

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

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**4 Abstract**

5 The maximum depth of colonization ( $Z_c$ ) is a useful measure of seagrass growth that  
6 describes response to light attenuation in the water column. However, lack of standardization  
7 among methods for estimating  $Z_c$  has limited the description of habitat requirements at spatial  
8 scales most relevant for environmental management. An algorithm is presented for estimating  
9 seagrass  $Z_c$  using geospatial datasets that are commonly available for coastal regions. A defining  
10 characteristic of the algorithm is its ability to estimate  $Z_c$  using an adjustable spatial region such  
11 that the estimated values can be interpreted for specific areas of interest. These spatially-resolved  
12 estimates of  $Z_c$  can then be related to light attenuation to evaluate factors that affect seagrass  
13 growth, such as light requirements. Four distinct coastal regions of Florida were evaluated,  
14 describing seagrass growth patterns on relatively small spatial scales in each region. The analysis  
15 was extended to entire bay systems using  $Z_c$  and estimates of light attenuation ( $K_d$ ) to quantify  
16 minimum light requirements derived from satellite remote sensing. Sensitivity analyses indicated  
17 that estimates of  $Z_c$  were generally robust for each case study, although confidence intervals  
18 varied with sample size and number of points containing seagrass.  $Z_c$  estimates also varied along  
19 water quality gradients such that seagrass growth was more limited near locations with reduced  
20 water clarity. Site-specific characteristics that contributed to variation in growth patterns were  
21 easily distinguished using the algorithm as compared to less spatially-resolved estimates of  $Z_c$ .  
22 Light requirements for the Indian River Lagoon (13.4%) on the Atlantic Coast were substantially  
23 lower than those for Tampa Bay (30.4%) and Choctawhatchee Bay (47.1%) on the Gulf Coast.  
24 More importantly, the algorithm characterized spatial variation in light requirements within bays,  
25 with values ranging from 4.2 – 26.4% in the Indian River Lagoon, 15.6 – 78.3% in the  
26 Choctawhatchee Bay, and 4.8 – 50% in Tampa Bay. Higher light requirements in Gulf Coast  
27 estuaries may indicate regional differences in species composition or additional factors, such as  
28 epiphyte growth, that further reduce light availability at the leaf surface. A spatially-resolved  
29 characterization of seagrass  $Z_c$  is possible for other regions because the algorithm is transferable  
30 with minimal effort to novel datasets.

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

## **32    1    Introduction**

33       Seagrasses are ecologically valuable components of aquatic systems that have a critical  
34      role in shaping aquatic habitat. These ‘ecosystem engineers’ influence multiple characteristics of  
35      aquatic systems through interactions with many biological and abiotic components (Jones et al.  
36      1994, Koch 2001). For example, seagrass beds create habitat for juvenile fish and invertebrates by  
37      reducing wave action and stabilizing sediment (Williams and Heck 2001, Hughes et al. 2009).

38       Seagrasses also respond to changes in water clarity via physiological linkages with light  
39      availability. Seagrass communities in productive aquatic systems may decline in deeper waters as  
40      increased nutrient loading reduces water clarity through increased algal concentration (Duarte  
41      1995). Empirical relationships between nutrient loading, water clarity, light requirements, and the  
42      maximum depth of seagrass colonization have been identified (Duarte 1991, Kenworthy and  
43      Fonseca 1996, Choice et al. 2014) and are often used to characterize light regimes sufficient to  
44      maintain seagrass habitat (Steward et al. 2005). Seagrass depth limits have also been used to  
45      establish quantitative targets for nutrient loading that will maintain water quality (Janicki and  
46      Wade 1996). Seagrasses are integrative of conditions over time in relation to changes in nutrient  
47      regimes (Duarte 1995) and are often preferred biological endpoints to describe ecosystem  
48      responses to perturbations relative to more variable components of the ecosystem (e.g.,  
49      phytoplankton). Quantifying the relationship between seagrasses and water clarity is a useful  
50      approach to understanding ecological characteristics of aquatic systems with potential insights  
51      into system response to disturbance (Greve and Krause-Jensen 2005).

52       Many different approaches have been used to estimate seagrass depth limits. For example,  
53      a common in situ approach is to sample seagrass along depth transects until the outer limit is  
54      adequately characterized (e.g., Spears et al. 2009). Alternative techniques include underwater  
55      photos or videos, aquascope identification, or hydroacoustic assessments (Zhu et al. 2007,  
56      Søndergaard et al. 2013). Such efforts have been useful for site-specific approaches where the  
57      analysis needs are driven by a particular question (e.g., Iverson and Bittaker 1986, Hale et al.  
58      2004). The availability of geospatial data that describe areal seagrass and bathymetric coverage  
59      suggests standardized techniques can be developed that could be applied across broad areas.  
60      However, an additional challenge is that estimates from geospatial data are typically applied to

61 predefined management units that may prevent generalization outside of the study area (e.g.,  
62 [Steward et al. 2005](#)). For example, coastal regions and estuaries in Florida are partitioned using a  
63 segmentation scheme based on salinity distributions. Fig. 1a shows variation in seagrass  
64 distribution for a management segment (thick polygon) in the Big Bend region of Florida. The  
65 maximum depth colonization, as a red countour line, is based on a segment-wide estimate of all  
66 seagrasses within the polygon. Although the estimate is not inaccurate for the segment,  
67 substantial variation in growth patterns at smaller spatial scales is not adequately described. depth  
68 of colonization ( $Z_c$ ) is greatly over-estimated at the outflow of the Steinhatchee River (northeast  
69 portion of the segment) where high concentrations of dissolved organic matter reduce water  
70 clarity and naturally limit seagrass growth (personal communication, Nijole Wellendorf, Florida  
71 Department of Environmental Protection). Consequently, methods for estimating seagrass depth  
72 limits should have sufficient flexibility based on the characteristics of the study region and the  
73 desired spatial context for evaluation. Such techniques can facilitate comparisons between regions  
74 given the spatial and temporal coverage of most geospatial data sources.

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

90 Products from remote sensing can provide useful estimates of water clarity by covering

91 spatial scales relevant to coastal ecosystems and providing coverage at regular and frequent time  
92 intervals. As such, water clarity data from satellite remote sensing products could be combined  
93 with depth of colonization estimates to develop a spatial description of seagrass light  
94 requirements. Although algorithms have been developed for coastal waters to estimate surface  
95 reflectance from satellite data (Woodruff et al. 1999, Chen et al. 2007), this information has rarely  
96 been used to describe seagrass light requirements at a spatial resolution consistent with most  
97 remote sensing products. Conversely, secchi observations can provide reliable measures of water  
98 clarity (USEPA 2006), although data can be unbalanced by location and time. Aquatic resources  
99 with greater recreational or economic importance may be over-sampled relative to those that may  
100 have more ecological significance (Wagner et al. 2008, Lottig et al. 2014). Moreover, field  
101 measurements that are limited to discrete time periods are more descriptive of short-term  
102 variability rather than long-term trends in water clarity (Elsdon and Connell 2009). Seagrass  
103 growth patterns are integrative of seasonal and inter-annual patterns in water clarity, such that  
104 estimates of light requirements may be limited if water clarity measurements inadequately  
105 describe temporal variation. Satellite remote sensing products can provide reliable estimates of  
106 water clarity and could be used to develop a more complete description of relevant ecosystem  
107 characteristics.

108 Quantitative and flexible methods for estimating seagrass depth limits and light  
109 requirements can improve descriptions of aquatic habitat, thus enabling potentially novel insights  
110 into ecological characteristics of aquatic systems. This article describes a method for estimating  
111 seagrass depth of colonization using geospatial datasets describing seagrass coverage and satellite  
112 remote sensing data of light attenuation in the water column to create a spatially-resolved and  
113 flexible measure. An algorithm is described that estimates seagrass depth limits from coverage  
114 maps and bathymetric data using an *a priori* defined area of influence. These estimates are  
115 combined with measures of water clarity to develop a spatial characterization of light  
116 requirements. Study objectives are to 1) describe the method for estimating seagrass depth of  
117 colonization, 2) apply the technique to four distinct regions of Florida to illustrate improved  
118 quantification of seagrass growth patterns with respect to depth, and 3) develop a spatial  
119 description of depth limits, water clarity, and light requirements for the case studies. The method  
120 is first illustrated using four relatively small areas of larger coastal regions followed by extension

121 to entire estuaries to characterize spatial variation in light requirements, within and between  
122 regions.

## 123 **2 Methods**

### 124 **2.1 Study sites and data sources**

125 Four coastal locations in Florida were used as study sites: the Big Bend region (northeast  
126 Gulf Coast), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf Coast), and Indian River  
127 Lagoon (Atlantic coast) (Table 1 and Fig. 2). These sites were chosen to represent a regional  
128 distribution of estuarine areas in Florida and to ensure sites had adequate data. One segment  
129 within each region and smaller spatial units defined by the algorithm were first evaluated to  
130 illustrate use of the method. A second analysis focused on quantifying seagrass depth limits for  
131 all of Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon to describe the spatial  
132 pattern of light requirements.

133 Geospatial data describing seagrass areal coverage and bathymetry were used to estimate  
134  $Z_c$ . These data products are publically available for coastal regions of Florida through the US  
135 Geological Survey, Florida Department of Environmental Protection, Florida Fish and Wildlife  
136 Conservation Commission, and many watershed management districts. Seagrass coverage maps  
137 were obtained for a recent year in each of the study sites (Table 1). The original coverage maps  
138 were produced by photo-interpreting aerial images to categorize seagrass as absent, discontinuous  
139 (patchy), or continuous. We considered only present (continuous and patchy) and absent  
140 categories since differences between continuous and patchy coverage were often inconsistent  
141 between data sources.

142 Bathymetry data were obtained from the National Oceanic and Atmospheric  
143 Administration's (NOAA) National Geophysical Data Center (<http://www.ngdc.noaa.gov/>) as  
144 either Digital Elevation Models (DEMs) or as raw sounding data from hydroacoustic or other  
145 surveys. Tampa Bay data provided by the Tampa Bay National Estuary Program are described in  
146 Tyler et al. (2007). Bathymetry for the Indian River Lagoon was obtained from the St. John's  
147 Water Management District (Coastal Planning and Engineering 1997). Vertical datums varied  
148 among data sources. NOAA products were referenced to mean lower low water. Tampa Bay data,  
149 however, were referenced to the North American Vertical Datum of 1988 (NAVD88) and the

150 Indian River Lagoon data were referenced to mean sea level. Prior to analysis, all bathymetric data  
151 were vertically adjusted to local mean sea level (MSL) using the NOAA VDatum tool  
152 (<http://vdatum.noaa.gov/>) for comparability between data sources. Adjusted data were combined  
153 with seagrass coverage layers using standard union techniques for raster and vector layers in  
154 ArcMap 10.1 (ESRI (Environmental Systems Research Institute) 2012). To reduce computation  
155 time, bathymetry layers were first masked using a 1 km buffer of the seagrass coverage layer.  
156 Raster bathymetric layers were converted to vector point layers to combine with seagrass  
157 coverage maps, described below.

## 158 **2.2 Quantifying water clarity**

159 Spatial variation in water clarity were explored for the entire areas of Choctawhatchee  
160 Bay, Tampa Bay, and the Indian River Lagoon. Limited clarity data in the Big Bend region  
161 prohibited analysis in this location. Satellite images were used to create a gridded 1 km<sup>2</sup> map of  
162 estimated water clarity (m, Tampa Bay) or light extinction ( $K_d$ , m<sup>-1</sup>, Choctawhatchee Bay).  
163 Secchi data were used directly to evaluate light requirements for the Indian River Lagoon because  
164 satellite data were inestimable.

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

179 Satellite estimates of water clarity were unobtainable in the Indian River Lagoon because

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

## 188 **2.3 Estimating seagrass depth of colonization**

189 Seagrass depth of colonization estimates used combined seagrass coverage maps and  
190 bathymetric depth data described above. The combined layer was a point shapefile with attributes  
191 describing location (latitude, longitude), depth (m), and seagrass (present, absent). Seagrass  $Z_c$   
192 values were estimated from these data by quantifying the proportion of points with seagrass at  
193 each observed depth. Three unique measures obtained from these data are minimum ( $Z_{c,min}$ ),  
194 median ( $Z_{c,med}$ ), and maximum ( $Z_{c,max}$ ) depth of colonization. Operationally, these terms  
195 describe characteristics of the seagrass coverage map with quantifiable significance.  $Z_{c,max}$  is the  
196 deepest depth at which a significant coverage of mappable seagrasses occurred independent of  
197 outliers, whereas  $Z_{c,med}$  is the median depth occurring at the deep water edge.  $Z_{c,min}$  is the depth  
198 at which seagrass coverage begins to decline with increasing depth and may not be statistically  
199 distinguishable from zero depth, particularly in turbid waters.

200 The spatially-resolved approach for estimating  $Z_c$  begins by choosing an explicit location  
201 in cartesian coordinates within the general boundaries of the available data. Seagrass depth data  
202 (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the  
203 chosen location are selected for estimating seagrass  $Z_c$  values (sample areas in Fig. 1). The  
204 estimate for each location is quantified from the proportion of sampled points that contain  
205 seagrass at decreasing 0.1 meter depth bins from the surface to the maximum depth in the sample  
206 (Fig. 3a). Although the chosen radius for selecting data is problem-specific, the minimum radius  
207 should be large enough to sample a sufficient number of points for estimating  $Z_c$ . In general, a  
208 sufficient radius will produce a plot that indicates a decrease in the proportion of points that are  
209 occupied by seagrass with increasing depth. Plots with insufficient data may indicate a reduction

210 of seagrass with depth has not occurred (e.g., nearshore areas) or seagrasses simply are not  
211 present. If more than one location is used to estimate  $Z_c$  (as in Fig. 1), radii for each point should  
212 be chosen to reduce overlap with the seagrass depth data sampled by neighboring points.

213 For each location, a curve is fit to the sampled depth points using non-linear regression to  
214 characterize the reduction in seagrass as a function of depth (Fig. 3b). Specifically, a decreasing  
215 logistic growth curve is used with the assumption that seagrass decline with increasing depth is  
216 monotonic from the minimum depth of colonization followed by a gradual decline at the  
217 maximum depth. The function is asymptotic at the minimum and maximum depths of  
218 colonization to constrain the estimates within the data domain. The curve is fit by minimizing the  
219 residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992) with  
220 starting parameters estimated from the observed data that are initial approximations of the curve  
221 characteristics. The model has the following form:

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

222 where the proportion of points occupied by seagrass at each depth,  $Z$ , is defined by a logistic  
223 curve with an asymptote  $\alpha$ , a midpoint inflection  $\beta$ , and a scale parameter  $\gamma$ . Finally, a simple  
224 linear curve is fit through the inflection point ( $\beta$ ) of the logistic curve to estimate the three  
225 measures of depth of colonization (Fig. 3c). The inflection point is considered the depth at which  
226 seagrass are decreasing at a maximum rate and is used as the slope of the linear curve. The  
227 maximum depth of seagrass colonization,  $Z_{c,max}$ , is the x-axis intercept of the linear curve. The  
228 minimum depth of seagrass growth,  $Z_{c,min}$ , is the location where the linear curve intercepts the  
229 upper asymptote of the logistic growth curve. The median depth of seagrass colonization,  $Z_{c,med}$ ,  
230 is the halfway between  $Z_{c,min}$  and  $Z_{c,max}$ .  $Z_{c,med}$  is not always the inflection point of the logistic  
231 growth curve.

232 Estimates for each of the three  $Z_c$  measures were obtained only if specific criteria were  
233 met. These criteria were implemented as a safety measure that ensures a sufficient amount and  
234 appropriate quality of data were sampled within the chosen radius. First, estimates were provided  
235 only if a sufficient number of seagrass depth points were present in the sampled data to estimate a  
236 logistic growth curve. This criteria applies to the sample size as well as the number of points with

237 seagrass in the sample. Second, estimates were provided only if an inflection point was present on  
238 the logistic curve within the range of the sampled depth data. This criteria applied under two  
239 scenarios where the curve was estimated but a trend was not adequately described by the sampled  
240 data. That is, estimates were unavailable if the logistic curve described only the initial decrease in  
241 points occupied as a function of depth. The opposite scenario occurred when a curve was  
242 estimated but only the deeper locations beyond the inflection point were present in the sample.  
243 Third, the estimate for  $Z_{c,min}$  was set to zero depth if the linear curve through the inflection point  
244 intercepted the upper asymptote of the logistic curve at x-axis values less than zero. The estimate  
245 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  
246 fixed at zero. Finally, estimates were considered invalid if the 95% confidence interval for  $Z_{c,max}$   
247 included zero. In such cases, the three measures are not statistically distinguishable, although a  
248 useful estimate for  $Z_{c,max}$  is provided. Methods to determine confidence bounds are described  
249 below.

## 250 2.4 Estimating uncertainty

251 Confidence intervals for the  $Z_c$  values were estimated using a Monte Carlo simulation  
252 approach that used the variance-covariance matrix of the logistic model parameters (Hilborn and  
253 Mangel 1997). Confidence intervals were constructed by repeated sampling of a multivariate  
254 normal distribution to evaluate the uncertainty in the inflection point in eq. (1). The sampling  
255 distribution assumes:

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

256 where  $x$  is a predictor variable used in eq. (1) (depth) that follows a multivariate normal  
257 distribution with mean  $\mu$ , and variance-covariance matrix  $\Sigma$ . The mean values are set at the depth  
258 value corresponding to the inflection point on the logistic curve from the observed model, whereas  
259  $\Sigma$  is the variance-covariance matrix of the model parameters ( $\alpha, \beta, \gamma$ ). A large number of samples  
260 ( $n = 10000$ ) were drawn from the distribution to characterize the uncertainty of the depth value of  
261 the inflection point. The 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the sample were considered bounds on the  
262 95% confidence interval. This approach was used because uncertainty from the logistic curve is  
263 directly related to uncertainty in each of the  $Z_c$  estimates that are based on the linear curve  
264 through the inflection point. Upper and lower limits for each  $Z_c$  estimate were obtained by fitting

265 new linear curves through the upper and lower limits of the initial depth value. (i.e., Fig. 3c).

266 Nonlinear least squares models were based on the `nls` and `SSlogis` functions that used  
267 a self-starting logistic growth model (Bates and Chambers 1992, ?). Multivariate normal  
268 distributions were simulated using functions in the MASS package (Venables and Ripley 2002).  
269 Geospatial data were imported and processed using functions in the `rgeos` and `sp` packages  
270 (Bivand et al. 2008, Bivand and Rundel 2014).

## 271 **2.5 Evaluation of spatial heterogeneity of seagrass depth limits**

272 Spatially-resolved estimates of  $Z_c$  were obtained for several locations in each of the four  
273 segments described above (Fig. 2). A regular grid of locations for estimating each of the three  $Z_c$   
274 values was created for each segment. Spacing between sample points was 0.01 decimal degrees  
275 ( $\approx 1$  km at 30 degrees N latitude) and the sampling radius for each location was set to 0.02  
276 decimal degrees. The sample radius allowed complete utilization of the seagrass data while  
277 minimizing overlap. Finally, a single segment-wide estimate using all data at each study site was  
278 used for comparisons. Departures from the segment-wide estimate at finer scales were considered  
279 evidence of spatial heterogeneity in seagrass growth and improved clarity of description as a  
280 result.

## 281 **2.6 Relating depth of colonization and water clarity**

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

$$I_z = I_O \cdot \exp(-K_d \cdot Z) \quad (3)$$

288 such that the irradiance of incident light at depth  $Z$  ( $I_z$ ) can be estimated from the irradiance at  
289 the surface ( $I_O$ ) and a light extinction coefficient ( $K_d$ ). Light requirements of seagrass can be  
290 estimated by rearranging eq. (3):

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

291 where the percent light requirements are a function of the estimated  $Z_{c,max}$  and light extinction. If  
292  $K_d$  estimates are unavailable, a conversion factor can be used to estimate the light extinction  
293 coefficient from secchi depth  $Z_{secchi}$ , such that  $c = K_d \cdot Z_{secchi}$ , where  $c$  has been estimated as 1.7  
294 (Poole and Atkins 1929, Idso and Gilbert 1974):

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

295 Two approaches were used to estimate light requirements based on the availability of  
296 satellite data or in situ water clarity (see section 2.2). For locations with satellite data  
297 (Choctawhatchee and Tampa Bay), a regular grid of sampling points was created as before to  
298 estimate  $Z_{c,max}$  and sample the continuous layer of satellite-derived water clarity. Grid spacing  
299 was different in each bay (0.005 for Choctawhatchee Bay, 0.01 for Tampa Bay) to account for  
300 variation in spatial scales of seagrass coverage. Equation (4) was used to estimate light  
301 requirements at each point for Choctawhatchee Bay and eq. (5) was used for Tampa Bay.  
302 Similarly, the geographic coordinates for each in situ secchi measurement in the Indian River  
303 Lagoon were used as locations for estimating  $Z_{c,max}$  and light requirements using eq. (5).  
304 Excessively small estimates for light requirements were removed for Indian River Lagoon which  
305 were likely caused by shallow secchi observations that were not screened during initial data  
306 processing. A critical difference between the satellite and secchi data was that a more complete  
307 spatial description of light requirements was possible in the former case due to continuous  
308 coverage, whereas descriptions using secchi data were confined to the original sampling  
309 locations. Sampling radii for locations in each bay were chosen to maximize the number of points  
310 with estimable values for  $Z_{c,max}$  (as described in section 2.3), while limiting the upper radius to  
311 adequately describe variation in seagrass growth patterns for emphasizing gradients in light  
312 requirements. Radii were fixed at 0.04 decimal degrees for Choctawhatchee Bay, 0.1 decimal  
313 degrees for Tampa Bay, and 0.15 decimal degrees for Indian River Lagoon.

314 **3 Results**

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

316        Each coastal region varied by several characteristics that potentially explain variation of  
317        seagrass growth (Table 1). Mean surface area was 191.2 square kilometers, with area decreasing  
318        for the Big Bend (271.4 km), Upper Indian River Lagoon (228.5 km), Old Tampa Bay (205.5  
319        km), and Choctawhatchee Bay (59.4 km) segments. Mean depth was less than 5 meters for each  
320        segment, excluding Western Choctawhatchee Bay which was slightly deeper than the other  
321        segments (5.3 m). Maximum depths were considerably deeper for Choctawhatchee Bay (11.9 m)  
322        and Old Tampa Bay (10.4 m), as compared to the Big Bend (3.6 m) and Indian River Lagoon (1.4  
323        m) segments. Seagrasses covered a majority of the surface area for the Big Bend segment (74.8  
324        %), whereas coverage was much less for Upper Indian River Lagoon (32.8 %), Old Tampa Bay  
325        (11.9 %), and Western Choctawhatchee Bay (5.9 %). Visual examination of the seagrass coverage  
326        maps for the respective year of each segment indicated that seagrasses were not uniformly  
327        distributed (Fig. 2). Seagrasses in Western Choctawhatchee Bay were sparse with the exception  
328        of a large patch located to the west of the inlet connection with the Gulf of Mexico. Seagrasses in  
329        the Big Bend segment were located throughout with noticeable declines near the outflow of the  
330        Steinhatchee River, whereas seagrasses in Old Tampa Bay and Upper Indian River Lagoon were  
331        generally confined to shallow areas near the shore. Seagrass coverage showed a partial decline  
332        toward the northern ends of both Old Tampa Bay and Upper Indian River Lagoon segments.  
333        Water clarity as indicated by average secchi depths was similar between the segments (1.5 m),  
334        although Choctawhatchee Bay had a slightly higher average (2.1 m).

335        The segment-wide estimates of  $Z_c$  indicated that seagrasses generally did not grow deeper  
336        than three meters in any of the segments (Table 2). Maximum and median depth of colonization  
337        were deepest for the Big Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old  
338        Tampa Bay (1.1 and 0.9 m), whereas the minimum depth of colonization was deepest for Western  
339        Choctawhatchee Bay (1.8 m) and shallowest for Old Tampa Bay (0.6 m). In most cases, the  
340        averages of all grid-based estimates were less than the whole segment estimates, indicating a  
341        left-skewed distribution of estimates at finer spatial scales. For example, the average of all grid  
342        estimates for  $Z_{c, max}$  in the Big Bend region indicated seagrasses grew to approximately 2.1 m,

343 which was 1.6 m less than the whole segment estimate. Although reductions were not as severe  
344 for the average grid estimates for the remaining segments, considerable within-segment variation  
345 was observed depending on grid location. For example, the deepest estimate for  $Z_{c,min}$  (2 m) in  
346 the Upper Indian River Lagoon exceeded the average of all grid locations for  $Z_{c,max}$  (1.7 m).  
347  $Z_{c,min}$  also had minimum values of zero meters for the Big Bend and Old Tampa Bay segments,  
348 suggesting that seagrasses declined continuously from the surface for several locations.

349 Visual interpretations of the grid estimates provided further information on the  
350 distribution of seagrasses in each segment (Fig. 4). Spatial heterogeneity in depth limits was  
351 particularly apparent for the Big Bend and Upper Indian River Lagoon segments. As expected,  
352 depth estimates indicated that seagrasses grew deeper at locations far from the outflow of the  
353 Steinhatchee River in the Big Bend segment. Similarly, seagrasses were limited to shallower  
354 depths at the north end of the Upper Indian River Lagoon segment near the Merrit Island National  
355 Wildlife Refuge. Seagrasses were estimated to grow at maximum depths up to 2.2 m on the  
356 eastern portion of the Upper Indian River Lagoon segment. Spatial heterogeneity was less distinct  
357 for the remaining segments although some patterns were apparent. Seagrasses in Old Tampa Bay  
358 grew slightly deeper in the northeast portion of the segment and declined to shallower depths near  
359 the inflow at the northern edge. Spatial variation in Western Choctawhatchee Bay was minimal,  
360 although the maximum  $Z_c$  estimate was observed in the northeast portion of the segment. As  
361 expected,  $Z_c$  values could not be estimated where seagrasses were sparse or absent, nor where  
362 seagrasses were present but the sampled points did not show a decline with depth. The former  
363 scenario was most common in Old Tampa Bay and Western Choctawhatchee Bay where  
364 seagrasses were unevenly distributed or confined to shallow areas near the shore. The latter  
365 scenario was most common in the Big Bend segment where seagrasses were abundant but  
366 locations near the shore were inestimable given that seagrasses did not decline appreciably within  
367 the depths that were sampled.

368 Uncertainty in  $Z_{c,max}$  indicated that confidence intervals were generally acceptable (i.e.,  
369 greater than zero), although the ability to discriminate between the three depth estimates varied by  
370 segment (Fig. 4 and Table 3). Uncertainty for all estimates as the average width of the 95%  
371 confidence intervals for all segments was 0.2 m. Greater uncertainty was observed for Western  
372 Choctawhatchee Bay (mean width was 0.5 m) and Old Tampa Bay (0.4 m), compared to the Big

373 Bend (0.1 m) and Upper Indian River Lagoon (0.1 m) segments. The largest confidence interval  
374 for each segment was 1.4 m for Old Tampa Bay, 1.6 m for Western Choctawhatchee Bay, 0.5 m  
375 for the Big Bend, and 0.8 m for the Upper Indian River Lagoon segments. Most confidence  
376 intervals for the remaining grid locations were much smaller than the maximum in each segment  
377 (e.g., an extreme central location of the Upper Indian River Lagoon, Fig. 4). A comparison of  
378 overlapping confidence intervals for  $Z_{c,min}$ ,  $Z_{c,med}$ , and  $Z_{c,max}$  at each grid location indicated  
379 that not every measure was unique. Specifically, only 11.1% of grid points in Choctawhatchee  
380 Bay and 28.2% in Old Tampa Bay had significantly different estimates, whereas 82.4% of grid  
381 points in the Indian River Lagoon and 96.2% of grid points in the Big Bend segments had  
382 estimates that were significantly different. By contrast, all grid estimates in Choctawhatchee Bay  
383 and Indian River Lagoon had  $Z_{c,max}$  estimates that were significantly greater than zero, whereas  
384 all but 12.4% of grid points in Old Tampa Bay and 8% of grid points in the Big Bend segment had  
385  $Z_{c,max}$  estimates significantly greater than zero.

### 386 **3.2 Evaluation of seagrass light requirements**

387 Estimates of water clarity, seagrass depth limits, and corresponding light requirements for  
388 all locations in Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon indicated  
389 substantial variation, both between and within the different bays. Satellite-derived estimates of  
390 light attenuation for Choctawhatchee Bay (as  $K_d$ , Fig. 5) and Tampa Bay (as clarity, Fig. 6)  
391 indicated variation between years and along major longitudinal and lateral axes. For  
392 Choctawhatchee Bay,  $K_d$  estimates for western and central segments were substantially smaller  
393 than those for the more shallow, eastern segment. Maximum  $K_d$  values were also observed in  
394 earlier years (e.g., 2003, 2004). Clarity estimates for Tampa Bay also showed an increase towards  
395 more seaward segments, with particularly higher clarity along the mainstem. Clarity in 2006 was  
396 relatively lower than other years, with noticeable increases in 2007 and 2008. In situ secchi  
397 observations for the Indian River Lagoon followed a clear latitudinal gradient with higher values  
398 in more southern segments (Fig. 9). Very few measurements were available for the Upper Indian  
399 River Lagoon and Banana River segments, likely due to water clarity exceeding the maximum  
400 depth in shallow areas.

401 Seagrass  $Z_c$  estimates were obtained for 259 locations in Choctawhatchee Bay, 566  
402 locations in Tampa Bay, and 37 locations in the Indian River Lagoon (Table 4 and Figs. 7 to 9).

403 Mean  $Z_{c,max}$  for each bay was 2.5, 1.7, and 1.3 m for Choctawhatchee Bay, Tampa Bay, and  
404 Indian River Lagoon, respectively, with all values being significantly different between bays  
405 (ANOVA,  $F = 326.9$ ,  $df = 2, 859$ ,  $p < 0.001$ , followed by Tukey multiple comparison,  
406  $p < 0.001$  for all). Generally, spatial variation in  $Z_{c,max}$  followed variation in light requirements  
407 for broad spatial scales with more seaward segments or areas near inlets having lower light  
408 requirements. Mean light requirements were significantly different between all bays (ANOVA,  
409  $F = 463.7$ ,  $df = 2, 859$ ,  $p < 0.001$ , Tukey  $p < 0.001$  for all), with a mean requirement of 47.1%  
410 for Choctawhatchee Bay, 30.4% for Tampa Bay, and 13.4% for Indian River Lagoon. Significant  
411 differences in light requirements between segments within each bay were also observed  
412 (ANOVA,  $F = 12.1$ ,  $df = 2, 256$ ,  $p < 0.001$  for Choctawhatchee Bay,  $F = 84.6$ ,  $df = 3, 562$ ,  
413  $p < 0.001$  for Tampa Bay,  $F = 7.6$ ,  $df = 6, 30$ ,  $p < 0.001$  for Indian River Lagoon). Post-hoc  
414 evaluation of all pair-wise comparisons of mean light requirements between segments within each  
415 bay indicated that significant differences were apparent for several locations. Significant  
416 differences were observed between all segments in Choctawhatchee Bay ( $p < 0.001$  for all),  
417 except the central and western segments (Fig. 7). Similarly, significant differences in Tampa Bay  
418 were observed between all segments ( $p < 0.05$  for all), except Middle Tampa Bay and Old Tampa  
419 Bay (Fig. 8). Finally, for the Indian River Lagoon, significant differences were observed only  
420 between the Lower Central Indian River Lagoon and the Upper ( $p < 0.001$ ) and Lower Mosquito  
421 Lagoons ( $p = 0.023$ ), the Lower Indian River Lagoon and the Upper ( $p < 0.001$ ) and Lower  
422 Mosquito Lagoons ( $p = 0.013$ ), and the Upper Central Indian River and the Upper Mosquito  
423 Lagoon ( $p = 0.018$ ) (Fig. 9). Small sample sizes likely reduced the ability to distinguish between  
424 segments in the Indian River Lagoon.

## 425 **4 Discussion**

426 Seagrass depth of colonization is tightly coupled to variation in water quality such that an  
427 accurate method for estimating  $Z_{c,max}$  provides a biologically-relevant description of aquatic  
428 habitat. Accordingly, the ability to estimate seagrass depth of colonization and associated light  
429 requirements from relatively inexpensive sources of information has great value for developing an  
430 understanding of potentially limiting factors that affect ecosystem condition. To these ends, this  
431 study presented an approach for estimating seagrass depth of colonization from existing

432 geospatial datasets that has the potential to greatly improve clarity of description within multiple  
433 spatial contexts. We evaluated four distinct coastal regions of Florida to illustrate utility of the  
434 method for describing seagrass depth limits at relatively small spatial scales and extended the  
435 analysis to entire bay systems by combining estimates with water clarity to characterize spatial  
436 variation in light requirements. The results indicated that substantial variation in seagrass depth  
437 limits were observed, even within relatively small areas of interest. Estimated light requirements  
438 also indicated substantial heterogeneity within and between entire bays, suggesting uneven  
439 distribution of factors that limit seagrass growth patterns. To our knowledge, such an approach  
440 has yet to be implemented in widespread descriptions of aquatic habitat and there is great  
441 potential to expand the method beyond the current case studies. The reproducible nature of the  
442 algorithm also enables a context-dependent approach given the high level of flexibility. Overall,  
443 these methods inform the description of seagrass growth patterns by developing a more spatially  
444 relevant characterization of aquatic habitat.

#### 445 **4.1 Evaluation of the algorithm**

446 The algorithm for estimating seagrass depth of colonization has three primary advantages  
447 that facilitated a description of aquatic habitat in each of the case studies. First, the application of  
448 non-linear least squares regression provided an empirical means to characterize the reduction of  
449 seagrass coverage with increasing depth. This approach was necessary for estimating each of the  
450 three depth limits ( $Z_{c,min}$ ,  $Z_{c,med}$ ,  $Z_{c,max}$ ) using the maximum slope of the curve. The maximum  
451 rate of decline describes a direct and estimable physiological response of seagrass to decreasing  
452 light availability such that each measure provided an operational characterization of growth  
453 patterns (see section 2.3). The regression approach also allowed an estimation of confidence in  $Z_c$   
454 values by accounting for uncertainty in each of the three parameters of the logistic growth curve  
455 ( $\alpha$ ,  $\beta$ ,  $\gamma$ ). Indications of uncertainty are required components of any esimation technique that  
456 provide a direct evaluation of the quality of data used to determine he model fit. By default,  
457 estimates with confidence intervals for  $Z_{c,max}$  that included zero were discarded to remove highly  
458 imprecise estimates. Despite this restriction, some examples had exceptionally large confidence  
459 intervals relative to neighboring estimates (e.g., center of Upper Indian River Lagoon, Fig. 4),  
460 which suggests not all locations are suitable for applying the algorithm. The ability to estimate  $Z_c$   
461 and to discriminate between the three measures depended on several factors, the most important

462 being the extent to which the sampled seagrass points described a true reduction of seagrass  
463 coverage with depth. Sampling method (e.g., chosen radius) as well as site-specific characteristics  
464 (e.g., bottom-slope, actual occurrence of seagrass) are critical factors that directly influence  
465 confidence in  $Z_c$  estimates. A pragmatic approach should be used when applying the algorithm to  
466 novel data such that the location and chosen sample radius should be defined by the limits of the  
467 analysis objectives.

468 A second advantage is that the algorithm is highly flexible depending on the desired  
469 spatial context. Although this attribute directly affects confidence intervals, the ability to choose a  
470 sampling radius based on a problem of interest can greatly improve the description of aquatic  
471 habitat given site-level characteristics. The previous example described for the Big Bend region  
472 highlights this flexibility, such that a segment-wide estimate was inadequate for characterizing  
473  $Z_{c,max}$  that was limited near the outflow of the Steinhatchee river. The ability to choose a smaller  
474 sampling radius more appropriate for the location indicated that  $Z_{c,max}$  reflected known  
475 differences in water clarity near the outflow relative to other locations in the segment. However,  
476 an important point is that a segment-wide estimate is not necessarily biased such that a sampling  
477 radius that covers a broad spatial area could be appropriate depending on the analysis needs. If  
478 the effect of water clarity near the outflow was not a concern, the segment-wide estimate could  
479 describe seagrass growth patterns for the larger area without inducing descriptive bias. However,  
480 water quality standards as employed by management agencies are commonly based on predefined  
481 management units, which may not be appropriate for all locations. The flexibility of the algorithm  
482 could facilitate the development of point-based standards that eliminate the need to develop or use  
483 a pre-defined classification scheme. In essence, the relevant management area can be defined a  
484 priori based on known site characteristics.

485 The ability to use existing geospatial datasets is a third advantage of the algorithm.  
486 Further, bathymetry data and seagrass coverage are the only requirements for describing  $Z_c$  in a  
487 spatial context. These datasets are routinely collected by agencies at annual or semi-annual cycles  
488 for numerous coastal regions. Accordingly, data availability and the relatively simple method for  
489 estimating  $Z_c$  suggests that spatial descriptions could be developed for much larger regions with  
490 minimal effort. The availability of satellite-based products with resolutions appropriate for the  
491 scale of assessment could also facilitate a broader understanding of seagrass light requirements

492 when combined with  $Z_c$  estimates. However, data quality is always a relevant issue when using  
493 secondary information as a means of decision-making or addressing specific research questions.  
494 Methods for acquiring bathymetric or seagrass coverage data are generally similar between  
495 agencies such that the validity of comparisons from multiple sources is typically not a concern.  
496 However, one point of concern is the minimum mapping unit for each coverage layer, which is  
497 limited by the resolution of the original aerial photos and the comparability of photo-interpreted  
498 products created by different analysts. Seagrass maps routinely classify coverage as absent,  
499 patchy, or continuous. Discrepancies between the latter two categories between regions limited  
500 the analysis to a simple binary categorization of seagrass as present or absent. An additional  
501 evaluation of comparability between categories for different coverage maps could improve the  
502 descriptive capabilities of  $Z_c$  estimates.

## 503 **4.2 Heterogeneity in growth patterns and light requirements**

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

522        The use of light attenuation data, either as satellite-derived estimates or in situ secchi  
523        observations, combined with  $Z_c$  estimates provided detailed and previously unavailable  
524        characterizations of light requirements within the three estuaries. Requirements were lowest for  
525        the Indian River Lagoon, whereas estimates were higher for Tampa Bay and highest for  
526        Choctawhatchee Bay. Requirements for the Indian River Lagoon were generally in agreement  
527        with other Atlantic coastal systems (Dennison et al. 1993, Kemp et al. 2004), such that  
528        requirements typically did not exceed 25% with mean requirements for the whole bay estimated  
529        at 13.4%. However, light requirements for Indian River Lagoon were based on secchi  
530        observations with uneven spatial and temporal coverage, which potentially led to an incomplete  
531        description of true variation in light attenuation. Alternative measures to estimate  $K_d$  (e.g.,  
532        vertically-distributed PAR sensors) are required when bottom depth is shallower than maximum  
533        water clarity, although scalability remains an issue. Conversely, satellite-derived estimates were  
534        possible for Tampa and Choctawhatchee Bays where water column depth was sufficient and were  
535        preferred over in situ data given more complete spatial coverage. Mean light requirements for  
536        Tampa Bay were 30.4% of surface irradiance, which was in agreement with previously reported  
537        values (Dixon and Leverone 1995). Light requirements in Lower Tampa Bay were further verified  
538        using four locations from Dixon and Leverone (1995). Estimates using the current algorithm with  
539        2010 data were within 0.1% of the previously estimated light requirements of 22.5%, although  $Z_c$   
540        estimates were deeper suggesting improvements in water clarity. Estimates for Choctawhatchee  
541        Bay were substantially higher with a bay-wide average of 47.1%. The relatively higher light  
542        requirements for Gulf Coast esuaries, particularly Choctawhatchee Bay, may reflect the need for  
543        additional validation data for the conversion of satellite reflectance values to light attenuation.  
544        However, estuaries in the northern Gulf of Mexico are typically shallow and highly productive  
545        (Caffrey et al. 2013), such that high light requirements may in fact be related to the effects of high  
546        nutrient loads on water clarity. Further evaluation of seagrass light requirements in the northern  
547        Gulf of Mexico could clarify the extent to which our results reflect true differences relative to  
548        other coastal regions.

549        As previously noted, variation in seagrass light requirements can be attributed to  
550        differences in physiological requirements between species or regional effects of different light  
551        regimes (Choice et al. 2014). For example, *Halodule wrightii* is the most abundant seagrass in

552 Choctawhatchee Bay and occurs in the western polyhaline portion near the outflow with the Gulf  
553 of Mexico. Isolated patches of *Ruppia maritima* are also observed in the oligohaline eastern  
554 regions of the bay. Although  $Z_{c,max}$  was only estimable for a few points in eastern  
555 Choctawhatchee Bay, differences in species assemblages along a salinity gradient likely explain  
556 the differences in light requirements. The decline of *R. maritima* in eastern Choctawhatchee Bay  
557 has been attributed to species sensitivity to turbidity from high rainfall events, whereas losses of  
558 *H. wrightii* have primarily been attributed to physical stress during storm overwash and high wave  
559 energy (FLDEP 2012). The relatively high light requirements of eastern Choctawhatchee Bay  
560 likely reflect differing species sensitivity to turbidity, either through sediment resuspension from  
561 rainfall events or light attenuation from nutrient-induced phytoplankton production. Similarly,  
562 high light requirements may be related to epiphyte production at the leaf surface (Kemp et al.  
563 2004). Estimated light requirements based solely on water column light attenuation, as for secchi  
564 or satellite-derived values, may indicate unusually large light requirements if seagrasses are  
565 further limited by epiphytic growth at the leaf surface. Epiphyte limitation may be common for  
566 upper bay segments where nutrient inputs from freshwater inflows enhance algal production  
567 (Kemp et al. 2004). Additionally, lower light requirements for Hillsborough Bay relative to Old  
568 Tampa Bay may reflect a reduction in epiphyte load from long-term decreases in nitrogen inputs  
569 to northeast Tampa Bay (Dawes and Avery 2010).

### 570 4.3 Conclusions

571 Spatially-resolved estimates of  $Z_c$  combined with high-resolution measures of light  
572 attenuation provided an effective approach for evaluating light requirements. However, light  
573 requirements, although important, may only partially describe ecosystem characteristics that  
574 influence growth patterns. Seagrasses may be limited by additional physical, geological, or  
575 geochemical factors, including effects of current velocity, wave action, sediment grain size  
576 distribution, and sediment organic content (Koch 2001). Accordingly, spatially-resolved estimates  
577 of  $Z_c$  and associated light requirements must be evaluated in the context of multiple factors that  
578 may act individually or interactively with light attenuation. Extreme estimates of light  
579 requirements may suggest light attenuation is not the only determining factor for seagrass growth.  
580 An additional constraint is the quality of data that describe water clarity to estimate light  
581 requirements. Although the analysis used satellite-derived clarity to create a more complete

582 description relative to in situ data, the conversion of reflectance data from remote sensing  
583 products to attenuation estimates is not trivial. Further evaluation of satellite-derived data is  
584 needed to create a broader characterization of light requirements. However, the algorithm was  
585 primarily developed to describe maximum depth of colonization and the estimation of light  
586 requirements was a secondary product that illustrated an application of the method.

587 Spatially-resolved  $Z_c$  estimates can be a preliminary source of information for developing a more  
588 detailed characterization of seagrass habitat requirements and the potential to develop broad-scale  
589 descriptions has been facilitated as a result. Specifically, ? developed a more general approach for  
590 estimating  $Z_c$  for each coastal segment of Florida such that data are available to apply the current  
591 method on a much broader scale. Applications outside of Florida are also possible given the  
592 minimal requirements for geospatial data products to estimate depth of colonization.

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Table 1: Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates (see Fig. 2 for spatial distribution). Year is the date of the seagrass coverage and bathymetric data. Latitude and longitude are the geographic centers of each segment. Area and depth values are 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 <sup>a</sup>	OTB	UIRL	WCB
Year <sup>b</sup>	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

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

<sup>b</sup> Seagrass coverage data sources, see section 2.1 for bathymetry data sources:

BB: [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)

OTB: [http://www.swfwmd.state.fl.us/data/gis/layer\\_library/category/swim](http://www.swfwmd.state.fl.us/data/gis/layer_library/category/swim)

UIRL: <http://www.sjrwmd.com/gisdevelopment/docs/themes.html>

WCB [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)

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.

<b>Segment<sup>a</sup></b>	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>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
<b>WCB</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

<sup>a</sup>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. Summaries are based on the widths of 95% confidence intervals. The uncertainty values are equally applicable to each seagrass depth measure ( $Z_{c, min}$ ,  $Z_{c, med}$ ,  $Z_{c, max}$ ).

Segment <sup>a</sup>	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

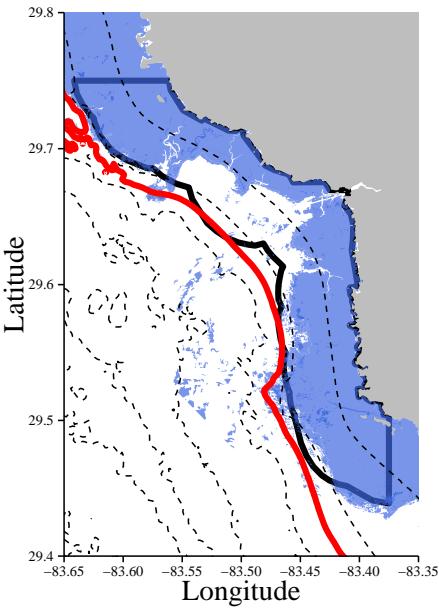
<sup>a</sup>BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Choctawhatchee Bay.

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.

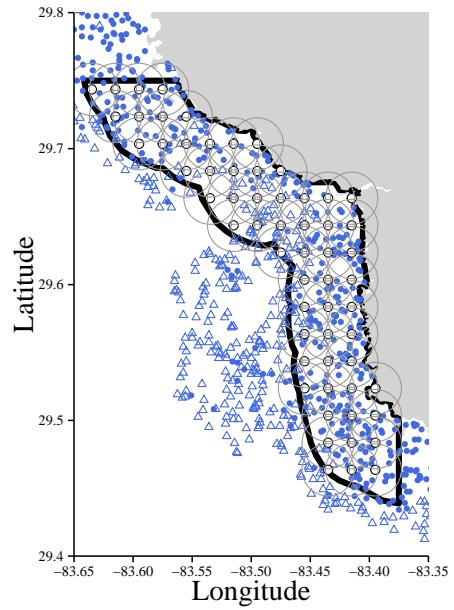
Segment <sup>a</sup>	n	$Z_{c,max}$				% light			
		Mean	St. Dev.	Min	Max	Mean	St. Dev.	Min	Max
<b>Choctawhatchee Bay</b>									
CCB	121	2.4	0.4	0.9	3.2	48.2	10.2	15.6	78.3
ECB	3	0.9	0.0	0.8	0.9	67.8	2.7	64.8	69.9
WCB	135	2.6	0.2	2.1	2.9	45.6	6.6	24.2	70.9
<b>Indian River Lagoon</b>									
BR	2	1.4	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		20.3	20.3
UML	3	0.9	0.1	0.8	1.0	23.3	2.8	20.9	26.4
<b>Tampa Bay</b>									
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

<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.

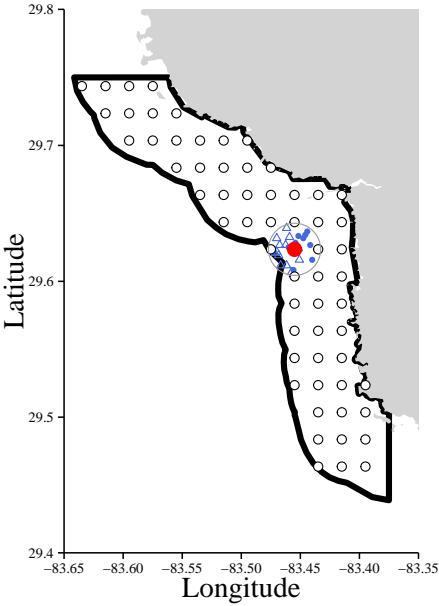
(a) Seagrass coverage and bathymetry for the segment



(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.

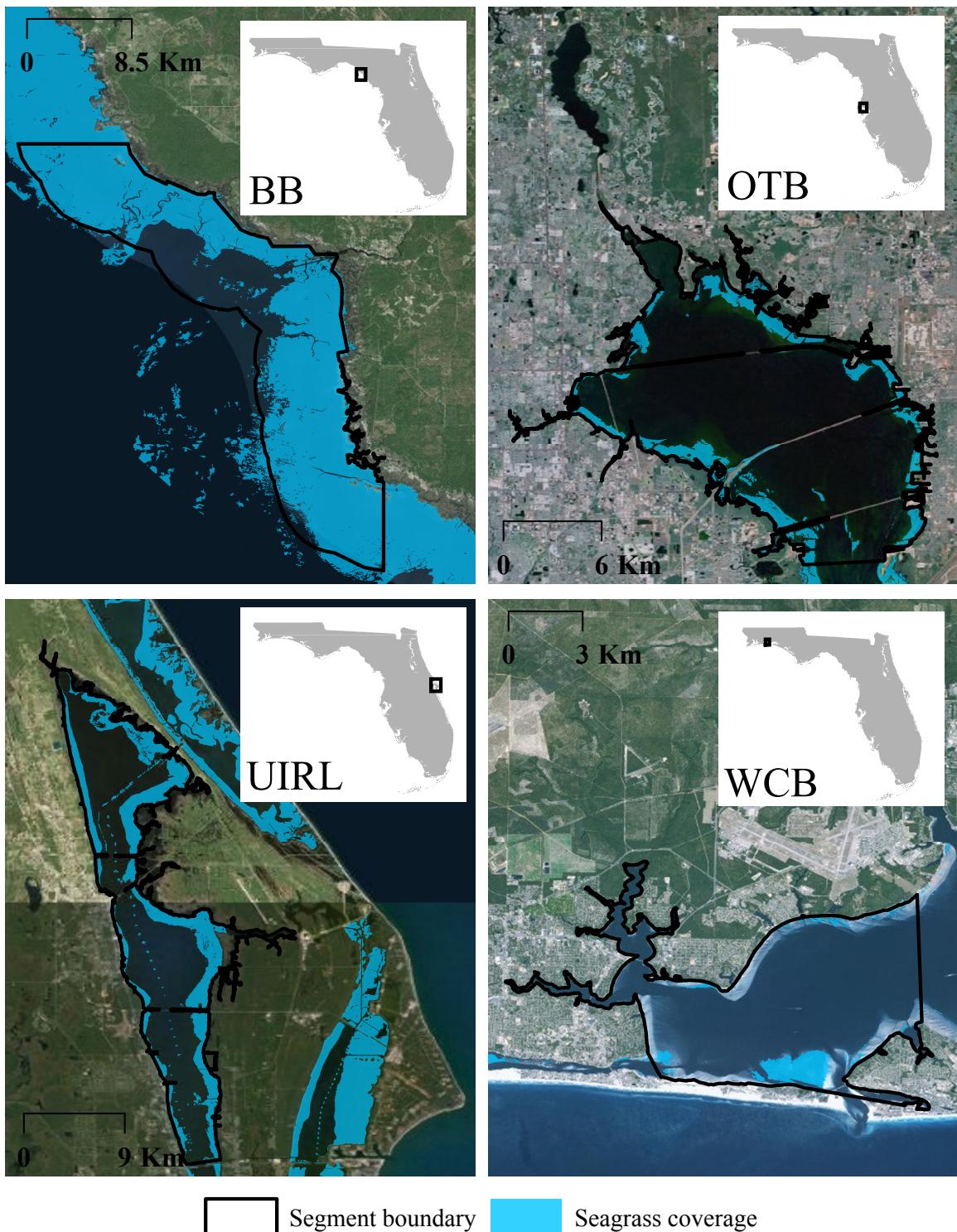
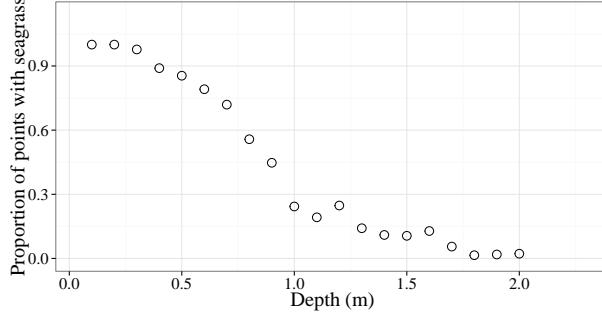
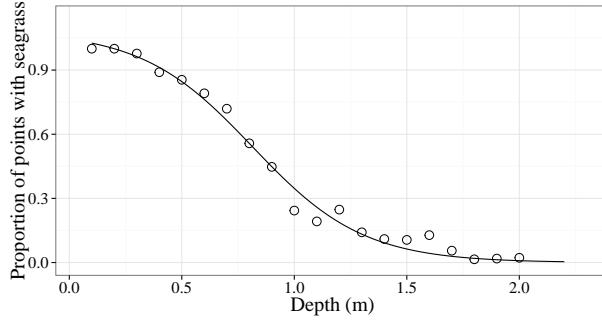


Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

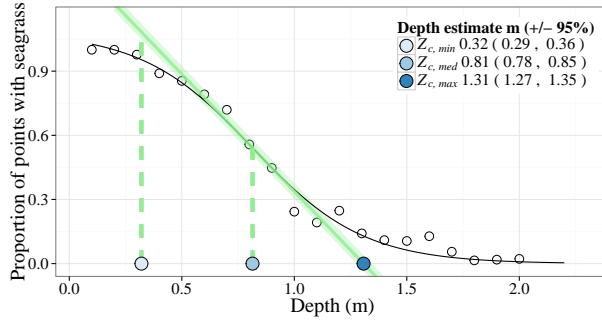


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test location in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit through the points. Fig. 3c shows three depth estimates based on a linear curve through the inflection point of logistic growth curve, including 95% confidence intervals based on the lighter green area around the linear curve.

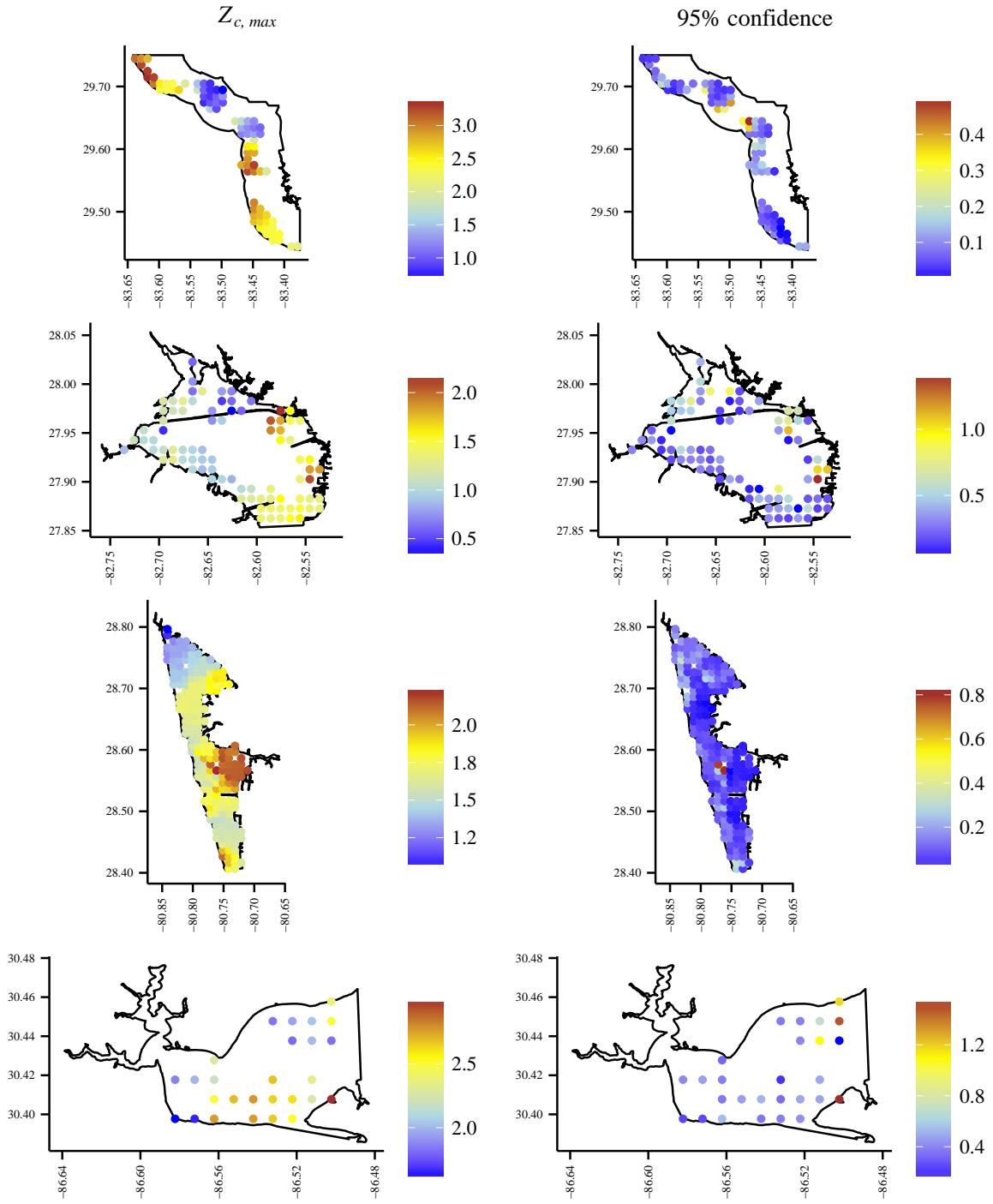


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ( $Z_{c, max}$ ) estimates are on the left and corresponding widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each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

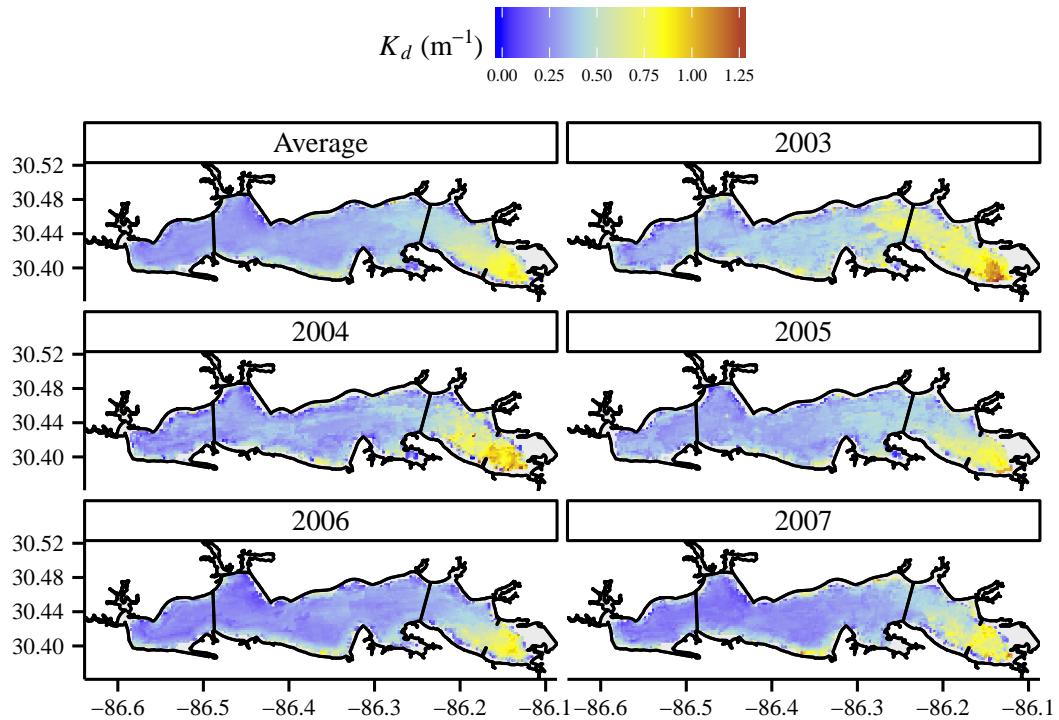


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment identification.

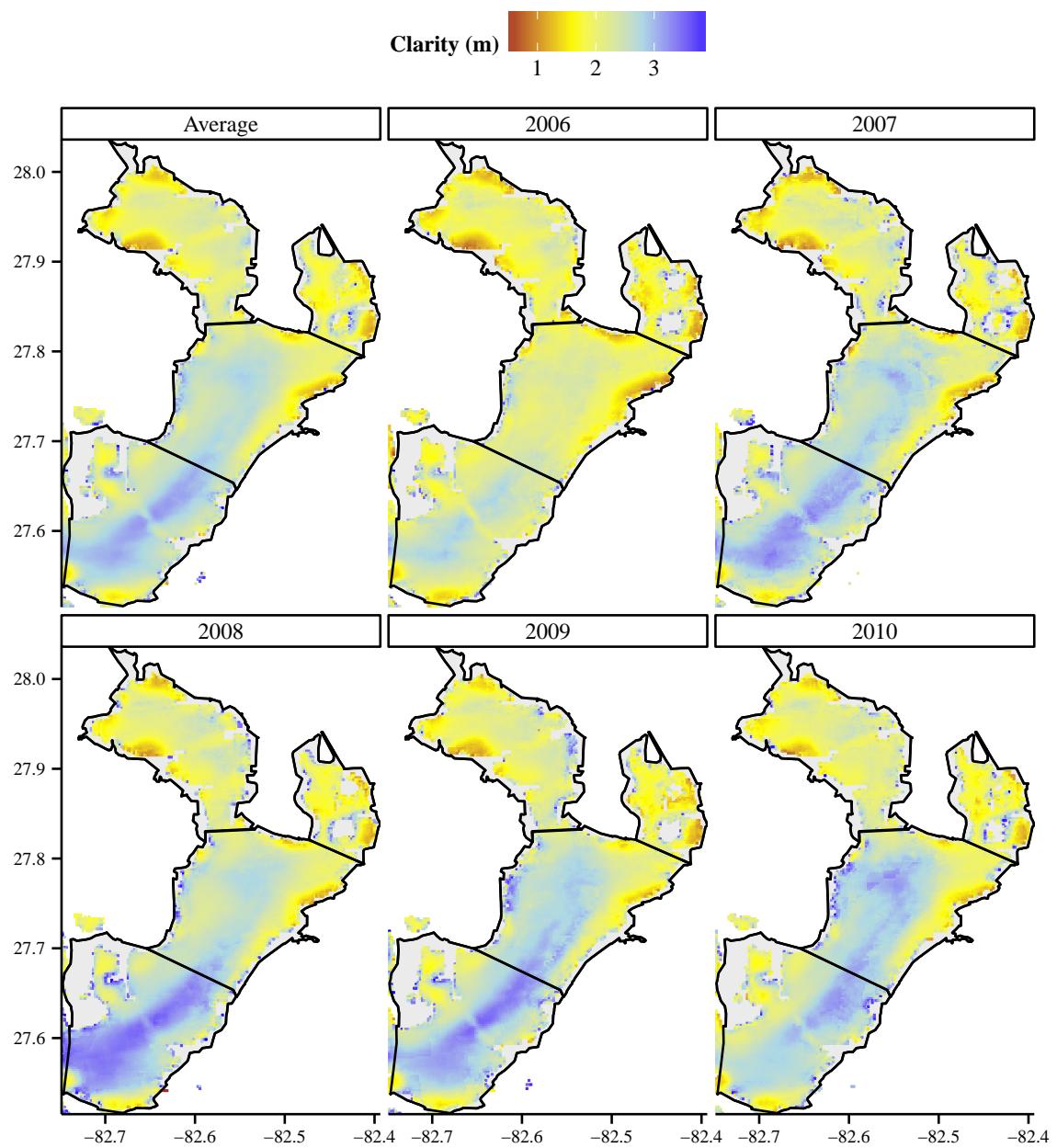


Fig. 6: Satellite estimated water clarity for Tampa Bay. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

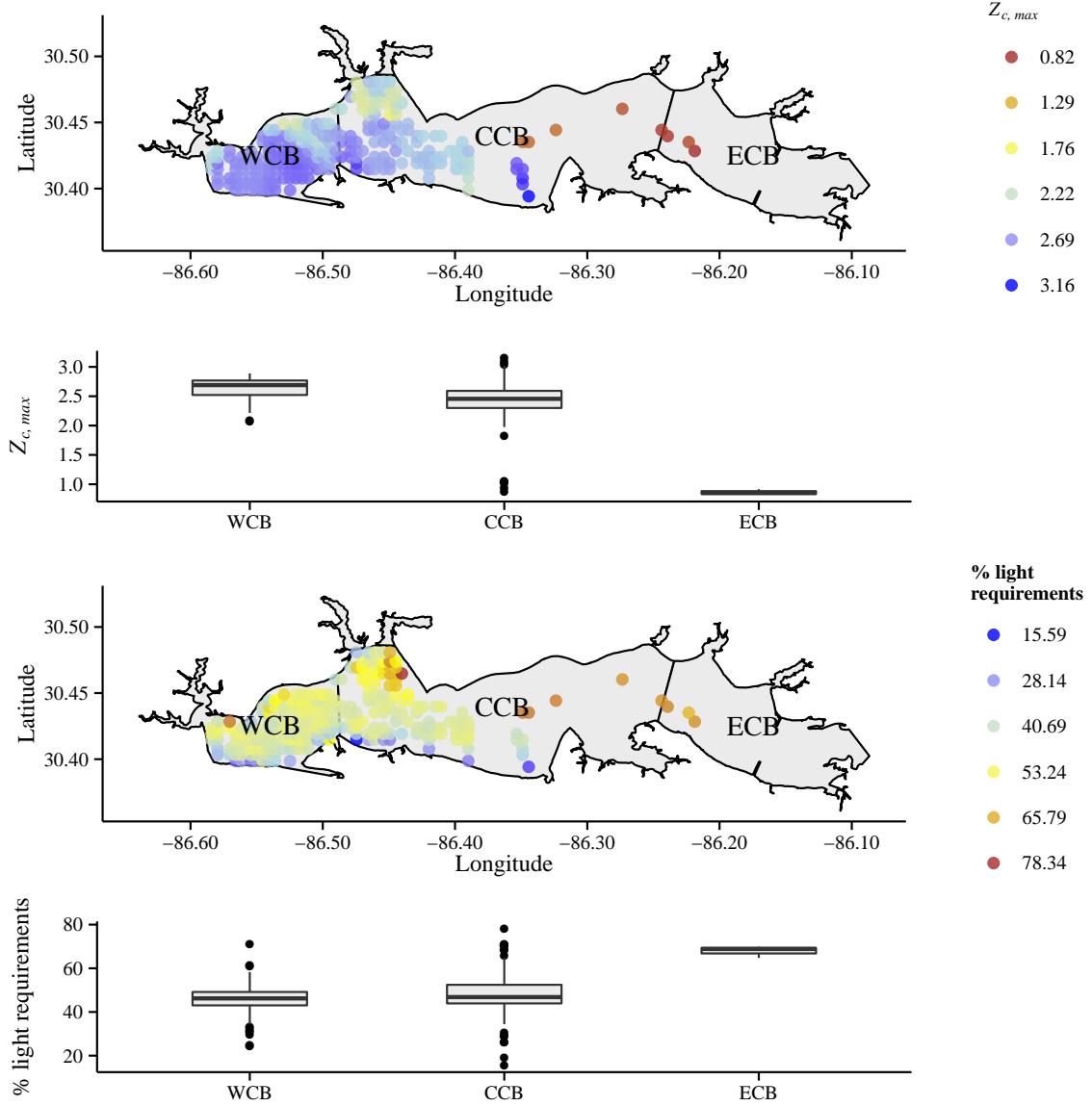


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.04 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.

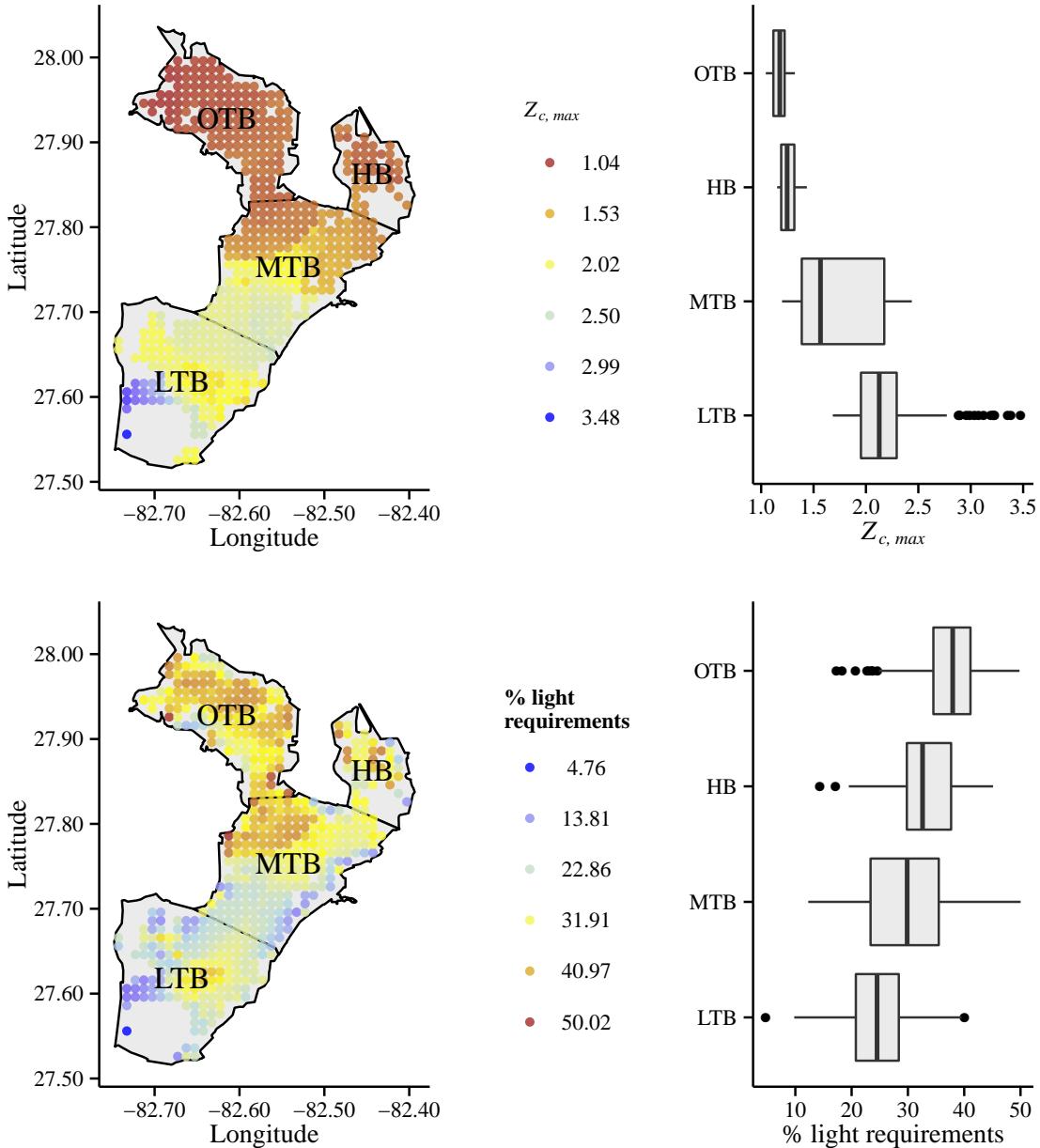


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots as in Fig. 7. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

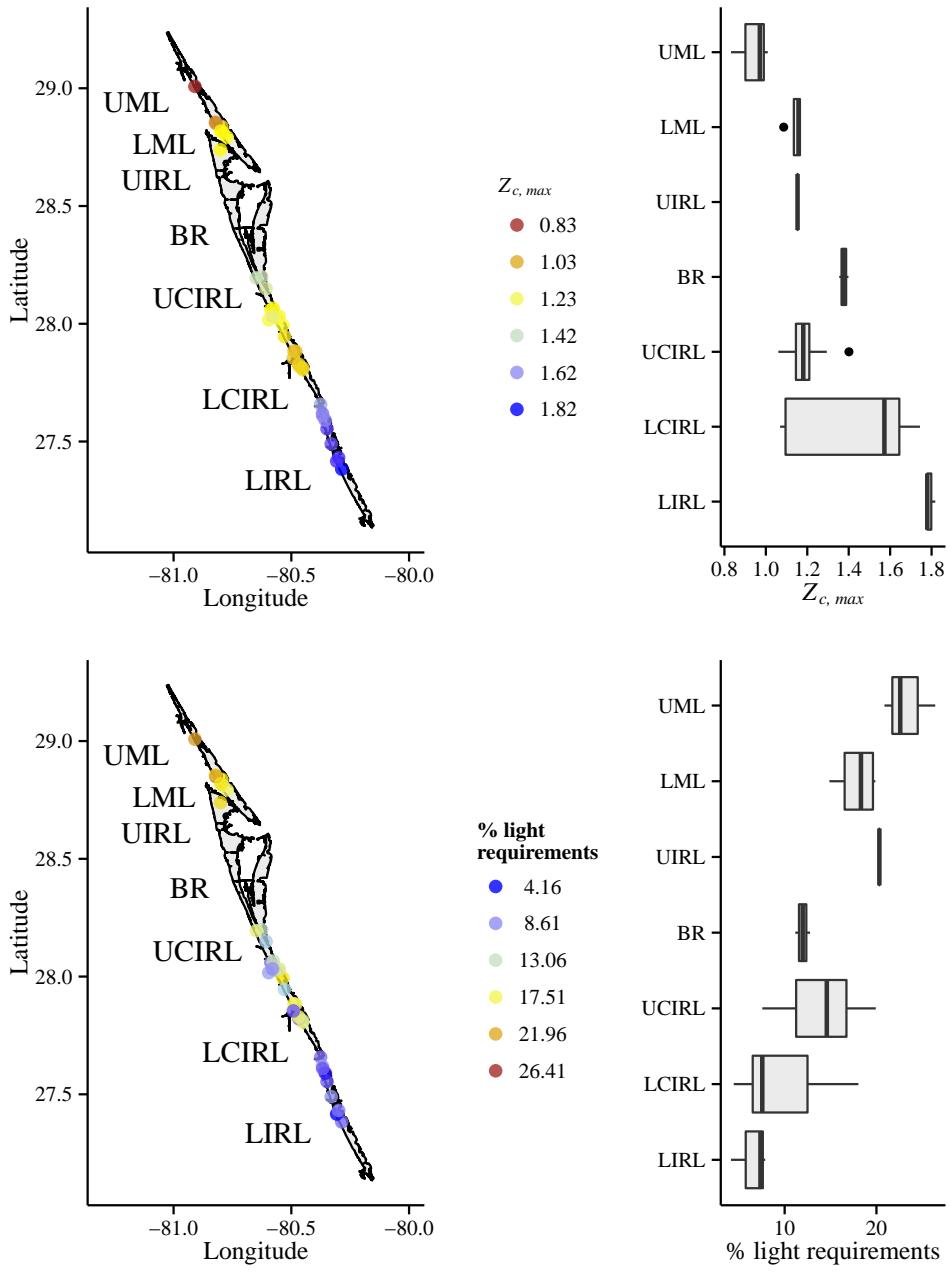


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment as boxplots as in Fig. 7. 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 0.15 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.