general, an  
201 appropriate radius will produce a plot that indicates a decrease in the proportion of points that are  
202 occupied by seagrass with increasing depth. If more than one location is used to estimate  $Z_c$ ,  
203 appropriate radii for each point would have minimal overlap with the seagrass depth data sampled  
204 by neighboring points.

205 A curve is fit to the sampled depth points using non-linear regression to characterize the  
206 reduction in seagrass as a function of depth (Fig. 3b). Specifically, a decreasing logistic growth  
207 curve is used with the assumption that seagrass decline with increasing depth is monotonic and  
208 asymptotic at the minimum and maximum depths of colonization. The curve is fit by minimizing  
209 the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992) with  
210 starting parameters estimated from the observed data that are initial approximations of the curve

211 characteristics. The model has the following form:

$$Proportion = \frac{\alpha}{1 + e^{(\beta - Z)/\gamma}} \quad (1) \quad \{eqn:prop\}$$

212 where the proportion of points occupied by seagrass at each depth,  $Z$ , is defined by a logistic  
213 curve with an asymptote  $\alpha$ , a midpoint inflection  $\beta$ , and a scale parameter  $\gamma$ . Finally, a simple  
214 linear curve is fit through the inflection point ( $\beta$ ) of the logistic curve to estimate the three  
215 measures of depth of colonization (Fig. 3c). The inflection point is considered the depth at which  
216 seagrass are decreasing at a maximum rate and is used as the slope of the linear curve. The  
217 maximum depth of seagrass colonization,  $Z_{c,max}$ , is the x-axis intercept of the linear curve. The  
218 minimum depth of seagrass growth,  $Z_{c,min}$ , is the location where the linear curve intercepts the  
219 upper asymptote of the logistic growth curve. The median depth of seagrass colonization,  $Z_{c,med}$ ,  
220 is the depth halfway between  $Z_{c,min}$  and  $Z_{c,max}$ .  $Z_{c,med}$  is typically the inflection point of the  
221 logistic growth curve.

222 Estimates for each of the three  $Z_c$  measures are obtained only if specific criteria are met.  
223 These criteria were implemented as a safety measure that ensures a sufficient amount and  
224 appropriate quality of data were sampled within the chosen radius. First, estimates were provided  
225 only if a sufficient number of seagrass depth points were present in the sampled data to estimate a  
226 logistic growth curve. This criteria applies to the sample size as well as the number of points with  
227 seagrass in the sample. Second, estimates were provided only if an inflection point was present on  
228 the logistic curve within the range of the sampled depth data. This criteria applied under two  
229 scenarios where the curve was estimated but a trend was not adequately described by the sampled  
230 data. That is, estimates were unavailable if the logistic curve described only the initial decrease  
231 in points occupied as a function of depth but the observed points do not occur at depths deeper  
232 than the predicted inflection point. The opposite scenario occurred when a curve was estimated  
233 but only the deeper locations beyond the inflection point were present in the sample. Third, the  
234 estimate for  $Z_{c,min}$  was set to zero depth if the linear curve through the inflection point  
235 intercepted the asymptote at x-axis values less than zero. The estimate for  $Z_{c,med}$  was also shifted  
236 to the depth value halfway between  $Z_{c,min}$  and  $Z_{c,max}$  if  $Z_{c,min}$  was fixed at zero. Finally,  
237 estimates were considered invalid if the 95% confidence interval for  $Z_{c,max}$  included zero.

238 Methods used to determine confidence bounds on  $Z_c$  estimates are described below.

## 239 2.3 Estimating uncertainty in depth of colonization estimates

240 Confidence intervals for the  $Z_c$  values were estimated using a Monte Carlo simulation  
241 approach that considered the variance and covariance between the model parameters (Hilborn and  
242 Mangel 1997). For simplicity, we assume that the variability associated with parameter estimates  
243 is the dominant source of uncertainty. A 95% confidence interval for each  $Z_c$  estimate was  
244 constructed by repeated sampling of a multivariate normal distribution followed by prediction of  
245 the proportion of points occupied by seagrass as in eq. (1). The sampling distribution assumes:

$$x \sim N(\mu, \Sigma) \quad (2)$$

246 where  $x$  is a predictor variable used in eq. (1) (depth) that follows a multivariate normal  
247 distribution with mean  $\mu$ , and variance-covariance matrix  $\Sigma$ . The mean values are set at the depth  
248 value corresponding to the inflection point on the logistic curve and the predicted model  
249 parameters (i.e.,  $\alpha$ ,  $\beta$ , and  $\gamma$ ), whereas  $\Sigma$  is the variance-covariance matrix of the model  
250 parameters. A large number of samples ( $n = 10000$ ) were drawn from the distribution to  
251 characterize the uncertainty of the depth value at the inflection point. The 2.5<sup>th</sup> and 97.5<sup>th</sup> quantile  
252 values of the sample were considered bounds on the 95% confidence interval.

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

263 The algorithm for estimating  $Z_c$  was implemented custom-made and pre-existing  
264 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. 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

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

$$I_z = I_O \cdot \exp(-K_d \cdot Z) \quad (3) \quad \{eqn:lambert\}$$

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):

$$\% \text{ light} = \exp(-K_d \cdot Z_{c, \max}) \quad (4) \quad \{\text{eqn:perc}\}$$

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). Thus,  $K_d$  can be replaced with the conversion factor and  $Z_{secchi}$ :

$$\% \text{ light} = \exp\left(-\left(\frac{1.7}{Z_{secchi}}\right) \cdot Z_{c, \max}\right) \quad (5) \quad \{\text{eqn:cperc}\}$$

Variation in seagrass light requirements by location can be considered biologically meaningful.

An evenly-spaced grid of sampling points was created for the spatial extent of Tampa Bay to estimate light requirements for seagrasses. Grid spacing was set at 0.01 decimal degrees as before. These points were used to sample the raster grid of satellite-derived water clarity and the seagrass depth points to estimate  $Z_{c, \max}$ . Similarly, the geographic coordinates for each available secchi measurement in the Indian River Lagoon were used as locations for estimating  $Z_{c, \max}$ . These estimates were compared with the averaged water clarity or secchi data for all preceding years to identify seagrass light requirements at each location (i.e., 2003–2010 for Tampa Bay and 1999–2009 for Indian River Lagoon). However, the relationship may vary depending on the specific radius around each sample point for estimating  $Z_{c, \max}$ . A sufficiently large radius was chosen that was an order of magnitude larger than that used for the individual segments given that  $Z_{c, \max}$  estimates were to be compared for whole bays rather than within segments. 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.

314 **3 Results**

315 **3.1 Segment characteristics and seagrass depth estimates**

316        Each of the four segments varied by several key characteristics that potentially explain  
317        within-segment variation of seagrass growth patterns (Table 1). Mean surface area was 191.2  
318        square kilometers, with area decreasing for the Big Bend (271.4 km), Indian River Lagoon (NA  
319        km), Old Tampa Bay (205.5 km), and Choctawhatchee Bay (59.4 km) segments. Seagrass  
320        coverage as a percentage of total surface area varied considerably by segment. Seagrasses covered  
321        a majority of the surface area for the Big Bend segment (74.8 %), whereas coverage was much  
322        less for Indian River Lagoon (NA %), Old Tampa Bay (11.9 %), and Choctawhatchee Bay (5.9  
323        %). Visual examination of the seagrass coverage maps for the respective year of each segment  
324        suggested that seagrasses were not uniformly distributed (Fig. 2). Seagrasses in the  
325        Choctawhatchee Bay segments were generally sparse with the exception of a large patch located  
326        to the west of the inlet connection with the Gulf of Mexico. Seagrasses in the Big Bend segment  
327        were located throughout the segment with noticeable declines near the outflow of the  
328        Steinhatchee River, whereas seagrasses in Old Tampa Bay and the Indian River Lagoon segment  
329        were generally confined to shallow areas near the shore. Seagrass coverage showed a partial  
330        decline toward the northern ends of both Old Tampa Bay and the Indian River Lagoon segments.  
331        Mean depth was less than 5 meters for each segment, excluding Choctawhatchee Bay which was  
332        slightly deeper than the other segments on average (5.3 m). Maximum depths were considerably  
333        deeper for Choctawhatchee Bay (11.9 m) and Old Tampa Bay (10.4 m), as compared to the Big  
334        Bend (3.6 m) and Indian River Lagoon (NA m) segments. Water clarity as indicated by average  
335        secchi depths was similar between the segments (1.5 m), although Choctawhatchee Bay had a  
336        slightly higher average (2.1 m).

337        Estimates of seagrass  $Z_c$  using a segment-wide approach that did not consider spatially  
338        explicit locations indicated that seagrasses generally did not grow deeper than three meters in any  
339        of the segments (Table 2). Maximum and median depth of colonization were deepest for the Big  
340        Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old Tampa Bay (1.1 and 0.9 m),  
341        whereas the minimum depth of colonization was deepest for Choctawhatchee Bay (1.8 m) and  
342        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 2.1 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 continuously 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. Seagrasses were estimated to grow at maximum depths up to 2.2 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 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 Choctawhatchee Bay where seagrasses were unevenly distributed or confined to shallow areas near the shore. The former scenario was most common in

373 the Big Bend segment where seagrasses were abundant but locations near the shore were  
374 inestimable given that seagrasses did not decline appreciably within the depths that were sampled.

375 Uncertainty for estimates of  $Z_{c,max}$  indicated that confidence intervals were generally  
376 acceptable (i.e., greater than zero), although the ability to discriminate between the three depth  
377 estimates varied by segment (Fig. 4 and Table 3). Mean uncertainty for all estimates in each  
378 segment measured as the width of a 95% confidence interval was 0.2 m. Greater uncertainty was  
379 observed for Choctawhatchee Bay (mean width of all confidence intervals was 0.5 m) and Old  
380 Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Indian River Lagoon (0.1 m)  
381 segments. The largest confidence interval for each segment was 1.4 m for Old Tampa Bay, 1.6 m  
382 for Choctawhatchee Bay, 0.5 m for the Big Bend, and 0.8 m for the Indian River Lagoon  
383 segments. However, most confidence intervals for the remaining grid locations were much  
384 smaller than the maximum in each segment. A comparison of overlapping confidence intervals  
385 for  $Z_{c,min}$ ,  $Z_{c,med}$ , and  $Z_{c,max}$  at each grid location indicated that not every measure was unique.  
386 Specifically, only 11.1% of grid points in Choctawhatchee Bay and 28.2% in Old Tampa Bay had  
387 significantly different estimates, whereas 82.4% of grid points in the Indian River Lagoon and  
388 96.2% of grid points in the Big Bend segments had estimates that were significantly different. By  
389 contrast, all grid estimates in Choctawhatchee Bay and Indian River Lagoon had  $Z_{c,max}$  estimates  
390 that were significantly greater than zero, whereas all but 12.4% of grid points in Old Tampa Bay  
391 and 8% of grid points in the Big Bend segment had  $Z_{c,max}$  estimates significantly greater than  
392 zero.

### 393 3.2 Evaluation of seagrass light requirements

394 Estimates of seagrass depth limits and corresponding light requirements for all segments  
395 of Tampa Bay and the Indian River Lagoon indicated substantial variation, both between and  
396 within the different bays (?? and Figs. 8 and 9). Seagrass  $Z_c$  estimates were obtained for 566  
397 locations in Tampa Bay and 37 locations in the Indian River Lagoon where secchi observations  
398 were available in the Florida IWR database. Mean secchi depth for all recorded observations was  
399 2.3 m ( $n = 566$ ) for Tampa Bay and NA m ( $n = 37$ ) for Indian River Lagoon. Mean light  
400 requirements were significantly different between the bays (two-sided t-test,  $t = 16.8$ ,  $df = 46.8$ ,  
401  $p < 0.001$ ) with a mean requirement of 30.4% for Tampa Bay and 13.4% for Indian River  
402 Lagoon. Within each bay, light requirements were significantly different between segments

<sup>403</sup> (ANOVA,  $F = 84.6$ ,  $df = 3, 562$ ,  $p = 0.00$  for Tampa Bay,  $F = 7.6$ ,  $df = 6, 30$ ,  $p = 0.000$  for  
<sup>404</sup> Indian River Lagoon). However, post-hoc evaluation of all pair-wise comparisons of mean light  
<sup>405</sup> requirements indicated that significant differences were only observed between a few segments  
<sup>406</sup> within each bay. Significant differences in Tampa Bay were observed between Old Tampa Bay  
<sup>407</sup> and Hillsborough Bay (Tukey multiple comparisons,  $p = 0.003$ ). Significant differences in the  
<sup>408</sup> Indian River Lagoon were observed between the Upper Indian River Lagoon and Banana River  
<sup>409</sup> ( $p = 0.616$ ), the Upper Indian River Lagoon and Lower Indian River Lagoon ( $p = 0.070$ ), and  
<sup>410</sup> Upper Indian River Lagoon and Lower St. Lucie ( $p = \text{NA}$ ) segments. In general, spatial variation  
<sup>411</sup> of light requirements in Tampa Bay suggested that seagrasses were less light-limited (i.e., lower  
<sup>412</sup> percent light requirements at  $Z_{c, max}$ ) in Hillsborough Bay and western areas of Lower Tampa Bay  
<sup>413</sup> near the Gulf of Mexico (Fig. 8). Seagrassess in the Indian River Lagoon were generally less  
<sup>414</sup> light-limited towards the south and in the Banana River segment (Fig. 9).

<sup>415</sup> **4 Discussion**

416 **References**

- 417 Barko JW, Hardin DG, Matthews MS. 1982. Growth and morphology of submersed freshwater  
418 macrophytes in relation to light and temperature. Canadian Journal of Botany, 60(6):877–887.
- 419 Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors,  
420 Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.
- 421 Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R  
422 package version 0.3-8.
- 423 Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer,  
424 New York, New York.
- 425 Chen Z, Muller-Karger FE, Hu C. 2007. Remote sensing of water clarity in Tampa Bay. Remote  
426 Sensing of Environment, 109(2):249–259.
- 427 Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from  
428 historical records of light attenuation along the Gulf coast of peninsular Florida. Marine  
429 Pollution Bulletin, 81(1):94–102.
- 430 Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report  
431 to St. John's River Water Management District. Technical Report Contract 95W142, Coastal  
432 Planning and Engineering, Palatka, Florida.
- 433 Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA.  
434 1993. Assessing water quality with submersed aquatic vegetation. BioScience, 43(2):86–94.
- 435 Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.
- 436 Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes.  
437 Ophelia, 41:87–112.
- 438 Elsdon TS, Connell SD. 2009. Spatial and temporal monitoring of coastal water quality: refining  
439 the way we consider, gather, and interpret patterns. Aquatic Biology, 5(2):157–166.
- 440 Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.
- 441 Greve T, Krause-Jensen D. 2005. Stability of eelgrass (*Zostera marina L.*) depth limits:  
442 influence of habitat type. Marine Biology, 147(3):803–812.
- 443 Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.
- 444 Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species  
445 along Florida's central gulf coast: Iverson and Bittaker revisited. Estuaries, 27(1):36–43.
- 446 Hall MO, Durako MJ, Fourqurean JW, Zieman JC. 1990. Decadal changes in seagrass  
447 distribution and abundance in Florida Bay. Estuaries, 22(2B):445–459.

- 448 Hilborn R, Mangel M. 1997. The Ecological Detective: Confronting Models with Data.  
449 Princeton University Press, Princeton, New Jersey.
- 450 Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern:  
451 declining seagrasses and threatened dependent species. *Frontiers in Ecology and the*  
452 *Environment*, 7(5):242–246.
- 453 Idso SB, Gilbert RG. 1974. On the universality of the Poole and Atkins secchi disk-light  
454 extinction equation. *Journal of Applied Ecology*, 11(1):399–401.
- 455 Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico  
456 coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5):577–602.
- 457 Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary:  
458 An empirically based approach to setting management targets. Technical Report 06-96, Tampa  
459 Bay National Estuary Program, St. Petersburg, Florida.
- 460 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *OIKOS*,  
461 69(3):373–386.
- 462 Kemp WC, Batiuk R, Bartleson R, Bergstrom P, Carter V, Gallegos CL, Hunley W, Karrh L, Koch  
463 EW, Landwehr JM, Moore KA, Murray L, Naylor M, Rybicki NB, Stevenson JC, Wilcox DJ.  
464 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water  
465 quality, light regime, and physical-chemical factors. *Estuaries*, 27(3):363–377.
- 466 Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and  
467 *Syringodium filiforme* derived from the relationship between diffuse light attenuation and  
468 maximum depth distribution. *Estuaries*, 19(3):740–750.
- 469 Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible  
470 submersed aquatic vegetation habitat requirements. *Estuaries*, 24(1):1–17.
- 471 Lottig NR, Wagner T, Henry EN, Cheruvellil KS, Webster KE, Downing JA, Stow CA. 2014.  
472 Long-term citizen-collected data reveal geographical patterns and temporal trends in water  
473 clarity. *PLoS ONE*, 9(4):e95769.
- 474 Poole HH, Atkins WRG. 1929. Photo-electric measurements of submarine illumination  
475 throughout the year. *Journal of the Marine Biological Association of the United Kingdom*,  
476 16:297–324.
- 477 R Development Core Team. 2014. R: A language and environment for statistical computing,  
478 v3.1.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- 479 Spears BM, Gunn IDM, Carvalho L, Winfield IJ, Dudley B, Murphy K, May L. 2009. An  
480 evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven,  
481 Scotland. *Aquatic Botany*, 91(2):75–81.
- 482 Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light  
483 targets for the Indian River Lagoon system, Florida. *Estuaries*, 28(6):923–935.

- 484 Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007.
- 485 Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051
- 486 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.
- 487 USEPA (US Environmental Protection Agency). 2006. Volunteer estuary monitoring: A methods
- 488 manual, second edition. Technical Report EPA-842-B-06-003, Washington, DC.
- 489 Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Springer, New York, New
- 490 York, fourth edition.
- 491 Wagner T, Soranno PA, Cheruvellil KS, Renwick WH, Webster KE, Vaux P, Abbott RJ. 2008.
- 492 Quantifying sample biases of inland lake sampling programs in relation to lake surface area and
- 493 land use/cover. *Environmental Monitoring and Assessment*, 141(1-3):131–147.
- 494 Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay
- 495 ME, editors, *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts.
- 496 Woodruff DL, Stumpf RP, Scope JA, Paerl HW. 1999. Remote estimation of water clarity in
- 497 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.<sup>tab:seg\_summ</sup>

	Big Bend	Choctawhatchee Bay	Old Tampa Bay	Upper Indian R. Lagoon
Year <sup>a</sup>	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

<sup>a</sup> 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](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](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](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.<sup>tab:est\_summ</sup>

Segment <sup>a</sup>	Whole segment	Mean	St. Dev.	Min	Max
<b>BB</b>					
$Z_{c, min}$	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
<b>CB</b>					
$Z_{c, min}$	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
<b>OTB</b>					
$Z_{c, min}$	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
<b>UIRL</b>					
$Z_{c, min}$	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

<sup>a</sup>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. 4. The uncertainty values are equally applicable to each seagrass depth measure ( $Z_{c, min}$ ,  $Z_{c, med}$ ,  $Z_{c, max}$ ).<sup>tab:sens\_summ</sup>

Segment <sup>a</sup>	Mean	St. Dev	Min	Max
BB	0.10	0.09	0.01	0.49
CB	0.53	0.37	0.12	1.57
OTB	0.38	0.26	0.06	1.40
UIRL	0.10	0.10	0.00	0.81

<sup>a</sup>BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon.

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

Segment <sup>a</sup>	<i>n</i>	Mean	St. Dev.	Min	Max
<b>Choctawhatchee Bay</b>					
CCB	130	2.47	0.29	0.95	3.11
ECB	5	0.80	0.11	0.65	0.93
WCB	136	2.64	0.19	2.06	2.88
<b>Indian River Lagoon</b>					
BR	2	1.38	0.03	1.35	1.40
LCIRL	11	1.40	0.30	1.07	1.74
LIRL	3	1.79	0.02	1.78	1.82
LML	4	1.14	0.04	1.09	1.17
UCIRL	13	1.19	0.09	1.06	1.40
UIRL	1	1.15		1.15	1.15
UML	3	0.94	0.09	0.83	1.01
<b>Tampa Bay</b>					
HB	43	1.26	0.08	1.15	1.44
LTB	158	2.19	0.37	1.68	3.48
MTB	215	1.74	0.39	1.20	2.44
OTB	150	1.17	0.07	1.04	1.32

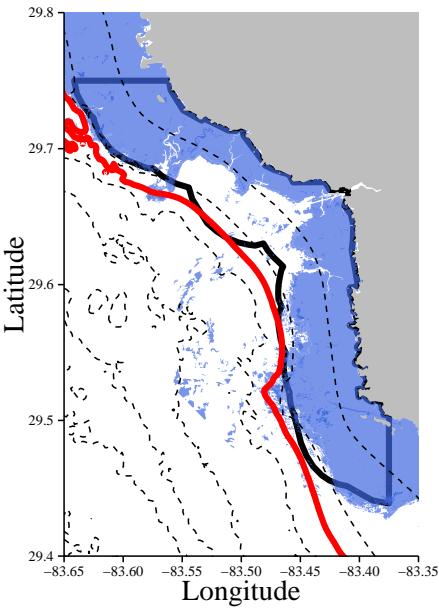
<sup>a</sup>CCB: Central Choctawhatchee Bay, ECB: Eastern Choctawhatchee Bay, WCB: Western Choctawhatchee Bay, BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon, HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

Table 5: Summary of estimated light requirements as percentage of surface irradiance for all bay segments of Choctawhatchee Bay, Indian River Lagoon, and Tampa Bay. See Figs. 7 to 9 for spatial distribution of the results.<sup>[tab:light\\_summ](#)</sup>

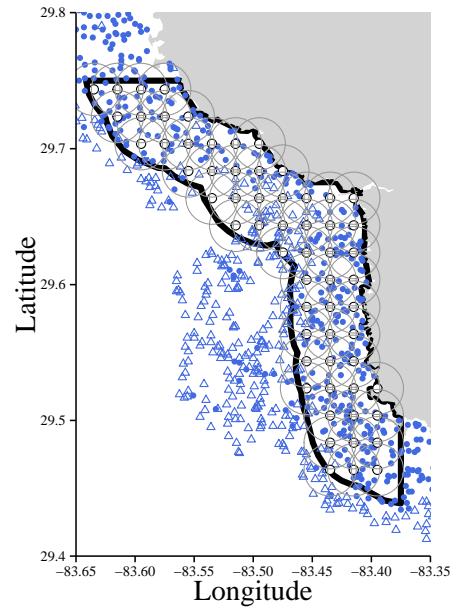
Segment <sup>a</sup>	n	Mean	St. Dev.	Min	Max
<b>Choctawhatchee Bay</b>					
CCB	130	46.71	8.71	23.33	82.56
ECB	5	71.78	7.72	65.72	85.22
WCB	136	45.26	6.27	24.43	64.38
<b>Indian River Lagoon</b>					
BR	2	11.96	1.13	11.16	12.77
LCIRL	11	9.72	4.75	4.45	18.04
LIRL	3	6.47	2.02	4.16	7.88
LML	4	17.84	2.34	14.88	19.88
UCIRL	13	14.11	4.19	7.57	19.92
UIRL	1	20.32		20.32	20.32
UML	3	23.29	2.83	20.87	26.41
<b>Tampa Bay</b>					
HB	43	32.74	7.42	14.34	45.13
LTB	158	24.33	6.67	4.76	40.02
MTB	215	29.76	8.01	12.30	50.02
OTB	150	37.00	5.82	17.32	49.82

<sup>a</sup>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.

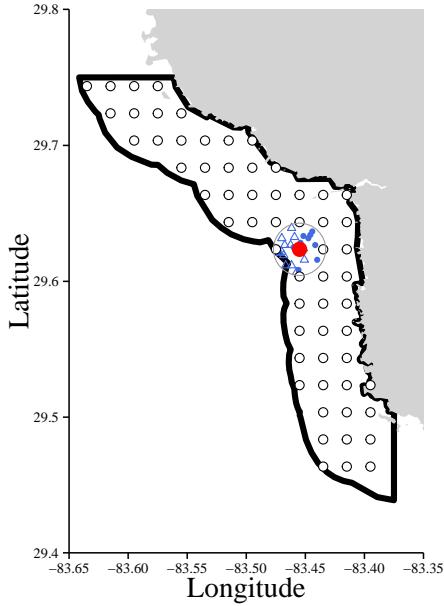
(a) Seagrass coverage and bathymetry for the segment



(b) Grid of locations and sample areas for estimates



(c) Sampled seagrass data for a test point



- Seagrass coverage
- 2 m depth contours
- Estimated depth limit for segment
- ▨ Segment polygon

- △ Seagrass absent
- Seagrass present

- Estimation grid
- Test point
- Sample area

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:buff\_}

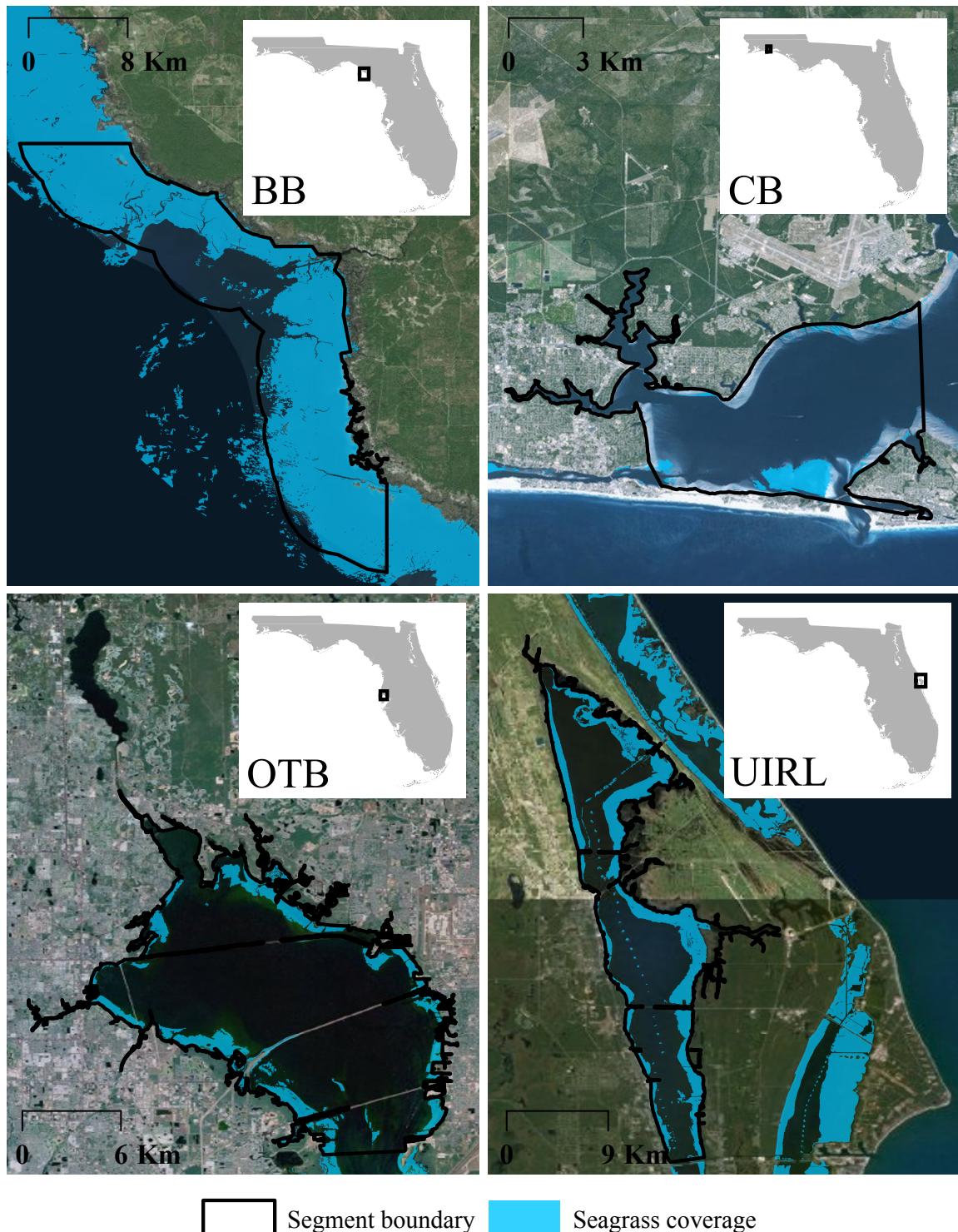
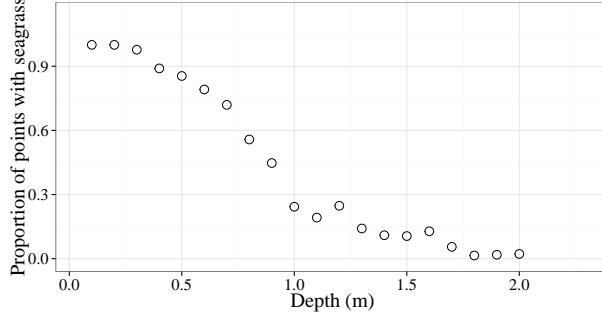


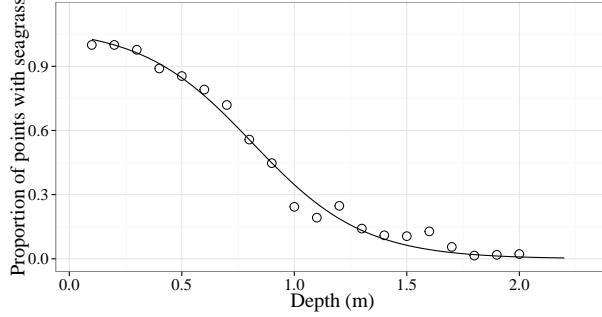
Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (CB: Choctawhatchee Bay), 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), and 2009 (UIRL: Upper Indian R. Lagoon).

{fig:seg\_a}

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

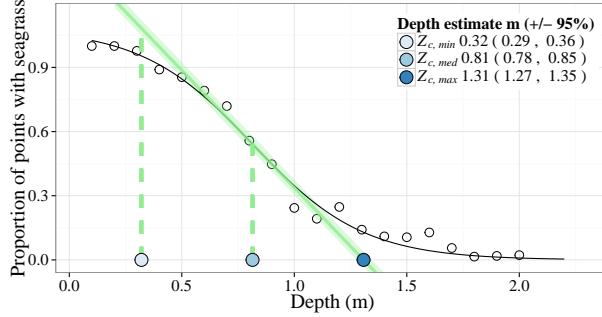


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit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

{fig:est\_e}

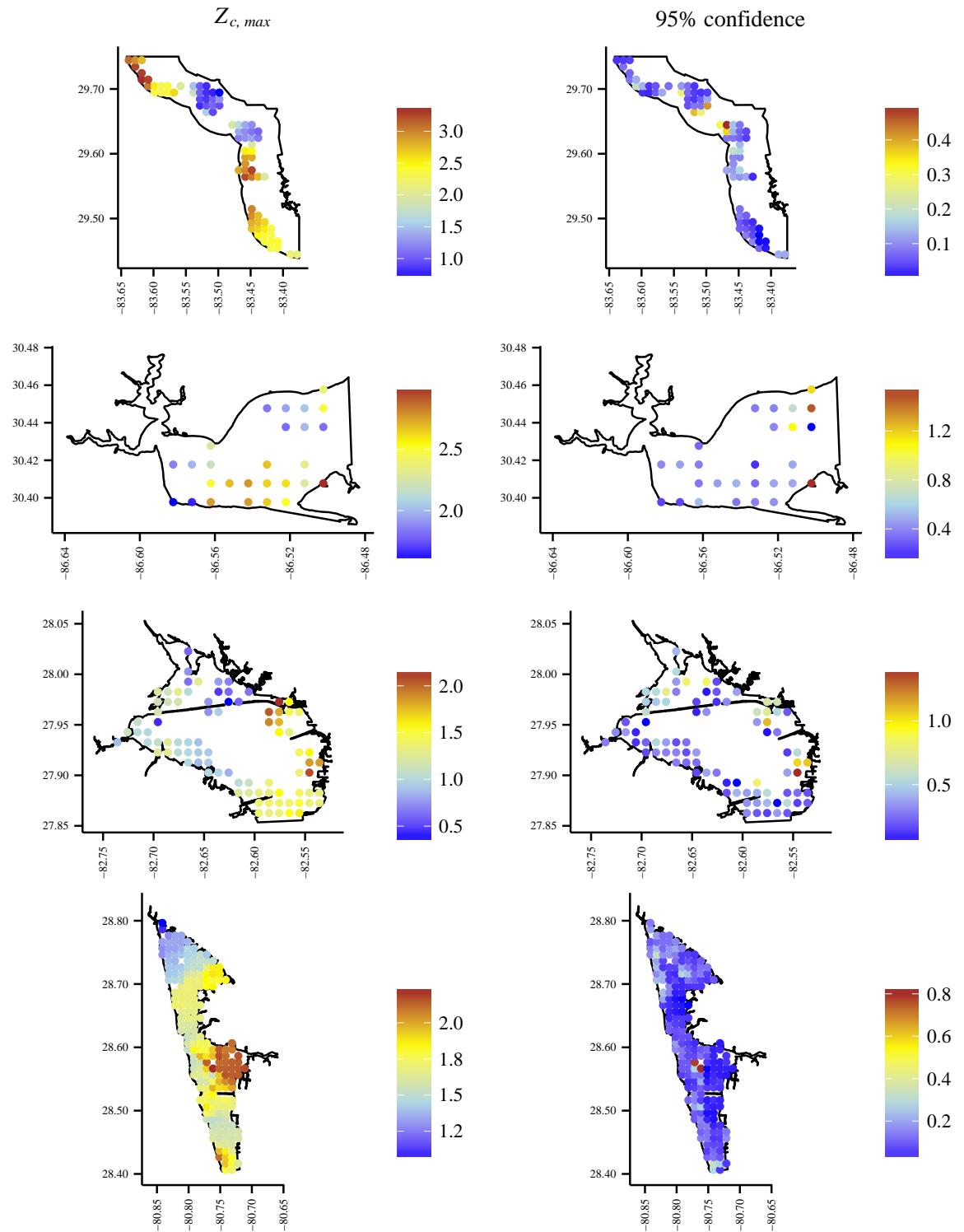


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ( $Z_{c, max}$ ) estimates are on the left and correspondings widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each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

{fig:all\_e}

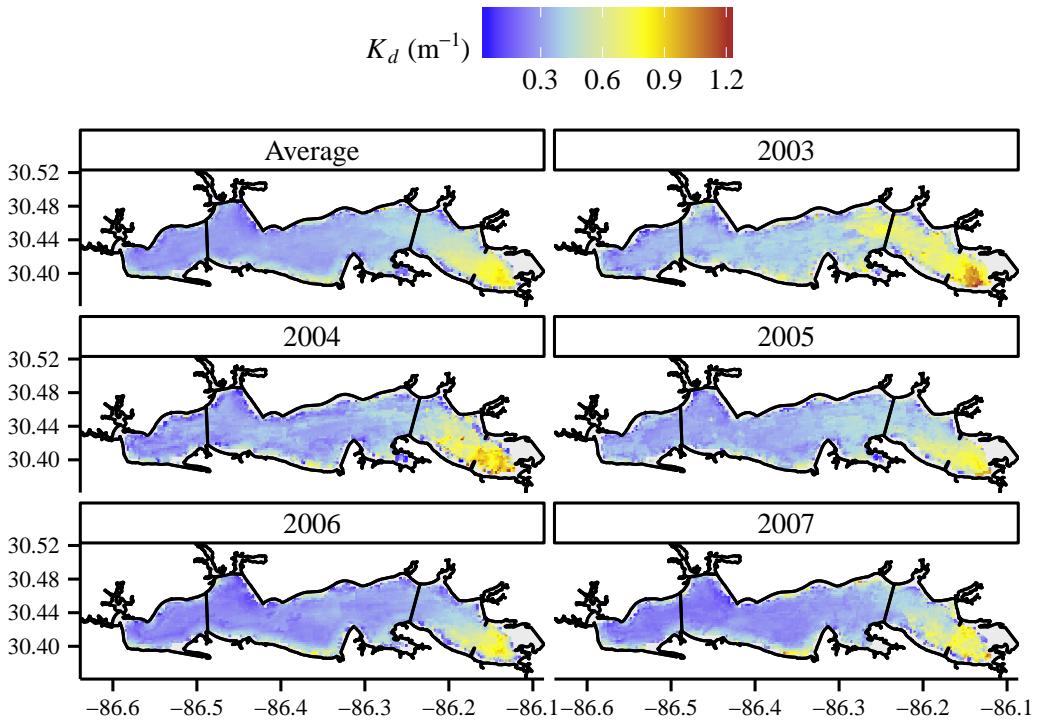


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate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

{fig:kd\_cl}

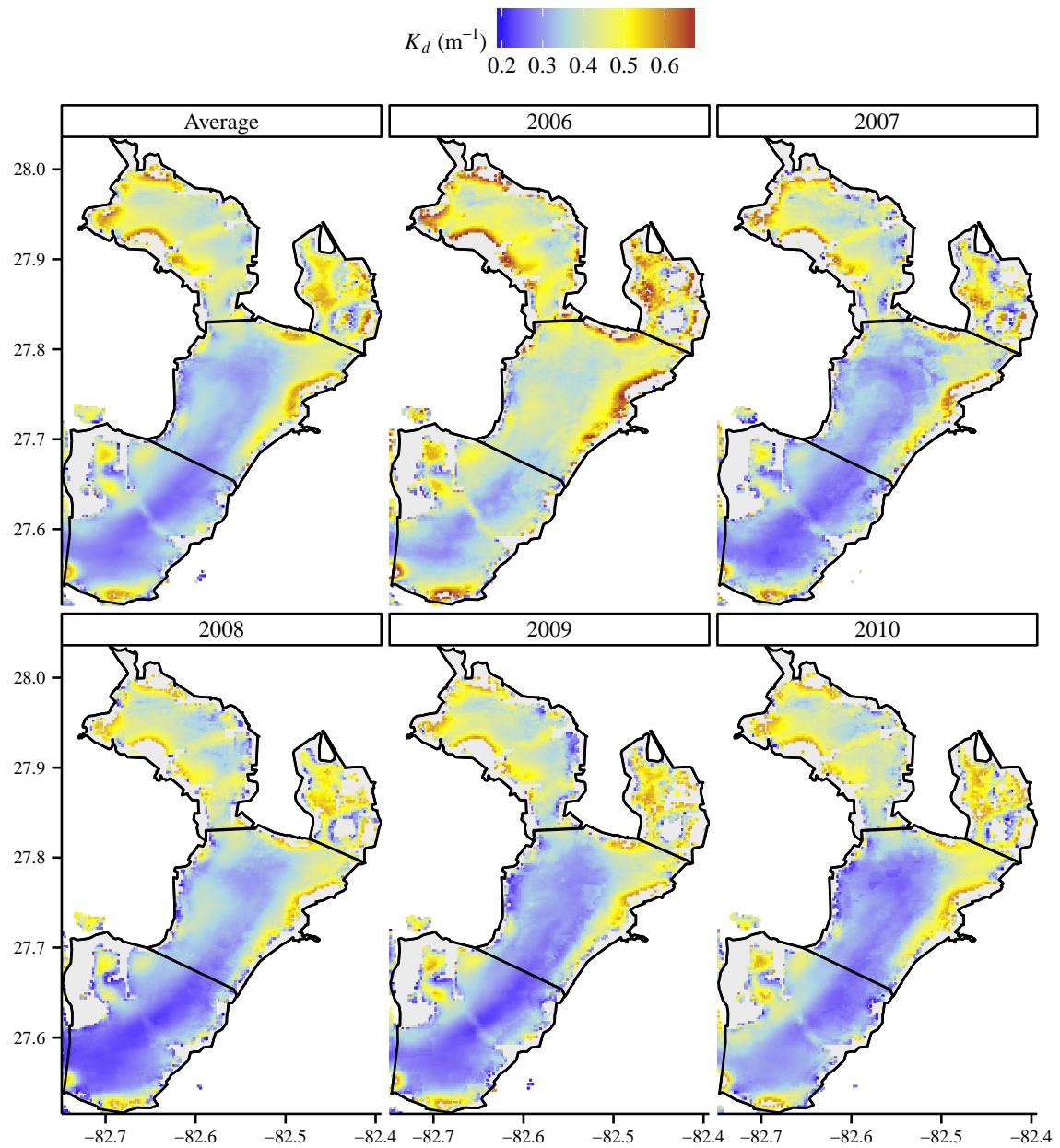


Fig. 6: Satellite estimated water clarity for Tampa Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment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

{fig:kd\_tk}

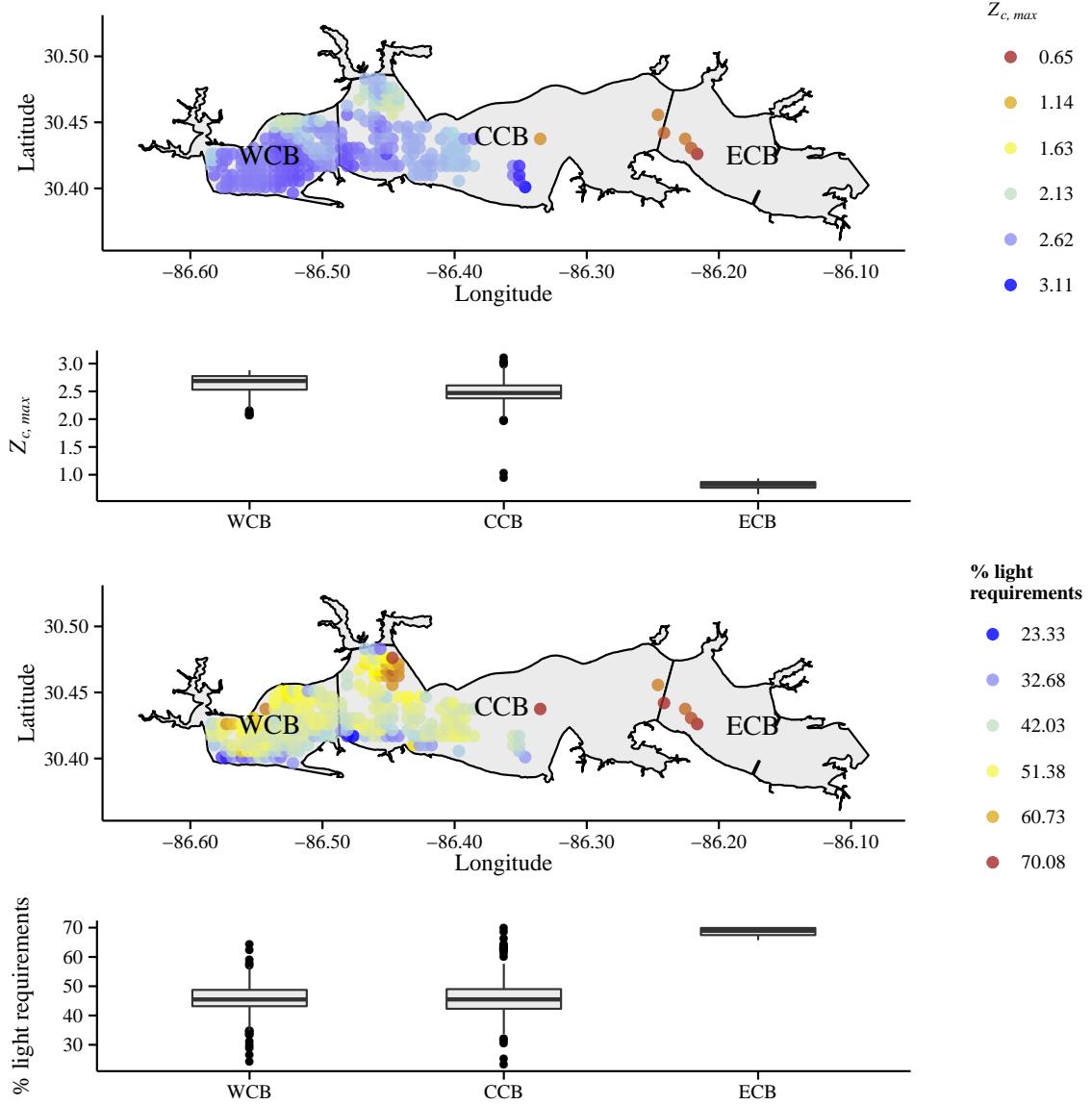


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25<sup>th</sup> percentile, median, and 75<sup>th</sup> 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:light}

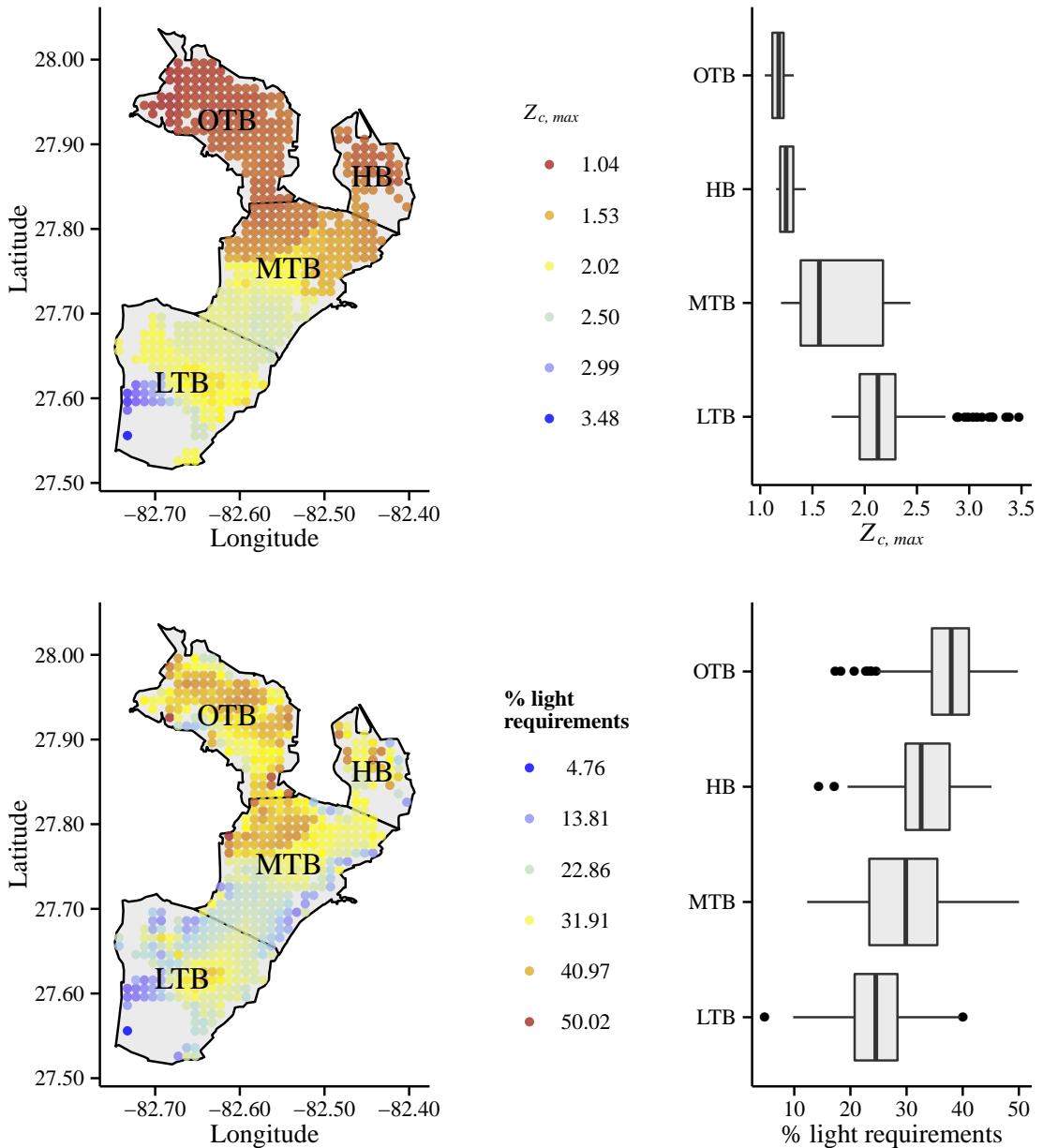


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25<sup>th</sup> percentile, median, and 75<sup>th</sup> 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:light}

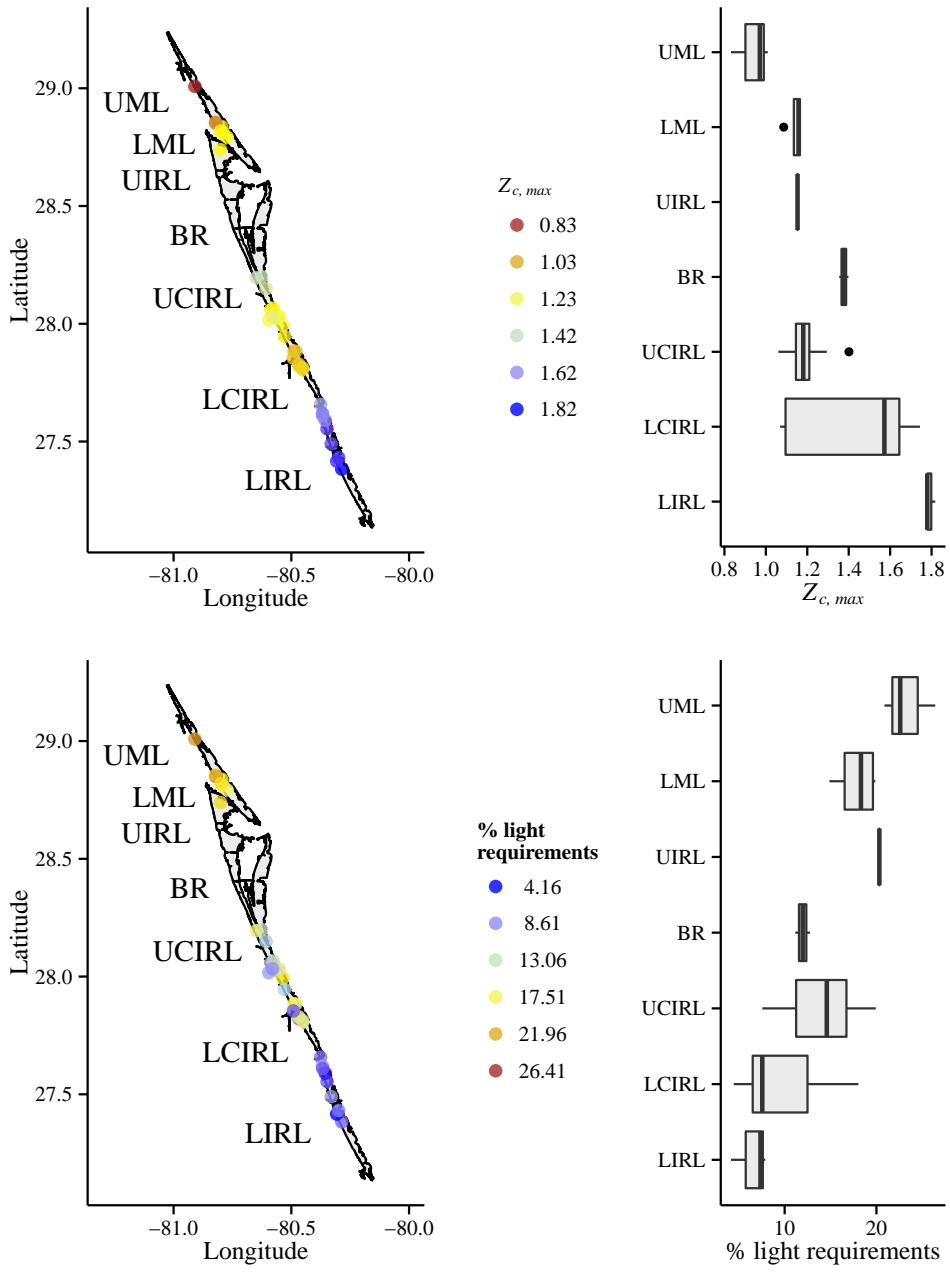


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment 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.

{fig:light}