

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

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4 Abstract

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

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

32 ***I 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 through physiological linkages with light
39 availability. Seagrass communities in productive aquatic systems may be light-limited 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 taxa (e.g., phytoplankton). Quantifying the
49 relationship of seagrasses with water clarity is a useful approach to understanding ecological
50 characteristics of aquatic systems with potential insights into system response to disturbance
51 (Greve and Krause-Jensen 2005).

52 Many techniques have been developed for estimating seagrass depth limits to better
53 understand water quality dynamics. Such efforts have been useful for site-specific approaches
54 where the analysis needs are driven by a particular question (e.g., Iverson and Bittaker 1986, Hale
55 et al. 2004). However, lack of standardization among methods has prevented broad-scale
56 comparisons between regions and has even contributed to discrepancies between measures based
57 on the technique used to measure depth of colonization (Spears et al. 2009). The availability of
58 geospatial data that describe areal seagrass and bathymetric coverage suggests standardized
59 techniques can be developed that could be applied across broad areas. Conversely, site-specific
60 approaches with such datasets typically quantify habitat requirements within predefined

61 management units that may prevent generalizations outside of the study area. For example,
62 Steward et al. (2005) describe use of a segmentation scheme for the Indian River Lagoon to
63 estimate seagrass depth limits for 19 distinct geospatial units. Although useful for the specific
64 study goals, substantial variation in growth patterns and water quality characteristics at different
65 spatial scales may prevent more detailed analyses. Methods for estimating seagrass depth limits
66 should also be reproducible for broad-scale comparisons, while also maintaining flexibility based
67 on the objectives. Such techniques can facilitate comparisons between regions given the spatial
68 coverage and annual availability of many geospatial data sources.

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

83 Water clarity data from satellite remote sensing products could be combined with depth of
84 colonization estimates to develop a spatial description of seagrass light requirements. Although
85 algorithms have been developed for coastal waters to estimate surface reflectance from satellite
86 data (Woodruff et al. 1999, Chen et al. 2007), this information has rarely been used to describe
87 seagrass light requirements at a spatial resolution consistent with most remote sensing products.
88 Conversely, secchi observations can provide reliable measures of water clarity (USEPA 2006),
89 although data can be biased by location and time. Monitoring programs may have unbalanced
90 coverage of aquatic resources with greater perceived importance relative to those that may have

more ecological significance (Wagner et al. 2008, Lottig et al. 2014). Moreover, infrequent field measurements that are limited to discrete time periods are more descriptive of short-term variability rather than long-term trends in water clarity (Elsdon and Connell 2009). Seagrasses growth patterns are integrative of seasonal and inter-annual patterns in water clarity, such that estimates of light requirements may be limited if water clarity measurements inadequately describe temporal variation. Satellite remote sensing products can provide reliable estimates of water clarity and could be used to develop a more complete description of relevant ecosystem characteristics.

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

2 **Methods**

2.1 **Study sites and data sources**

Four coastal locations in Florida were used as study sites: the Big Bend region (northeast Gulf Coast), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf Coast), and Indian River

120 Lagoon (Atlantic coast) (Table 1 and Fig. 2). Sites were chosen to represent a regional
121 distribution of coastal habitat in Florida, in addition to having available data and observed
122 gradients in water quality.

123 Coastal regions and estuaries in Florida are partitioned using a predefined segmentation
124 scheme for developing numeric nutrient criteria. These management segments were used for
125 comparison to evaluate variation in growth patterns at different spatial scales. For example,
126 Fig. 1a shows variation in seagrass distribution for a management segment (thick polygon) in the
127 Big Bend region of Florida. The maximum depth colonization, as a red countour line, is based on
128 a segment-wide estimate of all seagrasses within the polygon. Although the estimate is not
129 inaccurate, substantial variation in seagrass growth patterns at smaller spatial scales is not
130 adequately described. depth of colonization (Z_c) is greatly over-estimated at the outflow of the
131 Steinhatchee River (northeast portion of the segment) where high concentrations of dissolved
132 organic matter reduce water clarity and naturally limit seagrass growth (personal communication,
133 Nijole Wellendorf, Florida Department of Environmental Protection). One segment within each
134 region and smaller spatial units defined by the algorithm were first evaluated to illustrate use of
135 the method. Segments chosen for each region are shown in Fig. 2. A second analysis focused on
136 quantifying seagrass depth limits for all of Choctawhatchee Bay, Tampa Bay, and the Indian River
137 Lagoon to describe the spatial pattern of light requirements.

138 Geospatial data describing seagrass areal coverage combined with co-located bathymetric
139 depth maps were used to estimate Z_c . These products are publically available in coastal regions of
140 Florida through the US Geological Survey, Florida Department of Environmental Protection,
141 Florida Fish and Wildlife Conservation Commission, and many watershed management districts.
142 Seagrass coverage maps were obtained for one chosen year in each of the study sites (Table 1).
143 The original coverage maps were produced using photo-interpretations of aerial images to
144 categorize seagrass as absent, discontinuous (patchy), or continuous. We considered only present
145 (continuous and patchy) and absent categories since differences between continuous and patchy
146 coverage were often inconsistent between data sources.

147 Bathymetric depth maps were obtained from the National Oceanic and Atmospheric
148 Administration's (NOAA) National Geophysical Data Center (<http://www.ngdc.noaa.gov/>) as
149 either Digital Elevation Models (DEMs) or raw sounding data from hydroacoustic surveys. Tampa

150 Bay data provided by the Tampa Bay National Estuary Program are described in Tyler et al.
151 (2007). Bathymetric data for the Indian River Lagoon were obtained from the St. John's Water
152 Management District (Coastal Planning and Engineering 1997). The vertical datums varied such
153 that NOAA products were referenced to mean lower low water, Tampa Bay data were referenced
154 to the North American Vertical Datum of 1988 (NAVD88), and the Indian River Lagoon data
155 were referenced to mean sea level. Prior to analysis, all bathymetric data were vertically adjusted
156 to local mean sea level (MSL) using the NOAA VDatum tool (<http://vdatum.noaa.gov/>) for
157 comparability between data sources. Adjusted data were combined with seagrass coverage layers
158 using standard union techniques for raster and vector layers in ArcMap 10.1 (Environmental
159 Systems Research Institute 2012). To reduce computation time, depth layers were first masked
160 using a 1 km buffer of the seagrass coverage layer. Raster bathymetric layers were converted to
161 vector point layers to combine with seagrass coverage maps, described below.

162 **2.2 Quantifying water clarity**

163 Spatial variation in light requirements were explored using Z_c and water clarity estimates
164 for the entire areas of Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon. Limited
165 clarity data in the Big Bend region prohibited analysis in this location. Satellite images were used
166 to create a gridded 1 km² map as estimated water clarity (m, Tampa Bay) or light extinction (K_d ,
167 m⁻¹, Choctawhatchee Bay). Secchi data were used directly to evaluate light requirements for the
168 Indian River Lagoon because satellite data were inestimable.

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

180 between the cumulative distribution of the in situ K_d estimates and the satellite estimated K_d at
181 the same locations. The 2010 correction was applied to all five years of annual mean satellite data
182 prior to averaging to create a single layer for further analysis.

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

192 **2.3 Estimating seagrass depth of colonization**

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

204 The spatially-resolved approach for estimating Z_c begins by choosing an explicit location
205 in cartesian coordinates within the general boundaries of the available data. Seagrass depth data
206 (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the
207 chosen location are selected for estimating seagrass Z_c values (sample areas in Fig. 1). The
208 estimate for each location is quantified from the proportion of sampled points that contain
209 seagrass at decreasing 0.1 meter depth bins from the surface to the maximum depth in the sample

(Fig. 3a). Although the chosen radius for selecting data is problem-specific, the minimum radius should be large enough to sample a sufficient number of points for estimating Z_c . In general, a sufficient radius will produce a plot that indicates a decrease in the proportion of points that are occupied by seagrass with increasing depth. Plots with insufficient data may indicate a reduction of seagrass with depth has not occurred (e.g., nearshore areas) or seagrasses simply are not present. If more than one location is used to estimate Z_c (as in Fig. 1), radii for each point should be chosen to reduce overlap with the seagrass depth data sampled by neighboring points.

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

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

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

Estimates for each of the three Z_c measures were obtained only if specific criteria were

met. These criteria were implemented as a safety measure that ensures a sufficient amount and appropriate quality of data were sampled within the chosen radius. First, estimates were provided only if a sufficient number of seagrass depth points were present in the sampled data to estimate a logistic growth curve. This criteria applies to the sample size as well as the number of points with seagrass in the sample. Second, estimates were provided only if an inflection point was present on the logistic curve within the range of the sampled depth data. This criteria applied under two scenarios where the curve was estimated but a trend was not adequately described by the sampled data. That is, estimates were unavailable if the logistic curve described only the initial decrease in points occupied as a function of depth. The opposite scenario occurred when a curve was estimated but only the deeper locations beyond the inflection point were present in the sample. Third, the estimate for $Z_{c,min}$ was set to zero depth if the linear curve through the inflection point intercepted the upper asymptote of the logistic curve at x-axis values less than zero. The estimate for $Z_{c,med}$ was also shifted to the depth value halfway between $Z_{c,min}$ and $Z_{c,max}$ if $Z_{c,min}$ was fixed at zero. Finally, estimates were considered invalid if the 95% confidence interval for $Z_{c,max}$ included zero. In such cases, the three measures are not statistically distinguishable, although a useful estimate for $Z_{c,max}$ is provided. Methods to determine confidence bounds are described below.

2.4 Estimating uncertainty

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

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

where x is a predictor variable used in eq. (1) (depth) that follows a multivariate normal distribution with mean μ , and variance-covariance matrix Σ . The mean values are set at the depth value corresponding to the inflection point on the logistic curve from the observed model, whereas Σ is the variance-covariance matrix of the model parameters (α, β, γ). A large number of samples ($n = 10000$) were drawn from the distribution to characterize the uncertainty of the depth value of

265 the inflection point. The 2.5th and 97.5th percentiles of the sample were considered bounds on the
266 95% confidence interval. This approach was used because uncertainty from the logistic curve is
267 directly related to uncertainty in each of the Z_c estimates that are based on the linear curve
268 through the inflection point. Upper and lower limits for each Z_c estimate were obtained by fitting
269 new linear curves through the upper and lower limits of the initial depth value. (i.e., Fig. 3c).

270 Nonlinear least squares models were based on the `nls` and `SSlogis` functions that used
271 a self-starting logistic growth model (Bates and Chambers 1992, R Development Core Team
272 2014). Multivariate normal distributions were simulated using functions in the MASS package
273 (Venables and Ripley 2002). Geospatial data were imported and processed using functions in the
274 rgeos and sp packages (Bivand et al. 2008, Bivand and Rundel 2014).

275 **2.5 Evaluation of spatial heterogeneity of seagrass depth limits**

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

285 **2.6 Relating depth of colonization and water clarity**

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

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

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

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

where the percent light requirements are a function of the estimated $Z_{c, max}$ and light extinction. If K_d estimates are unavailable, a conversion factor can be 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):

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

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

317 degrees for Tampa Bay, and 0.15 decimal degrees for Indian River Lagoon.

318 **3 Results**

319 **3.1 Segment characteristics and seagrass depth estimates**

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

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

estimates for $Z_{c,max}$ in the Big Bend region indicated seagrasses grew to approximately 2.1 m, which was 1.6 m less than the whole segment estimate. Although reductions were not as severe for the average grid estimates for the remaining segments, considerable within-segment variation was observed depending on grid location. For example, the deepest estimate for $Z_{c,min}$ (2 m) in the Upper Indian River Lagoon exceeded the average of all grid locations for $Z_{c,max}$ (1.7 m). $Z_{c,min}$ also had minimum values of zero meters for the Big Bend and Old Tampa Bay segments, suggesting that seagrasses declined continuously from the surface for several locations.

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

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

376 Choctawhatchee Bay (mean width was 0.5 m) and Old Tampa Bay (0.4 m), compared to the Big
377 Bend (0.1 m) and Upper Indian River Lagoon (0.1 m) segments. The largest confidence interval
378 for each segment was 1.4 m for Old Tampa Bay, 1.6 m for Western Choctawhatchee Bay, 0.5 m
379 for the Big Bend, and 0.8 m for the Upper Indian River Lagoon segments. Most confidence
380 intervals for the remaining grid locations were much smaller than the maximum in each segment
381 (e.g., an extreme central location of the Upper Indian River Lagoon, Fig. 4). A comparison of
382 overlapping confidence intervals for $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$ at each grid location indicated
383 that not every measure was unique. Specifically, only 11.1% of grid points in Choctawhatchee
384 Bay and 28.2% in Old Tampa Bay had significantly different estimates, whereas 82.4% of grid
385 points in the Indian River Lagoon and 96.2% of grid points in the Big Bend segments had
386 estimates that were significantly different. By contrast, all grid estimates in Choctawhatchee Bay
387 and Indian River Lagoon had $Z_{c,max}$ estimates that were significantly greater than zero, whereas
388 all but 12.4% of grid points in Old Tampa Bay and 8% of grid points in the Big Bend segment had
389 $Z_{c,max}$ estimates significantly greater than zero.

390 3.2 Evaluation of seagrass light requirements

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

405 Seagrass Z_c estimates were obtained for 259 locations in Choctawhatchee Bay, 566

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

4 Discussion

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

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

447 **4.1 Evaluation of the algorithm**

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

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

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

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

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

4.2 Heterogeneity in growth patterns and light requirements

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

The use of light attenuation data, either as satellite-derived estimates or in situ secchi

525 observations, combined with Z_c estimates provided detailed and previously unavailable
526 characterizations of light requirements within the three estuaries. Requirements were lowest for
527 the Indian River Lagoon, whereas estimates were higher for Tampa Bay and highest for
528 Choctawhatchee Bay. Requirements for the Indian River Lagoon were generally in agreement
529 with other Atlantic coastal systems (Dennison et al. 1993, Kemp et al. 2004), such that
530 requirements typically did not exceed 25% with mean requirements for whole bay estimated at
531 13.4%. However, light requirements for Indian River Lagoon were based on secchi observations
532 with uneven spatial and temporal coverage, which potentially led to an incomplete description of
533 true variation in light attenuation. Alternative measures to estimate K_d (e.g., vertically-distributed
534 PAR sensors) are required when bottom depth is shallower than maximum water clarity, although
535 scalability remains an issue. Conversely, satellite-derived estimates were possible for Tampa and
536 Choctawhatchee Bays where water column depth was sufficient and were preferred over in situ
537 data given more complete spatial coverage. Mean light requirements for Tampa Bay were 30.4%
538 of surface irradiance, which was in agreement with previously reported values, particularly for
539 Lower Tampa Bay (Dixon and Leverone 1995). Estimates for Choctawhatchee Bay were
540 substantially higher with a bay-wide average of 47.1%. The relatively higher light requirements
541 for Gulf Coast esuaries, particularly Choctawhatchee Bay, may reflect the need for additional
542 validation data for the conversion of satellite reflectance values to light attenuation. However,
543 estuaries in the northern Gulf of Mexico are typically shallow and highly productive (Caffrey
544 et al. 2014), such that high light requirements may in fact be related to the effects of high nutrient
545 loads on water clarity. Further evaluation of seagrass light requirements in the northern Gulf of
546 Mexico could clarify the extent to which our results reflect true differences relative to other
547 coastal regions.

548 As previously noted, variation in seagrass light requirements can be attributed to
549 differences in physiological requirements between species or regional effects of different light
550 regimes (Choice et al. 2014). For example, *Halodule wrightii* is the most abundant seagrass in
551 Choctawhatchee Bay and occurs in the western polyhaline portion near the outflow with the Gulf
552 of Mexico. Isolated patches of *Ruppia maritima* are also observed in the oligohaline eastern
553 regions of the bay. Although $Z_{c,max}$ was only estimable for a few points in eastern
554 Choctawhatchee Bay, differences in species assemblages along a salinity gradient likely explain

555 the differences in light requirements. The decline of *R. maritima* in eastern Choctawhatchee Bay
556 has been attributed to species sensitivity to turbidity from high rainfall events, whereas losses of
557 *H. wrightii* have primarily been attributed to physical stress during storm overwash and high wave
558 energy (FLDEP 2012). The relatively high light requirements of eastern Choctawhatchee Bay
559 likely reflect differing species sensitivity to turbidity, either through sediment resuspension from
560 rainfall events or light attenuation from nutrient-induced phytoplankton production. Similarly,
561 high light requirements may be related to epiphyte production at the leaf surface (Kemp et al.
562 2004). Estimated light requirements based solely on water column light attenuation, as for secchi
563 or satellite-derived values, may indicate unusually large light requirements if seagrasses are
564 further limited by epiphytic growth at the leaf surface. Epiphyte limitation may be common for
565 upper bay segments where nutrient inputs from freshwater inflows enhance algal production
566 (Kemp et al. 2004). Additionally, lower light requirements for Hillsborough Bay relative to Old
567 Tampa Bay may reflect a reduction in epiphyte load from long-term decreases in nitrogen inputs
568 to northeast Tampa Bay (Dawes and Avery 2010).

569 4.3 Conclusions

570 Spatially-resolved estimates of Z_c combined with high-resolution measures of light
571 attenuation provided an effective approach for evaluating light requirements. However, light
572 requirements, although important, may only partially describe ecosystem characteristics that
573 influence growth patterns. Seagrasses may be limited by additional physical, geological, or
574 geochemical factors, including effects of current velocity, wave action, sediment grain size
575 distribution, and sediment organic content (Koch 2001). Accordingly, spatially-resolved estimates
576 of Z_c and associated light requirements must be evaluated in the context of multiple factors that
577 may act individually or interactively with light attenuation. Extreme estimates of light
578 requirements may suggest light attenuation is not the only determining factor for seagrass growth.
579 An additional constraint is the quality of data that describe water clarity to estimate light
580 requirements. Although the analysis used satellite-derived clarity to create a more complete
581 description relative to in situ data, the conversion of reflectance data from remote sensing
582 products to attenuation estimates is not trivial. Further evaluation of satellite-derived data is
583 needed to create a broader characterization of light requirements. However, the algorithm was
584 primarily developed to describe maximum depth of colonization and the estimation of light

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

593 **References**

- 594 Barko JW, Hardin DG, Matthews MS. 1982. Growth and morphology of submersed freshwater
595 macrophytes in relation to light and temperature. Canadian Journal of Botany, 60(6):877–887.
- 596 Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors,
597 Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.
- 598 Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R
599 package version 0.3-8.
- 600 Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer,
601 New York, New York.
- 602 Caffrey JM, Murrell MC, Amacker KS, Harper J, Phipps S, Woodrey M. 2014. Seasonal and
603 inter-annual patterns in primary production, respiration and net ecosystem metabolism in 3
604 estuaries in the northeast Gulf of Mexico. Estuaries and Coasts, 37(1):222–241.
- 605 Chen Z, Muller-Karger FE, Hu C. 2007. Remote sensing of water clarity in Tampa Bay. Remote
606 Sensing of Environment, 109(2):249–259.
- 607 Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from
608 historical records of light attenuation along the Gulf coast of peninsular Florida. Marine
609 Pollution Bulletin, 81(1):94–102.
- 610 Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report
611 to St. John's River Water Management District. Technical Report Contract 95W142, Coastal
612 Planning and Engineering, Palatka, Florida.
- 613 Dawes C, Avery W. 2010. Epiphytes of the seagrass *halodule wrightii* in Hillsborough Bay,
614 Florida, a 14 year study in an estuary recovering from eutrophication. Florida Scientist,
615 73(3-4):185–195.
- 616 Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA.
617 1993. Assessing water quality with submersed aquatic vegetation. BioScience, 43(2):86–94.
- 618 Dixon LK, Leverone JR. 1995. Light requirements of *Thalassia testudinum* in Tampa Bay,
619 Florida. Technical report, Number 425, Mote Marine Lab, Sarasota, Florida.
- 620 Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.
- 621 Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes.
622 Ophelia, 41:87–112.
- 623 Elsdon TS, Connell SD. 2009. Spatial and temporal monitoring of coastal water quality: refeining
624 the way we consider, gather, and interpret patterns. Aquatic Biology, 5(2):157–166.
- 625 Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.

- 626 Florida Department of Environmental Protection (FLDEP). 2012. Site-specific information in
627 support of establishing numeric nutrient criteria for Choctawhatchee Bay. Technical report,
628 Florida Department of Environmental Protection, Tallahassee, Florida.
- 629 Greve T, Krause-Jensen D. 2005. Stability of eelgrass (*Zostera marina L.*) depth limits:
630 influence of habitat type. *Marine Biology*, 147(3):803–812.
- 631 Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.
- 632 Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species
633 along Florida's central gulf coast: Iverson and Bittaker revisited. *Estuaries*, 27(1):36–43.
- 634 Hall MO, Durako MJ, Fourqurean JW, Zieman JC. 1990. Decadal changes in seagrass
635 distribution and abundance in Florida Bay. *Estuaries*, 22(2B):445–459.
- 636 Hilborn R, Mangel M. 1997. *The Ecological Detective: Confronting Models with Data*.
637 Princeton University Press, Princeton, New Jersey.
- 638 Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern:
639 declining seagrasses and threatened dependent species. *Frontiers in Ecology and the
640 Environment*, 7(5):242–246.
- 641 Idso SB, Gilbert RG. 1974. On the universality of the Poole and Atkins secchi disk-light
642 extinction equation. *Journal of Applied Ecology*, 11(1):399–401.
- 643 Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico
644 coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5):577–602.
- 645 Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary:
646 An empirically based approach to setting management targets. Technical Report 06-96, Tampa
647 Bay National Estuary Program, St. Petersburg, Florida.
- 648 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *OIKOS*,
649 69(3):373–386.
- 650 Kemp WC, Batiuk R, Bartleson R, Bergstrom P, Carter V, Gallegos CL, Hunley W, Karrh L, Koch
651 EW, Landwehr JM, Moore KA, Murray L, Naylor M, Rybicki NB, Stevenson JC, Wilcox DJ.
652 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water
653 quality, light regime, and physical-chemical factors. *Estuaries*, 27(3):363–377.
- 654 Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and
655 *Syringodium filiforme* derived from the relationship between diffuse light attenuation and
656 maximum depth distribution. *Estuaries*, 19(3):740–750.
- 657 Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible
658 submersed aquatic vegetation habitat requirements. *Estuaries*, 24(1):1–17.
- 659 Lee ZP, Du KP, Arnone R. 2005. A model for the diffuse attenuation of downwelling irradiance.
660 *Journal of Geophysical Research*, 110(C2):10.

- 661 Lottig NR, Wagner T, Henry EN, Cheruvil KS, Webster KE, Downing JA, Stow CA. 2014.
662 Long-term citizen-collected data reveal geographical patterns and temporal trends in water
663 clarity. PLoS ONE, 9(4):e95769.
- 664 Poole HH, Atkins WRG. 1929. Photo-electric measurements of submarine illumination
665 throughout the year. Journal of the Marine Biological Association of the United Kingdom,
666 16:297–324.
- 667 R Development Core Team. 2014. R: A language and environment for statistical computing,
668 v3.1.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- 669 Spears BM, Gunn IDM, Carvalho L, Winfield IJ, Dudley B, Murphy K, May L. 2009. An
670 evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven,
671 Scotland. Aquatic Botany, 91(2):75–81.
- 672 Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light
673 targets for the Indian River Lagoon system, Florida. Estuaries, 28(6):923–935.
- 674 Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007.
675 Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051
676 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.
- 677 USEPA (US Environmental Protection Agency). 2006. Volunteer estuary monitoring: A methods
678 manual, second edition. Technical Report EPA-842-B-06-003, Washington, DC.
- 679 Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Springer, New York, New
680 York, fourth edition.
- 681 Wagner T, Soranno PA, Cheruvil KS, Renwick WH, Webster KE, Vaux P, Abbott RJ. 2008.
682 Quantifying sample biases of inland lake sampling programs in relation to lake surface area and
683 land use/cover. Environmental Monitoring and Assessment, 141(1-3):131–147.
- 684 Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay
685 ME, editors, Marine Community Ecology. Sinauer Associates, Sunderland, Massachusetts.
- 686 Woodruff DL, Stumpf RP, Scope JA, Paerl HW. 1999. Remote estimation of water clarity in
687 optically complex estuarine waters. Remote Sensing of Environment, 68(1):41–52.

Table 1: Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates (see Fig. 2 for spatial distribution). Year is the date of the seagrass coverage and bathymetric data. Latitude and longitude are the geographic centers of each segment. Area and depth values are meters and square kilometers, respectively. Secchi measurements (m) were obtained from the Florida Department of Environmental Protection’s Impaired Waters Rule (IWR) database, update number 40. Secchi mean and standard errors are based on all observations within the ten years preceding each seagrass survey.

	BB ^a	OTB	UIRL	WCB
Year ^b	2006	2010	2009	2007
Latitude	29.61	27.94	28.61	30.43
Longitude	-83.48	-82.62	-80.77	-86.54
Surface area	271.37	205.50	228.52	59.41
Seagrass area	203.02	24.48	74.89	3.51
Depth (mean)	1.41	2.56	1.40	5.31
Depth (max)	3.60	10.40	3.70	11.90
Secchi (mean)	1.34	1.41	1.30	2.14
Secchi (se)	0.19	0.02	0.02	0.08

^a BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon, WCB: Western Choctawhatchee Bay

^b Seagrass coverage data sources, see section 2.1 for bathymetry data sources:

BB: 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

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

WCB 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.

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

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

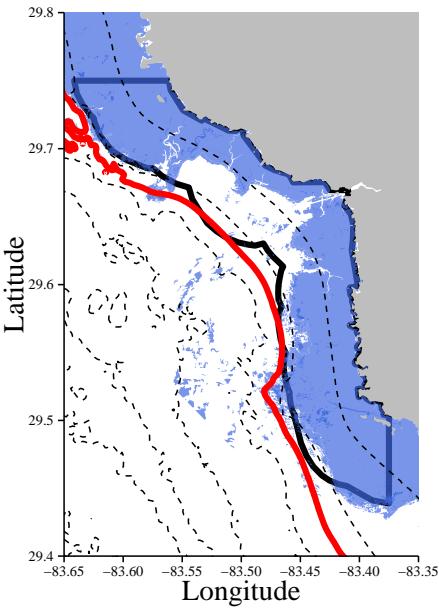
^aBB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Choctawhatchee Bay.

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

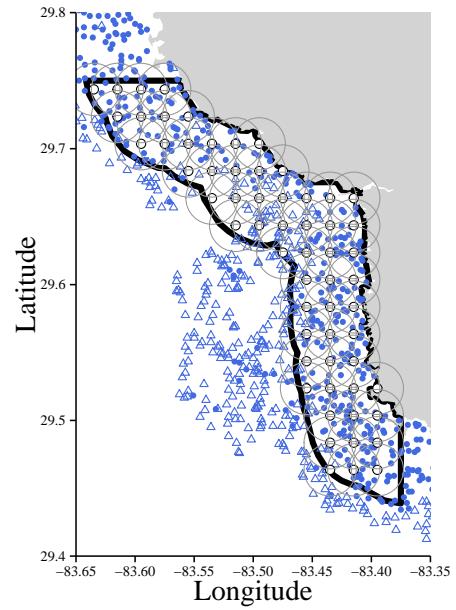
Segment ^a	n	$Z_{c,max}$				% light			
		Mean	St. Dev.	Min	Max	Mean	St. Dev.	Min	Max
Choctawhatchee Bay									
CCB	121	2.4	0.4	0.9	3.2	48.2	10.2	15.6	78.3
ECB	3	0.9	0.0	0.8	0.9	67.8	2.7	64.8	69.9
WCB	135	2.6	0.2	2.1	2.9	45.6	6.6	24.2	70.9
Indian River Lagoon									
BR	2	1.4	0.0	1.4	1.4	12.0	1.1	11.2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

^aCCB: 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.

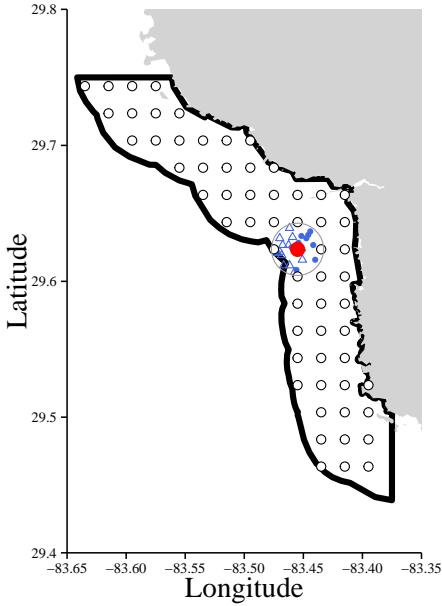
(a) Seagrass coverage and bathymetry for the segment



(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.

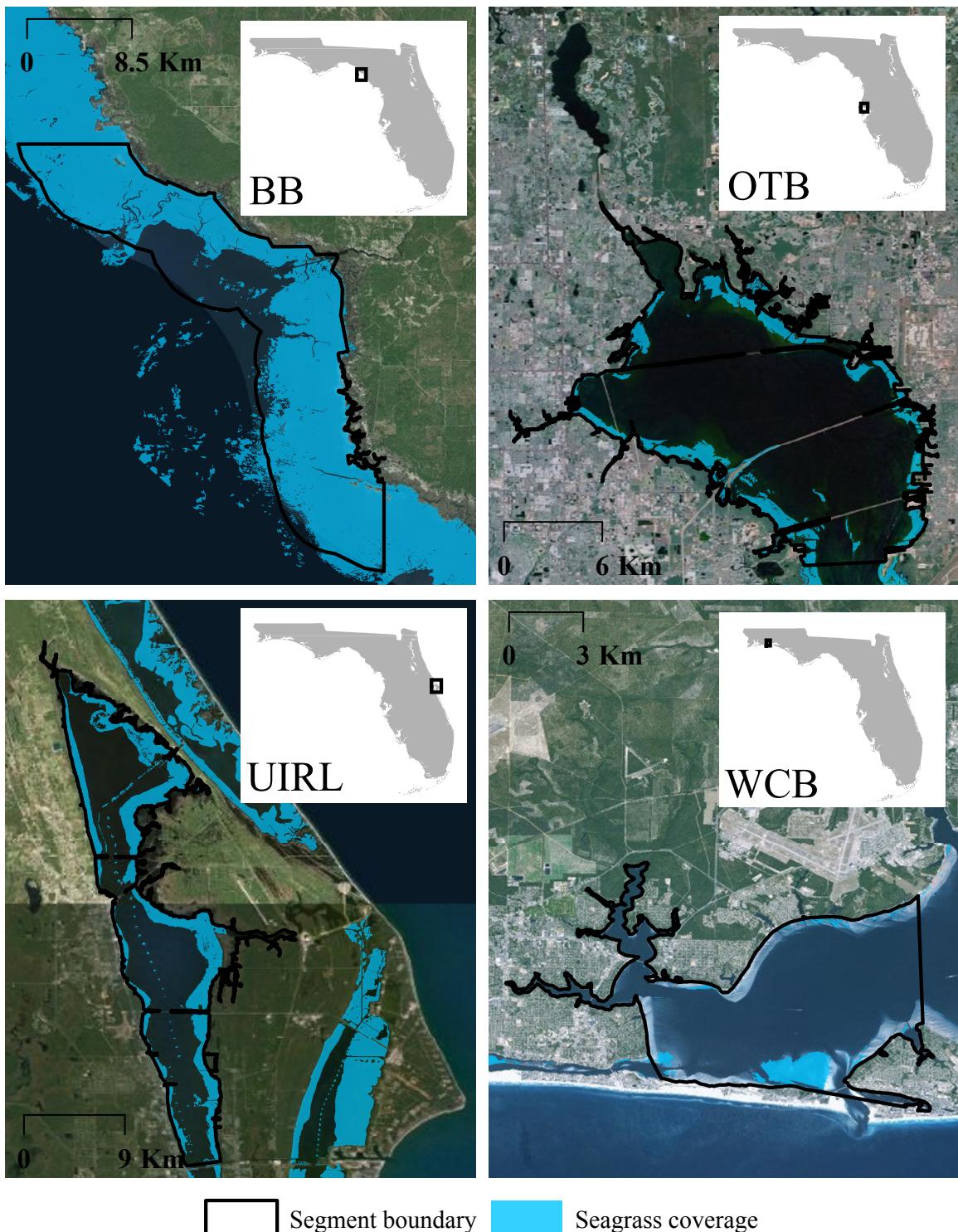
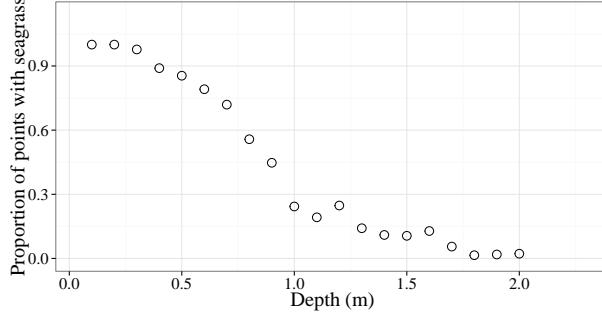
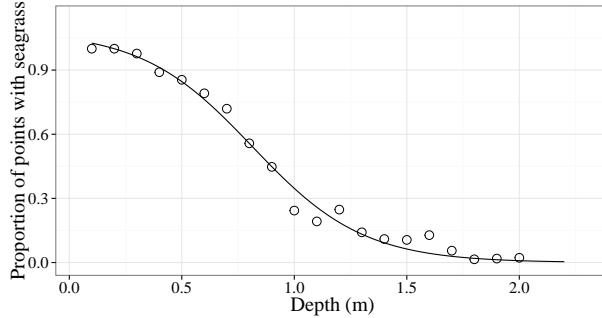


Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

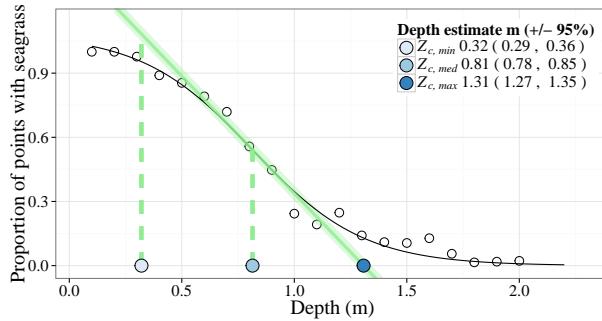


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test location in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit 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.

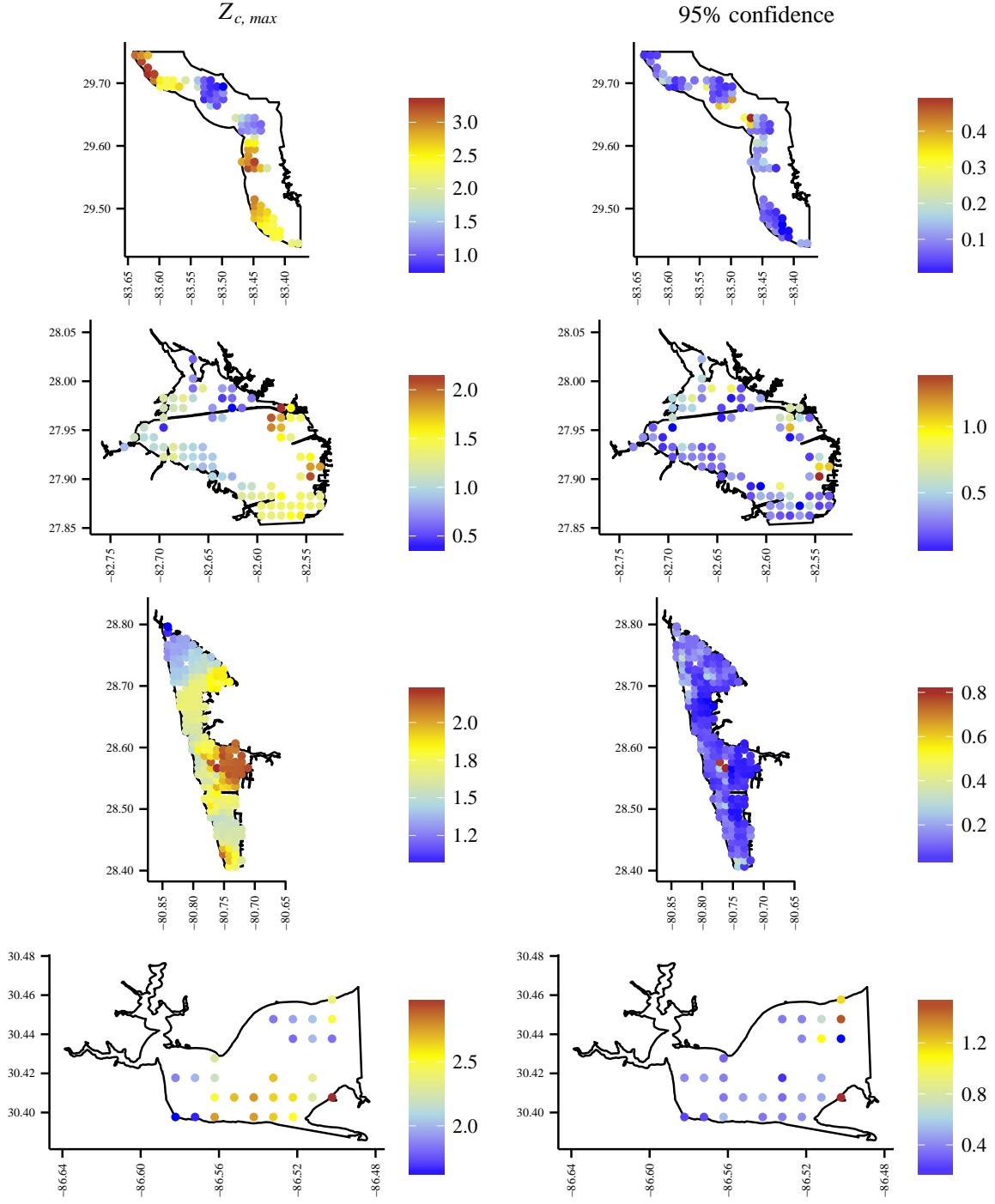


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ($Z_{c, max}$) estimates are on the left and correspondings widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each segment, where grid spacing was fixed at 0.02 decimal degrees. Radii for sampling seagrass bathymetric data around each grid location were fixed at 0.06 decimal degrees. From top to bottom: Big Bend, Old Tampa Bay, Upper Indian R. Lagoon, Western Choctawhatchee Bay.

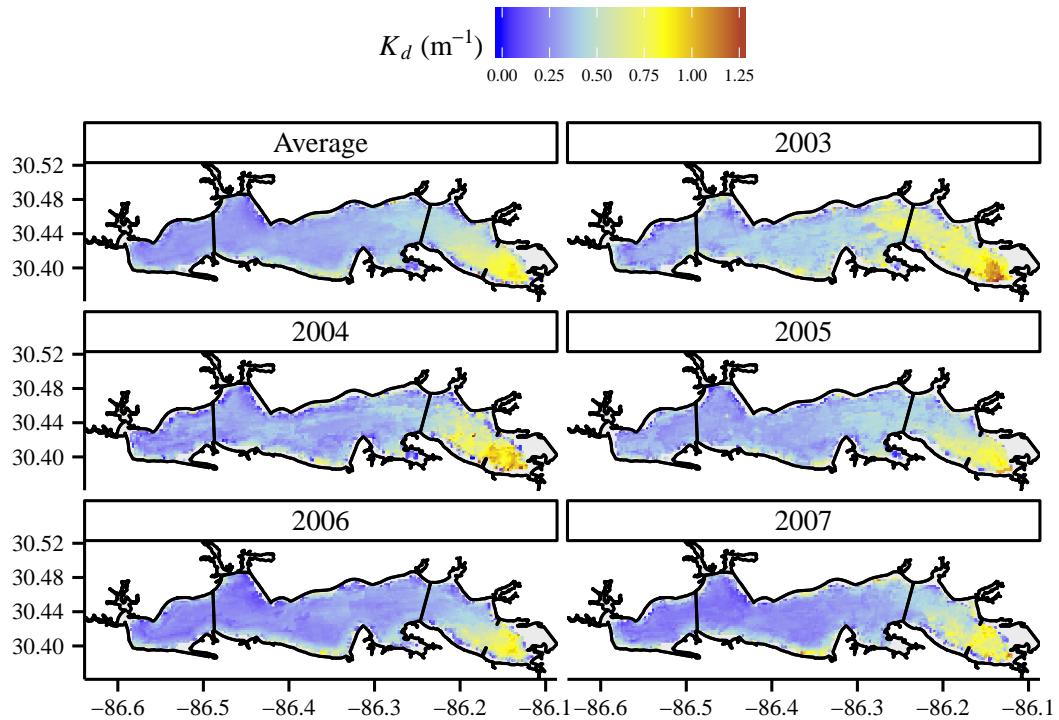


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment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

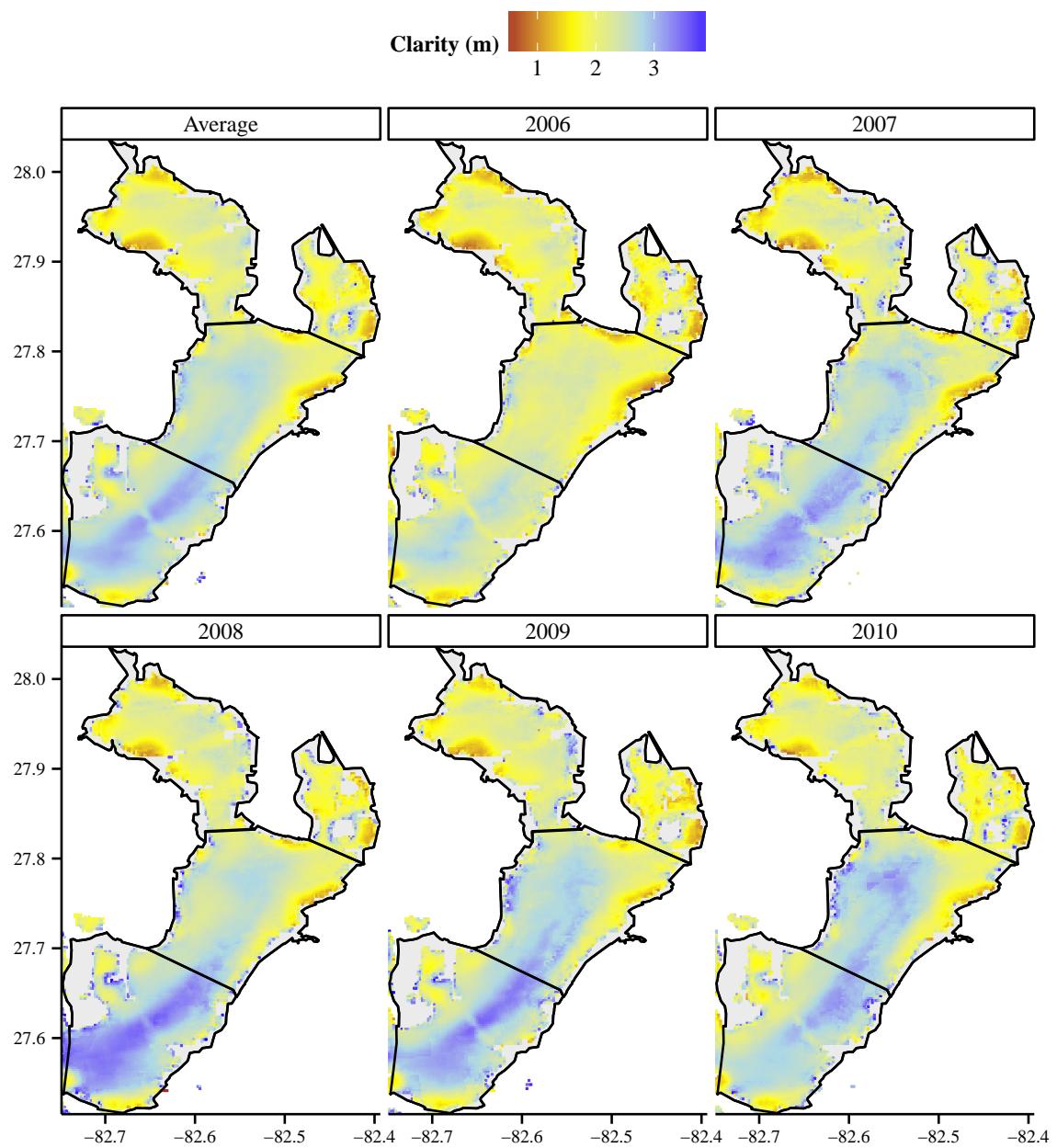


Fig. 6: Satellite estimated water clarity for Tampa Bay. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

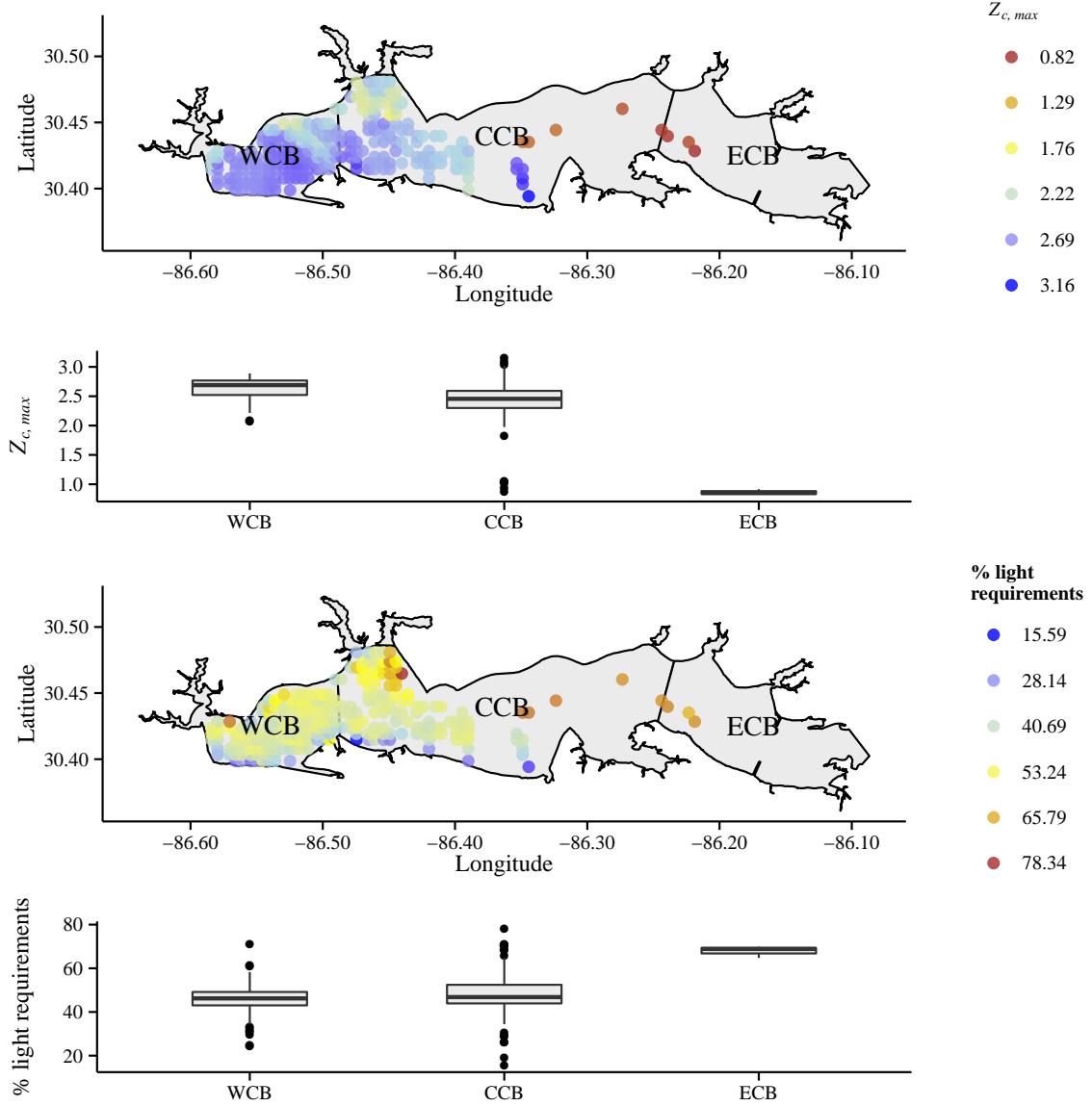


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.04 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. CCB: Central Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay.

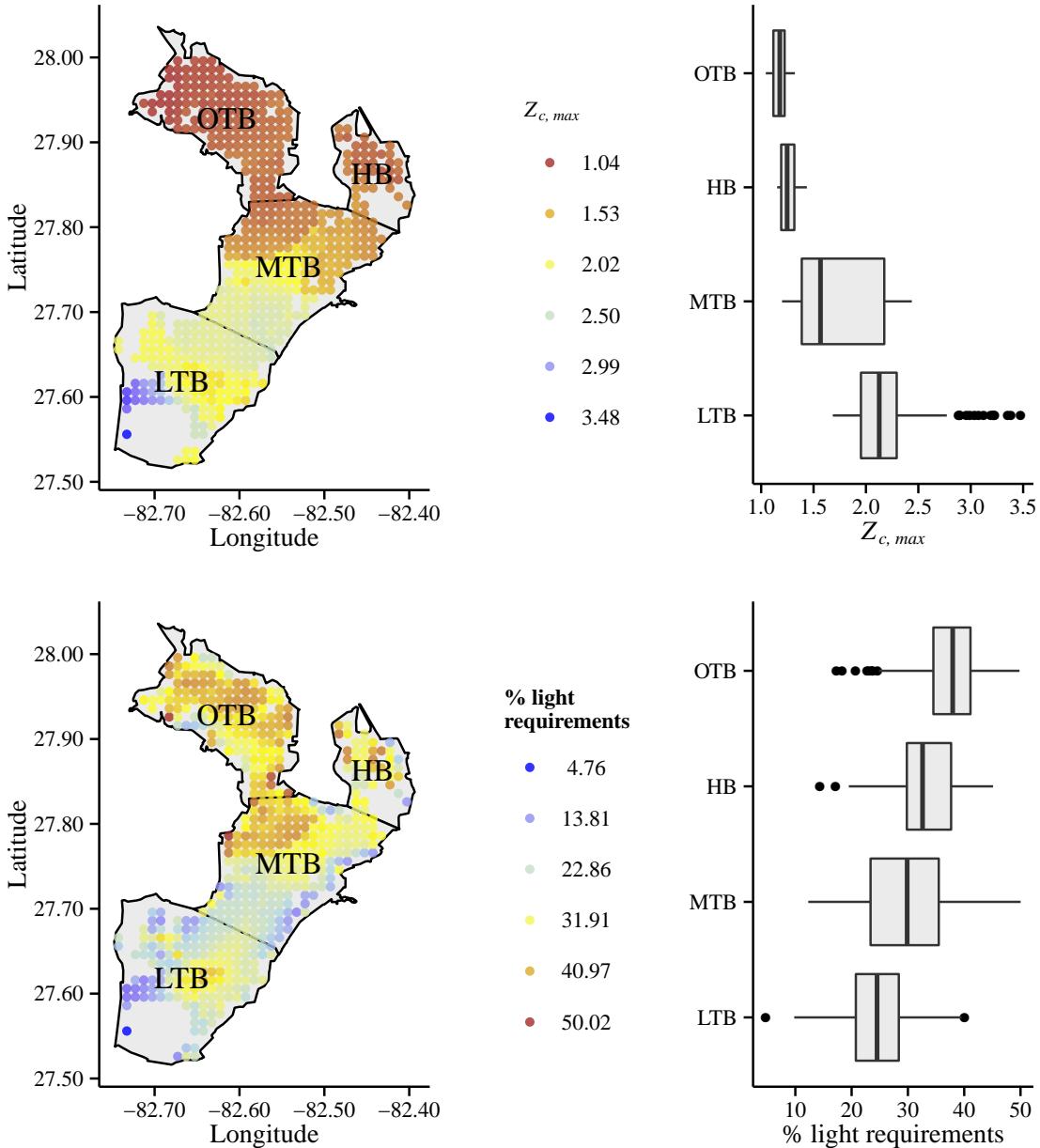


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees.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

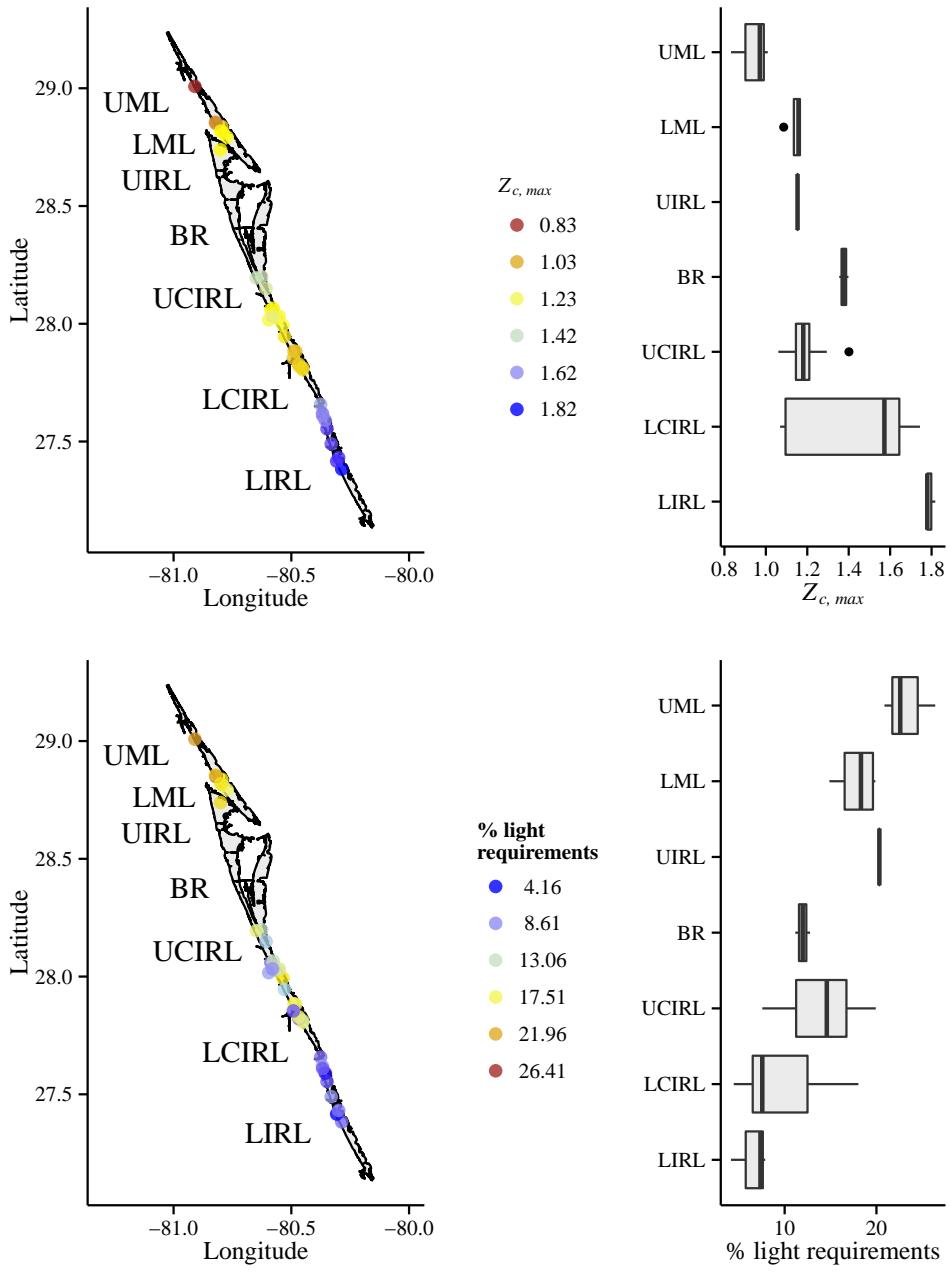


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment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