

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 habitat (Steward et al. 2005). Seagrass depth limits have also been used to establish
45 quantitative criteria for nutrient load targets for the maintenance of water quality (Janicki and
46 Wade 1996). Seagrasses are integrative of system-wide conditions over time in relation to
47 changes in nutrient regimes (Duarte 1995) and are often preferred biological endpoints to
48 describe ecosystem response to perturbations relative to more variable taxa (e.g., phytoplankton).

49 Quantifying the relationship of seagrasses with water clarity is a useful approach to understanding
50 ecological characteristics of aquatic systems with potential insights into system response to
51 disturbance (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 (Spears et al. 2009). The availability of geospatial data that describe areal
58 seagrass and bathymetric coverage suggests standardized techniques can be developed that could
59 be applied across broad areas. Conversely, site-specific approaches with such datasets typically
60 quantify habitat requirements within predefined management units that may prevent

61 generalizations outside of the study area. For example, Steward et al. (2005) describe use of a
62 segmentation scheme for the Indian River Lagoon on the Atlantic coast of Florida to assign
63 seagrass depth limits to 19 distinct geospatial units. Although useful for the specific study goals,
64 substantial variation in growth patterns and water quality characteristics at different spatial scales
65 may prevent more detailed analyses. Methods for estimating seagrass depth limits should also be
66 reproducible for broad-scale comparisons, while also maintaining flexibility based on the
67 objectives. Such techniques can facilitate comparisons between regions given the spatial coverage
68 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 In addition to accurate measures of depth of colonization, the availability of water clarity
84 data that are evenly distributed through space in time has also limited estimates of seagrass light
85 requirements. Secchi observations can provide reliable measures of water clarity (USEPA 2006),
86 although data can be biased by location. Monitoring programs may have unbalanced coverage of
87 aquatic resources with greater perceived importance relative to those that may have more
88 ecological significance (Wagner et al. 2008, Lottig et al. 2014). Moreover, infrequent field
89 measurements that are limited to discrete time periods are more descriptive of short-term
90 variability rather than long-term trends in water clarity (Elsdon and Connell 2009). Seagrasses

91 growth patterns are integrative of seasonal and inter-annual patterns in water clarity, such that
92 estimates of light requirements may be limited if water clarity measurements inadequately
93 describe temporal variation. Remote sensing products can provide reliable estimates of water
94 clarity and could be used to develop a more complete description of relevant ecosystem
95 characteristics. Although algorithms have been developed for coastal waters to estimate surface
96 reflectance from satellite data (Woodruff et al. 1999, Chen et al. 2007), this information has rarely
97 been used to describe seagrass light requirements at a spatial resolution consistent with most
98 remote sensing products.

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

115 **2 Methods**

116 Estimates of seagrass depth of colonization (Z_c) derived from relatively broad spatial
117 areas, such as predefined management units, may not fully describe relevant variation depending
118 on the question of interest. Fig. 1a shows variation in seagrass distribution for a management
119 segment (thick polygon) in the Big Bend region of Florida. The maximum depth colonization, as

120 a red countour line, is based on a segment-wide estimate of all seagrasses within the polygon.
121 Although the estimate is not inaccurate, substantial variation in seagrass growth patterns at
122 smaller spatial scales is not adequately described. In particular, Z_c is greatly over-estimated at the
123 outflow of the Steinhatchee River (northeast portion of the segment) where high concentrations of
124 dissolved organic matter reduce water clarity and naturally limit seagrass growth (personal
125 communication, Nijole Wellendorf, Florida Department of Environmental Protection). This
126 example suggests that it may be useful to have improved spatial resolution in Z_c , particularly
127 when site-specific characteristics require a more detailed description. The following is a summary
128 of data sources, methods, and rationale for developing the algorithm. Data and methods described
129 in [Hagy In review](#) are used as a foundation for developing the approach.

130 2.1 Data sources

131 2.1.1 Study sites

132 Four coastal locations in Florida were used as study sites: the Big Bend region (northeast
133 Gulf of Mexico), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf Coast), and Indian
134 River Lagoon (Atlantic coast) ([Table 1](#) and [Fig. 2](#)). Sites were chosen to represent a regional
135 distribution of coastal habitat in Florida, in addition to having available data and observed
136 gradients in water quality. Site-specific estimates of seagrass depth colonization and light
137 requirements were the focus of the current analysis, with emphasis on improved clarity of
138 description with changes in spatial context. However, coastal regions and estuaries in Florida are
139 partitioned using a predefined segmentation scheme for developing numeric nutrient criteria.
140 These management segments are used for comparison to evaluate variation in growth patterns at
141 difference spatial scales. One segment within each region and smaller spatial units defined by the
142 algorithm are first evaluated to illustrate use of the method. Segments in each region included a
143 location near the outflow of the Steinhatchee River for the Big Bend region, Old Tampa Bay,
144 Upper Indian River Lagoon, and Western Choctawhatchee Bay ([Fig. 2](#)). A second analysis
145 focused on describing seagrass depth limits for all of Choctawhatchee Bay, Tampa Bay, and the
146 Indian River Lagoon to develop a spatial description of light requirements.

147 2.1.2 Seagrass coverage and bathymetry

148 Geospatial data describing seagrass areal coverage combined with co-located bathymetric
149 depth maps were used to estimate Z_c . These products are publically available in coastal regions of

150 Florida through the US Geological Survey, Florida Department of Environmental Protection,
151 Florida Fish and Wildlife Conservation Commission, and many watershed management districts.
152 Seagrass coverage maps were obtained for one chosen year in each of the study sites (Table 1).
153 The original coverage maps were produced using photo-interpretations of aerial images to
154 categorize seagrass as absent, discontinuous (patchy), or continuous. We considered only present
155 (continuous and patchy) and absent categories since differences between continuous and patchy
156 coverage were often inconsistent between data sources.

157 Bathymetric depth maps were obtained from the National Oceanic and Atmospheric
158 Administration's (NOAA) National Geophysical Data Center (<http://www.ngdc.noaa.gov/>) as
159 either Digital Elevation Models (DEMs) or raw sounding data from hydroacoustic surveys.
160 Tampa Bay data provided by the Tampa Bay National Estuary Program are described in [Tyler](#)
161 [et al. \(2007\)](#). Bathymetric data for the Indian River Lagoon were obtained from the St. John's
162 Water Management District ([Coastal Planning and Engineering 1997](#)). The vertical datums varied
163 such that NOAA products were referenced to mean lower low water, Tampa Bay data were
164 referenced to the North American Vertical Datum of 1988 (NAVD88), and the Indian River
165 Lagoon data were referenced to mean sea level. All bathymetric data were vertically adjusted to
166 local mean sea level (MSL) using the NOAA VDatum tool (<http://vdatum.noaa.gov/>). Adjusted
167 data were combined with seagrass coverage layers using standard union techniques for raster and
168 vector layers in ArcMap 10.1 ([Environmental Systems Research Institute 2012](#)). To reduce
169 computation time, depth layers were first masked using a 1 km buffer of the seagrass coverage
170 layer. Raster bathymetric layers were converted to vector point layers to combine with seagrass
171 coverage maps, described below.

172 **2.1.3 Water clarity estimates**

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

179 Daily MODIS (Aqua level-2) satellite data for the preceding five years from the seagrass

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

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

202 **2.2 Estimation of seagrass depth of colonization**

203 The approach to estimating seagrass depth of colonization uses combined seagrass
204 coverage maps and bathymetric depth data described above. The combined layer was a point
205 shapefile with attributes describing location (latitude, longitude), depth (m), and seagrass
206 (present, absent). Seagrass Z_c values were estimated from these data by quantifying the
207 proportion of points with seagrass at each observed depth. Three unique measures obtained from
208 these data are minimum ($Z_{c,min}$), median ($Z_{c,med}$), and maximum ($Z_{c,max}$) depth of colonization.
209 Operationally, these terms describe characteristics of the seagrass coverage map with quantifiable

significance. $Z_{c, \max}$ is the deepest depth at which a significant coverage of mappable seagrasses occurred independent of outliers, whereas $Z_{c, \text{med}}$ is the median depth occurring at the deep water edge. $Z_{c, \min}$ is the depth at which seagrass coverage begins to decline with increasing depth and may not be statistically distinguishable from zero depth, particularly in turbid waters.

The spatially-resolved approach for estimating Z_c begins by choosing an explicit location in cartesian coordinates within the general boundaries of the available data. Seagrass depth data (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the chosen location are selected for estimating seagrass Z_c values (sample areas in Fig. 1). The estimate for each location is quantified from the proportion of sampled points that contain 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:

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

where the proportion of points occupied by seagrass at each depth, Z , is defined by a logistic

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

246 Estimates for each of the three Z_c measures are obtained only if specific criteria are met.
247 These criteria were implemented as a safety measure that ensures a sufficient amount and
248 appropriate quality of data were sampled within the chosen radius. First, estimates were provided
249 only if a sufficient number of seagrass depth points were present in the sampled data to estimate a
250 logistic growth curve. This criteria applies to the sample size as well as the number of points with
251 seagrass in the sample. Second, estimates were provided only if an inflection point was present on
252 the logistic curve within the range of the sampled depth data. This criteria applied under two
253 scenarios where the curve was estimated but a trend was not adequately described by the sampled
254 data. That is, estimates were unavailable if the logistic curve described only the initial decrease in
255 points occupied as a function of depth. The opposite scenario occurred when a curve was
256 estimated but only the deeper locations beyond the inflection point were present in the sample.
257 Third, the estimate for $Z_{c,min}$ was set to zero depth if the linear curve through the inflection point
258 intercepted the upper asymptote of the logistic curve at x-axis values less than zero. The estimate
259 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
260 fixed at zero. Finally, estimates were considered invalid if the 95% confidence interval for $Z_{c,max}$
261 included zero. In such cases, the three measures are not statistically distinguishable, although a
262 useful estimate for $Z_{c,max}$ is provided. Methods to determine confidence bounds are described
263 below.

264 2.3 Estimating uncertainty in depth of colonization estimates

265 Confidence intervals for the Z_c values were estimated using a Monte Carlo simulation
266 approach that used the variance-covariance matrix of the logistic model parameters (Hilborn and

267 Mangel 1997). Confidence intervals were constructed by repeated sampling of a multivariate
268 normal distribution to evaluate the uncertainty in the inflection point in eq. (1). The sampling
269 distribution assumes:

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

270 where x is a predictor variable used in eq. (1) (depth) that follows a multivariate normal
271 distribution with mean μ , and variance-covariance matrix Σ . The mean values are set at the depth
272 value corresponding to the inflection point on the logistic curve from the observed model, whereas
273 Σ is the variance-covariance matrix of the model parameters (α, β, γ). A large number of samples
274 ($n = 10000$) were drawn from the distribution to characterize the uncertainty of the depth value of
275 the inflection point. The 2.5th and 97.5th percentiles of the sample were considered bounds on the
276 95% confidence interval. This approach was used because uncertainty from the logistic curve is
277 directly related to uncertainty in each of the Z_c estimates that are based on the linear curve
278 through the inflection point. Upper and lower limits for each Z_c estimate were obtained by fitting
279 new linear curves through the upper and lower limits of the initial depth value. (i.e., Fig. 3c).

280 Nonlinear least squares models were based on the `nls` and `SSlogis` functions that used
281 a self-starting logistic growth model (Bates and Chambers 1992, R Development Core Team
282 2014). Multivariate normal distributions were simulated using functions in the MASS package
283 (Venables and Ripley 2002). Geospatial data were imported and processed using functions in the
284 rgeos and sp packages (Bivand et al. 2008, Bivand and Rundel 2014).

285 2.4 Evaluation of spatial heterogeneity of seagrass depth limits

286 Spatially-resolved estimates for seagrass Z_c were obtained for several locations in each of
287 the four segments described above (Fig. 2). A regular grid of locations for estimating each of the
288 three Z_c values was created for each segment. The grid was masked by the segment boundaries,
289 whereas seagrass depth points used to estimate Z_c extended slightly beyond the segment
290 boundaries to allow adequate sampling by grid points that occurred near the edge. Spacing
291 between sample points was chosen arbitrarily as 0.01 decimal degrees (1 km at 30 degrees N
292 latitude) and the sampling radius for each location was chosen as 0.02 decimal degrees. The
293 sample radius allowed for complete coverage of seagrass within the segment while also
294 minimizing redundancy of information described by each location. Finally, a single segment-wide

295 estimate using all data at each location was used for comparisons. Departures from the
296 segment-wide estimate at finer scales were considered evidence of spatial heterogeneity in
297 seagrass growth and improved clarity of description as a result.

298 **2.5 Estimating light requirements**

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

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

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

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

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

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

312 Two approaches were used to estimate light requirements based on the availability of
313 satellite data or in situ water clarity (see). For locations with satellite data (Choctawhatchee and
314 Tampa Bay), a regular grid of sampling points was created as before to estimate $Z_{c, max}$ and
315 sample the continuous layer of satellite-derived water clarity. Grid spacing was different in each
316 bay (0.005 for Choctawhatchee Bay, 0.01 for Tampa Bay) to account for variation in spatial scales
317 of seagrass coverage. Equation (4) was used to estimate light requirements at each point for

318 Choctawhatchee Bay and eq. (5) was used for Tampa Bay. Similarly, the geographic coordinates
319 for each in situ secchi measurement in the Indian River Lagoon were used as locations for
320 estimating $Z_{c,max}$ and light requirements using eq. (5). Excessively small estimates for light
321 requirements were removed for Indian River Lagoon which were likely caused by shallow secchi
322 observations that were not screened during initial data processing. A critical difference between
323 the satellite and secchi data was that a more complete spatial description of light requirements
324 was possible in the former case due to continuous coverage, whereas descriptions using secchi
325 data were confined to the original sampling locations. Sampling radii for locations in each bay
326 were chosen to maximize the number of points with estimable values for $Z_{c,max}$ (as described in
327 section 2.2), while limiting the upper radius to adequately describe variation in seagrass growth
328 patterns for emphasizing gradients in light requirements. Radii were fixed at 0.04 decimal degrees
329 for Choctawhatchee Bay, 0.1 decimal degrees for Tampa Bay, and 0.15 decimal degrees for
330 Indian River Lagoon.

331 **3 Results**

332 **3.1 Segment characteristics and seagrass depth estimates**

333 Each coastal region varied by several characteristics that potentially explain variation of
334 seagrass growth (Table 1). Mean surface area was 191.2 square kilometers, with area decreasing
335 for the Big Bend (271.4 km), Upper Indian River Lagoon (228.5 km), Old Tampa Bay (205.5
336 km), and Choctawhatchee Bay (59.4 km) segments. Mean depth was less than 5 meters for each
337 segment, excluding Western Choctawhatchee Bay which was slightly deeper than the other
338 segments (5.3 m). Maximum depths were considerably deeper for Choctawhatchee Bay (11.9 m)
339 and Old Tampa Bay (10.4 m), as compared to the Big Bend (3.6 m) and Indian River Lagoon (1.4
340 m) segments. Seagrasses covered a majority of the surface area for the Big Bend segment (74.8
341 %), whereas coverage was much less for Upper Indian River Lagoon (32.8 %), Old Tampa Bay
342 (11.9 %), and Western Choctawhatchee Bay (5.9 %). Visual examination of the seagrass coverage
343 maps for the respective year of each segment indicated that seagrasses were not uniformly
344 distributed (Fig. 2). Seagrasses in Western Choctawhatchee Bay were sparse with the exception
345 of a large patch located to the west of the inlet connection with the Gulf of Mexico. Seagrasses in
346 the Big Bend segment were located throughout with noticeable declines near the outflow of the

347 Steinhatchee River, whereas seagrasses in Old Tampa Bay and Upper Indian River Lagoon were
348 generally confined to shallow areas near the shore. Seagrass coverage showed a partial decline
349 toward the northern ends of both Old Tampa Bay and Upper Indian River Lagoon segments.
350 Water clarity as indicated by average secchi depths was similar between the segments (1.5 m),
351 although Choctawhatchee Bay had a slightly higher average (2.1 m).

352 The segment-wide estimates of Z_c indicated that seagrasses generally did not grow deeper
353 than three meters in any of the segments (Table 2). Maximum and median depth of colonization
354 were deepest for the Big Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old
355 Tampa Bay (1.1 and 0.9 m), whereas the minimum depth of colonization was deepest for Western
356 Choctawhatchee Bay (1.8 m) and shallowest for Old Tampa Bay (0.6 m). In most cases, the
357 averages of all grid-based estimates were less than the whole segment estimates, indicating a
358 left-skewed distribution of estimates at finer spatial scales. For example, the average of all grid
359 estimates for $Z_{c,max}$ in the Big Bend region indicated seagrasses grew to approximately 2.1 m,
360 which was 1.6 m less than the whole segment estimate. Although reductions were not as severe
361 for the average grid estimates for the remaining segments, considerable within-segment variation
362 was observed depending on grid location. For example, the deepest estimate for $Z_{c,min}$ (2 m) in
363 the Upper Indian River Lagoon exceeded the average of all grid locations for $Z_{c,max}$ (1.7 m).
364 $Z_{c,min}$ also had minimum values of zero meters for the Big Bend and Old Tampa Bay segments,
365 suggesting that seagrasses declined continuously from the surface for several locations.

366 Visual interpretations of the grid estimates provided further information on the
367 distribution of seagrasses in each segment (Fig. 4). Spatial heterogeneity in depth limits was
368 particularly apparent for the Big Bend and Upper Indian River Lagoon segments. As expected,
369 depth estimates indicated that seagrasses grew deeper at locations far from the outflow of the
370 Steinhatchee River in the Big Bend segment. Similarly, seagrasses were limited to shallower
371 depths at the north end of the Upper Indian River Lagoon segment near the Merrit Island National
372 Wildlife Refuge. Seagrasses were estimated to grow at maximum depths up to 2.2 m on the
373 eastern portion of the Upper Indian River Lagoon segment. Spatial heterogeneity was less distinct
374 for the remaining segments although some patterns were apparent. Seagrasses in Old Tampa Bay
375 grew slightly deeper in the northeast portion of the segment and declined to shallower depths near
376 the inflow at the northern edge. Spatial variation in Western Choctawhatchee Bay was minimal,

377 although the maximum Z_c estimate was observed in the northeast portion of the segment. As
378 expected, Z_c values could not be estimated where seagrasses were sparse or absent, nor where
379 seagrasses were present but the sampled points did not show a decline with depth. The former
380 scenario was most common in Old Tampa Bay and Western Choctawhatchee Bay where
381 seagrasses were unevenly distributed or confined to shallow areas near the shore. The latter
382 scenario was most common in the Big Bend segment where seagrasses were abundant but
383 locations near the shore were inestimable given that seagrasses did not decline appreciably within
384 the depths that were sampled.

385 Uncertainty in $Z_{c, max}$ indicated that confidence intervals were generally acceptable (i.e.,
386 greater than zero), although the ability to discriminate between the three depth estimates varied by
387 segment (Fig. 4 and Table 3). Uncertainty for all estimates as the average width of the 95%
388 confidence intervals for all segments was 0.2 m. Greater uncertainty was observed for Western
389 Choctawhatchee Bay (mean width was 0.5 m) and Old Tampa Bay (0.4 m), compared to the Big
390 Bend (0.1 m) and Upper Indian River Lagoon (0.1 m) segments. The largest confidence interval
391 for each segment was 1.4 m for Old Tampa Bay, 1.6 m for Western Choctawhatchee Bay, 0.5 m
392 for the Big Bend, and 0.8 m for the Upper Indian River Lagoon segments. Most confidence
393 intervals for the remaining grid locations were much smaller than the maximum in each segment
394 (e.g., an extreme central location of the Upper Indian River Lagoon, Fig. 4). A comparison of
395 overlapping confidence intervals for $Z_{c, min}$, $Z_{c, med}$, and $Z_{c, max}$ at each grid location indicated
396 that not every measure was unique. Specifically, only 11.1% of grid points in Choctawhatchee
397 Bay and 28.2% in Old Tampa Bay had significantly different estimates, whereas 82.4% of grid
398 points in the Indian River Lagoon and 96.2% of grid points in the Big Bend segments had
399 estimates that were significantly different. By contrast, all grid estimates in Choctawhatchee Bay
400 and Indian River Lagoon had $Z_{c, max}$ estimates that were significantly greater than zero, whereas
401 all but 12.4% of grid points in Old Tampa Bay and 8% of grid points in the Big Bend segment had
402 $Z_{c, max}$ estimates significantly greater than zero.

403 3.2 Evaluation of seagrass light requirements

404 Estimates of water clarity, seagrass depth limits, and corresponding light requirements for
405 all locations in Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon indicated
406 substantial variation, both between and within the different bays. Satellite-derived estimates of

407 light attenuation for Choctawhatchee Bay (as K_d , Fig. 5) and Tampa Bay (as clarity, Fig. 6)
408 indicated variation between years and along major longitudinal and lateral axes. For
409 Choctawhatchee Bay, K_d estimates for western and central segments were substantially smaller
410 than those for the more shallow, eastern segment. Maximum K_d values were also observed in
411 earlier years (e.g., 2003, 2004). Clarity estimates for Tampa Bay also showed an increase towards
412 more seaward segments, with particularly higher clarity along the mainstem. Clarity in 2006 was
413 relatively lower than other years, with noticeable increases in 2007 and 2008. In situ secchi
414 observations for the Indian River Lagoon followed a clear latitudinal gradient with higher values
415 in more southern segments (Fig. 9). Very few measurements were available for the Upper Indian
416 River Lagoon and Banana River segments, likely due to water clarity exceeding the maximum
417 depth in shallow areas.

418 Seagrass Z_c estimates were obtained for 259 locations in Choctawhatchee Bay, 566
419 locations in Tampa Bay, and 37 locations in the Indian River Lagoon (Table 4 and Figs. 7 to 9).
420 Mean $Z_{c,max}$ for each bay was 2.5, 1.7, and 1.3 m for Choctawhatchee Bay, Tampa Bay, and
421 Indian River Lagoon, respectively, with all values being significantly different between bays
422 (ANOVA, $F = 326.9$, $df = 2, 859$, $p < 0.001$, followed by Tukey multiple comparison,
423 $p < 0.001$ for all). Generally, spatial variation in $Z_{c,max}$ followed variation in light requirements
424 for broad spatial scales with more seaward segments or areas near inlets having lower light
425 requirements. Mean light requirements were significantly different between all bays (ANOVA,
426 $F = 463.7$, $df = 2, 859$, $p < 0.001$, Tukey $p < 0.001$ for all), with a mean requirement of 47.1%
427 for Choctawhatchee Bay, 30.4% for Tampa Bay, and 13.4% for Indian River Lagoon. Significant
428 differences in light requirements between segments within each bay were also observed
429 (ANOVA, $F = 12.1$, $df = 2, 256$, $p < 0.001$ for Choctawhatchee Bay, $F = 84.6$, $df = 3, 562$,
430 $p < 0.001$ for Tampa Bay, $F = 7.6$, $df = 6, 30$, $p < 0.001$ for Indian River Lagoon). Post-hoc
431 evaluation of all pair-wise comparisons of mean light requirements between segments within each
432 bay indicated that significant differences were apparent for several locations. Significant
433 differences were observed between all segments in Choctawhatchee Bay ($p < 0.001$ for all),
434 except the central and western segments (Fig. 7). Similarly, significant differences in Tampa Bay
435 were observed between all segments ($p < 0.05$ for all), except Middle Tampa Bay and Old Tampa
436 Bay (Fig. 8). Finally, for the Indian River Lagoon, significant differences were observed only

437 between the Lower Central Indian River Lagoon and the Upper ($p < 0.001$) and Lower Mosquito
438 Lagoons ($p = 0.023$), the Lower Indian River Lagoon and the Upper ($p < 0.001$) and Lower
439 Mosquito Lagoons ($p = 0.013$), and the Upper Central Indian River and the Upper Mosquito
440 Lagoon ($p = 0.018$) (Fig. 9). Small sample sizes likely reduced the ability to distinguish between
441 segments in the Indian River Lagoon.

442 **4 Discussion**

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

460 **4.1 Evaluation of the algorithm**

461 The algorithm for estimating seagrass depth of colonization has three primary advantages
462 that facilitated a description of aquatic habitat in each of the case studies. First, the application of
463 non-linear least squares regression provided an empirical means to characterize the reduction of
464 seagrass coverage with increasing depth. This approach was necessary for estimating each of the
465 three depth limits ($Z_{c, min}$, $Z_{c, med}$, $Z_{c, max}$) using the maximum slope of the curve. The maximum

466 rate of decline describes a direct and estimable physiological response of seagrass to decreasing
467 light availability such that each measure provided an operational characterization of growth
468 patterns (see section 2.2). The regression approach also allowed an estimation of confidence in Z_c
469 values by accounting for uncertainty in each of the three parameters of the logistic growth curve
470 (α , β , γ). Indications of uncertainty are required components of any esimation technique that
471 provide a direct evaluation of the quality of data used to determine he model fit. By default,
472 estimates with confidence intervals for $Z_{c,max}$ that included zero were discarded to remove highly
473 imprecise estimates. Despite this restriction, some examples had exceptionally large confidence
474 intervals relative to neighboring estimates (e.g., center of Upper Indian River Lagoon, Fig. 4),
475 which suggests not all locations are suitable for applying the algorithm. The ability to estimate Z_c
476 and to discriminate between the three measures depended on several factors, the most important
477 being the extent to which the sampled seagrass points described a true reduction of seagrass
478 coverage with depth. Sampling method (e.g., chosen radius) as well as site-specific characteristics
479 (e.g., bottom-slope, actual occurrence of seagrass) are critical factors that directly influence
480 confidence in Z_c estimates. A pragmatic approach should be used when applying the algorithm to
481 novel data such that the location and chosen sample radius should be defined by the limits of the
482 analysis objectives.

483 A second advantage is that the algorithm is highly flexible depending on the desired
484 spatial context. Although this attribute directly affects confidence intervals, the ability to choose a
485 sampling radius based on a problem of interest can greatly improve the description of aquatic
486 habitat given site-level characteristics. The previous example described for the Big Bend region
487 highlights this flexibility, such that a segment-wide estimate was inadequate for characterizing
488 $Z_{c,max}$ that was limited near the outflow of the Steinhatchee river. The ability to choose a smaller
489 sampling radius more appropriate for the location indicated that $Z_{c,max}$ reflected known
490 differences in water clarity near the outflow relative to other locations in the segment. However,
491 an important point is that a segment-wide estimate is not necesarily biased such that a sampling
492 radius that covers a broad spatial area could be appropriate depending on the analysis needs. If
493 the effect of water clarity near the outflow was not a concern, the segment-wide estimate could
494 describe seagrass growth patterns for the larger area without inducing descriptive bias. However,
495 water quality standards as employed by management agencies are commonly based on predefined

496 management units, which may not be appropriate for all locations. The flexibility of the algorithm
497 could facilitate the development of point-based standards that eliminate the need to develop or use
498 a pre-defined classification scheme. In essence, the relevant management area can be defined a
499 priori based on known site characteristics.

500 The ability to use existing geospatial datasets is a third advantage of the algorithm.
501 Further, bathymetry data and seagrass coverage are the only requirements for describing Z_c in a
502 spatial context. These datasets are routinely collected by agencies at annual or semi-annual cycles
503 for numerous coastal regions. Accordingly, data availability and the relatively simple method for
504 estimating Z_c suggests that spatial descriptions could be developed for much larger regions with
505 minimal effort. The availability of satellite-based products with resolutions appropriate for the
506 scale of assessment could also facilitate a broader understanding of seagrass light requirements
507 when combined with Z_c estimates. However, data quality is always a relevant issue when using
508 secondary information as a means of decision-making or addressing specific research questions.
509 Methods for acquiring bathymetric or seagrass coverage data are generally similar between
510 agencies such that the validity of comparisons from multiple sources is typically not a concern.
511 However, one point of concern is the minimum mapping unit for each coverage layer, which is
512 limited by the resolution of the original aerial photos and the comparability of photo-interpreted
513 products created by different analysts. Seagrass maps routinely classify coverage as absent,
514 patchy, or continuous. Discrepancies between the latter two categories between regions limited
515 the analysis to a simple binary categorization of seagrass as present or absent. An additional
516 evaluation of comparability between categories for different coverage maps could improve the
517 descriptive capabilities of Z_c estimates.

518 **4.2 Heterogeneity in growth patterns and light requirements**

519 Variation in Z_c for each of the case studies, as individual segments and whole bays, was
520 typically most pronounced along mainstem axes of each estuary or as distance from an inlet.
521 Greater depth of colonization was observed near seaward locations and was also most limited
522 near river inflows. Although an obvious conclusion would be that depth of colonization is
523 correlated with bottom depth, i.e., seagrasses grow deeper because they can, a more
524 biologically-relevant conclusion is that seagrass depth of colonization follows expected spatial
525 variation in water clarity. Shallow areas within an estuary are often near river outflows where

526 discharge is characterized by high sediment or nutrient loads that contribute to light scattering and
527 increased attenuation. Variation in Z_c along mainstem axes was not unexpected, although the
528 ability to characterize within-segment variation for each of the case studies was greatly improved
529 from more coarse estimates. Seagrasses may also be limited in shallow areas by tidal stress such
530 that a minimum depth can be defined that describes the upper limit related to dessication stress
531 from exposure at low tide. Coastal regions of Florida, particularly the Gulf Coast, are microtidal
532 with amplitudes not exceeding 0.5 meters. Accordingly, the effects of tidal stress on limiting the
533 minimum depth of colonization were not apparent for many locations in the case studies such that
534 $Z_{c,min}$ estimates were often observed at zero depth. Although this measure operationally defines
535 the depth at which seagrasses begin to decline with decreasing light availability, $Z_{c,min}$ could also
536 be used to describe the presence or absence of tidal stress.

537 The use of light attenuation data, either as satellite-derived estimates or in situ secchi
538 observations, combined with Z_c estimates provided detailed and previously unavailable
539 characterizations of light requirements within the three estuaries. Requirements were lowest for
540 the Indian River Lagoon, whereas estimates were higher for Tampa Bay and highest for
541 Choctawhatchee Bay. Requirements for the Indian River Lagoon were generally in agreement
542 with other Atlantic coastal systems (Dennison et al. 1993, Kemp et al. 2004), such that
543 requirements typically did not exceed 25% with mean requirements for whole bay estimated at
544 13.4%. However, light requirements for Indian River Lagoon were based on secchi observations
545 with uneven spatial and temporal coverage, which potentially led to an incomplete description of
546 true variation in light attenuation. Alternative measures to estimate K_d (e.g., vertically-distributed
547 PAR sensors) are required when bottom depth is shallower than maximum water clarity, although
548 scalability remains an issue. Conversely, satellite-derived estimates were possible for Tampa and
549 Choctawhatchee Bays where water column depth was sufficient and were preferred over in situ
550 data given more complete spatial coverage. Mean light requirements for Tampa Bay were 30.4%
551 of surface irradiance, which was in agreement with previously reported values, particularly for
552 Lower Tampa Bay (Dixon and Leverone 1995). Estimates for Choctawhatchee Bay were
553 substantially higher with a bay-wide average of 47.1%. The relatively higher light requirements
554 for Gulf Coast esuaries, particularly Choctawhatchee Bay, may reflect the need for additional
555 validation data for the conversion of satellite reflectance values to light attenuation. However,

556 estuaries in the northern Gulf of Mexico are typically shallow and highly productive (Caffrey
557 et al. 2014), such that high light requirements may in fact be related to the effects of high nutrient
558 loads on water clarity. Further evaluation of seagrass light requirements in the northern Gulf of
559 Mexico could clarify the extent to which our results reflect true differences relative to other
560 coastal regions.

561 As previously noted, variation in seagrass light requirements can be attributed to
562 differences in physiological requirements between species or regional effects of different light
563 regimes (Choice et al. 2014). For example, *Halodule wrightii* is the most abundant seagrass in
564 Choctawhatchee Bay and occurs in the western polyhaline portion near the outflow with the Gulf
565 of Mexico. Isolated patches of *Ruppia maritima* are also observed in the oligohaline eastern
566 regions of the bay. Although $Z_{c, max}$ was only estimable for a few points in eastern
567 Choctawhatchee Bay, differences in species assemblages along a salinity gradient likely explain
568 the differences in light requirements. The decline of *R. maritima* in eastern Choctawhatchee Bay
569 has been attributed to species sensitivity to turbidity from high rainfall events, whereas losses of
570 *H. wrightii* have primarily been attributed to physical stress during storm overwash and high wave
571 energy (FLDEP 2012). The relatively high light requirements of eastern Choctawhatchee Bay
572 likely reflect differing species sensitivity to turbidity, either through sediment resuspension from
573 rainfall events or light attenuation from nutrient-induced phytoplankton production. Similarly,
574 high light requirements may be related to epiphyte production at the leaf surface (Kemp et al.
575 2004). Estimated light requirements based solely on water column light attenuation, as for secchi
576 or satellite-derived values, may indicate unusually large light requirements if seagrasses are
577 further limited by epiphytic growth at the leaf surface. Epiphyte limitation may be common for
578 upper bay segments where nutrient inputs from freshwater inflows enhance algal production
579 (Kemp et al. 2004). Additionally, lower light requirements for Hillsborough Bay relative to Old
580 Tampa Bay may reflect a reduction in epiphyte load from long-term decreases in nitrogen inputs
581 to northeast Tampa Bay (Dawes and Avery 2010).

582 4.3 Conclusions

583 Spatially-resolved estimates of Z_c combined with high-resolution measures of light
584 attenuation provided an effective approach for evaluating light requirements. However, light
585 requirements, although important, may only partially describe ecosystem characteristics that

586 influence growth patterns. Seagrasses may be limited by additional physical, geological, or
587 geochemical factors, including effects of current velocity, wave action, sediment grain size
588 distribution, and sediment organic content (Koch 2001). Accordingly, spatially-resolved estimates
589 of Z_c and associated light requirements must be evaluated in the context of multiple factors that
590 may act individually or interactively with light attenuation. Extreme estimates of light
591 requirements may suggest light attenuation is not the only determining factor for seagrass growth.

592 An additional constraint is the quality of data that describe water clarity to estimate light
593 requirements. Although the analysis used satellite-derived clarity to create a more complete
594 description relative to in situ data, the conversion of reflectance data from remote sensing
595 products to attenuation estimates is not trivial. Further evaluation of satellite-derived data is
596 needed to create a broader characterization of light requirements. However, the algorithm was
597 primarily developed to describe maximum depth of colonization and the estimation of light
598 requirements was a secondary product that illustrated an application of the method.

599 Spatially-resolved Z_c estimates can be a preliminary source of information for developing a more
600 detailed characterization of seagrass habitat requirements and the potential to develop broad-scale
601 descriptions has been facilitated as a result. Specifically, [Hagy In review](#) developed a more
602 general approach for estimating Z_c for each coastal segment of Florida such that data are
603 available to apply the current method on a much broader scale. Applications outside of Florida
604 are also possible given the minimal requirements for geospatial data products to estimate depth of
605 colonization.

606 **References**

- 607 Barko JW, Hardin DG, Matthews MS. 1982. Growth and morphology of submersed freshwater
608 macrophytes in relation to light and temperature. Canadian Journal of Botany, 60(6):877–887.
- 609 Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors,
610 Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.
- 611 Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R
612 package version 0.3-8.
- 613 Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer,
614 New York, New York.
- 615 Caffrey JM, Murrell MC, Amacker KS, Harper J, Phipps S, Woodrey M. 2014. Seasonal and
616 inter-annual patterns in primary production, respiration and net ecosystem metabolism in 3
617 estuaries in the northeast Gulf of Mexico. Estuaries and Coasts, 37(1):222–241.
- 618 Chen Z, Muller-Karger FE, Hu C. 2007. Remote sensing of water clarity in Tampa Bay. Remote
619 Sensing of Environment, 109(2):249–259.
- 620 Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from
621 historical records of light attenuation along the Gulf coast of peninsular Florida. Marine
622 Pollution Bulletin, 81(1):94–102.
- 623 Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report
624 to St. John's River Water Management District. Technical Report Contract 95W142, Coastal
625 Planning and Engineering, Palatka, Florida.
- 626 Dawes C, Avery W. 2010. Epiphytes of the seagrass *halodule wrightii* in Hillsborough Bay,
627 Florida, a 14 year study in an estuary recovering from eutrophication. Florida Scientist,
628 73(3-4):185–195.
- 629 Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA.
630 1993. Assessing water quality with submersed aquatic vegetation. BioScience, 43(2):86–94.
- 631 Dixon LK, Leverone JR. 1995. Light requirements of *Thalassia testudinum* in Tampa Bay,
632 Florida. Technical report, Number 425, Mote Marine Lab, Sarasota, Florida.
- 633 Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.
- 634 Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes.
635 Ophelia, 41:87–112.
- 636 Elsdon TS, Connell SD. 2009. Spatial and temporal monitoring of coastal water quality: refeining
637 the way we consider, gather, and interpret patterns. Aquatic Biology, 5(2):157–166.
- 638 Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.

- 639 Florida Department of Environmental Protection (FLDEP). 2012. Site-specific information in
640 support of establishing numeric nutrient criteria for Choctawhatchee Bay. Technical report,
641 Florida Department of Environmental Protection, Tallahassee, Florida.
- 642 Greve T, Krause-Jensen D. 2005. Stability of eelgrass (*Zostera marina L.*) depth limits:
643 influence of habitat type. *Marine Biology*, 147(3):803–812.
- 644 Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.
- 645 Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species
646 along Florida's central gulf coast: Iverson and Bittaker revisited. *Estuaries*, 27(1):36–43.
- 647 Hall MO, Durako MJ, Fourqurean JW, Zieman JC. 1990. Decadal changes in seagrass
648 distribution and abundance in Florida Bay. *Estuaries*, 22(2B):445–459.
- 649 Hilborn R, Mangel M. 1997. *The Ecological Detective: Confronting Models with Data*.
650 Princeton University Press, Princeton, New Jersey.
- 651 Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern:
652 declining seagrasses and threatened dependent species. *Frontiers in Ecology and the
653 Environment*, 7(5):242–246.
- 654 Idso SB, Gilbert RG. 1974. On the universality of the Poole and Atkins secchi disk-light
655 extinction equation. *Journal of Applied Ecology*, 11(1):399–401.
- 656 Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico
657 coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5):577–602.
- 658 Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary:
659 An empirically based approach to setting management targets. Technical Report 06-96, Tampa
660 Bay National Estuary Program, St. Petersburg, Florida.
- 661 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *OIKOS*,
662 69(3):373–386.
- 663 Kemp WC, Batiuk R, Bartleson R, Bergstrom P, Carter V, Gallegos CL, Hunley W, Karrh L, Koch
664 EW, Landwehr JM, Moore KA, Murray L, Naylor M, Rybicki NB, Stevenson JC, Wilcox DJ.
665 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water
666 quality, light regime, and physical-chemical factors. *Estuaries*, 27(3):363–377.
- 667 Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and
668 *Syringodium filiforme* derived from the relationship between diffuse light attenuation and
669 maximum depth distribution. *Estuaries*, 19(3):740–750.
- 670 Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible
671 submersed aquatic vegetation habitat requirements. *Estuaries*, 24(1):1–17.
- 672 Lee ZP, Du KP, Arnone R. 2005. A model for the diffuse attenuation of downwelling irradiance.
673 *Journal of Geophysical Research*, 110(C2):10.

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

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

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

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

^b Seagrass coverage data sources, see section 2.1.2 for bathymetry data sources:

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

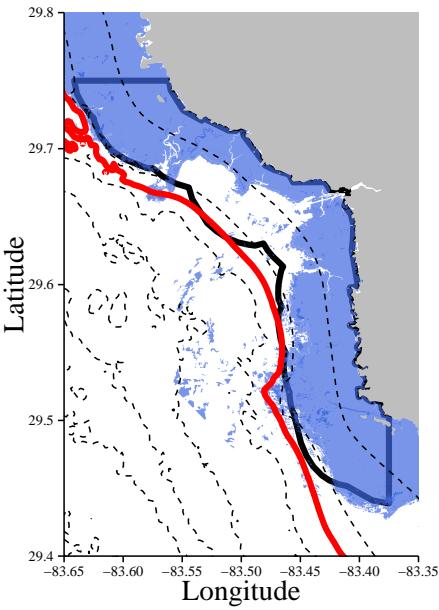
^aBB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Choctawhatchee Bay.

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.

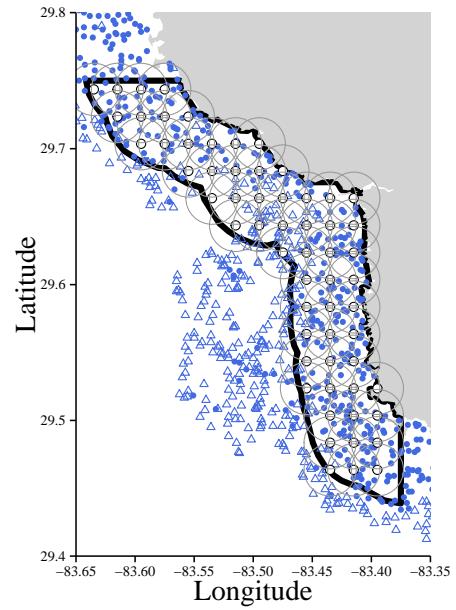
Segment ^a	n	$Z_{c,max}$				% light			
		Mean	St. Dev.	Min	Max	Mean	St. Dev.	Min	Max
Choctawhatchee Bay									
CCB	121	2.4	0.4	0.9	3.2	48.2	10.2	15.6	78.3
ECB	3	0.9	0.0	0.8	0.9	67.8	2.7	64.8	69.9
WCB	135	2.6	0.2	2.1	2.9	45.6	6.6	24.2	70.9
Indian River Lagoon									
BR	2	1.4	0.0	1.4	1.4	12.0	1.1	11.2	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.

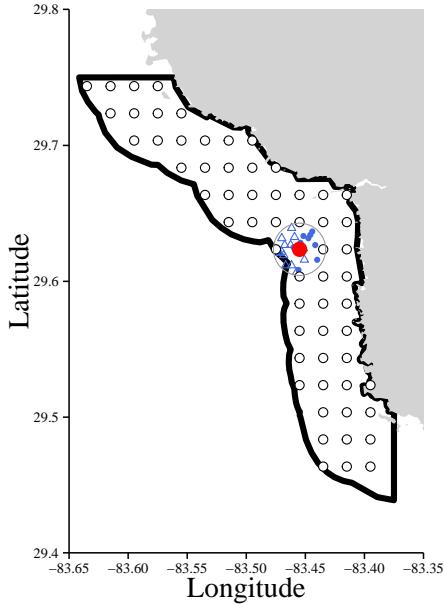
(a) Seagrass coverage and bathymetry for the segment



(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.

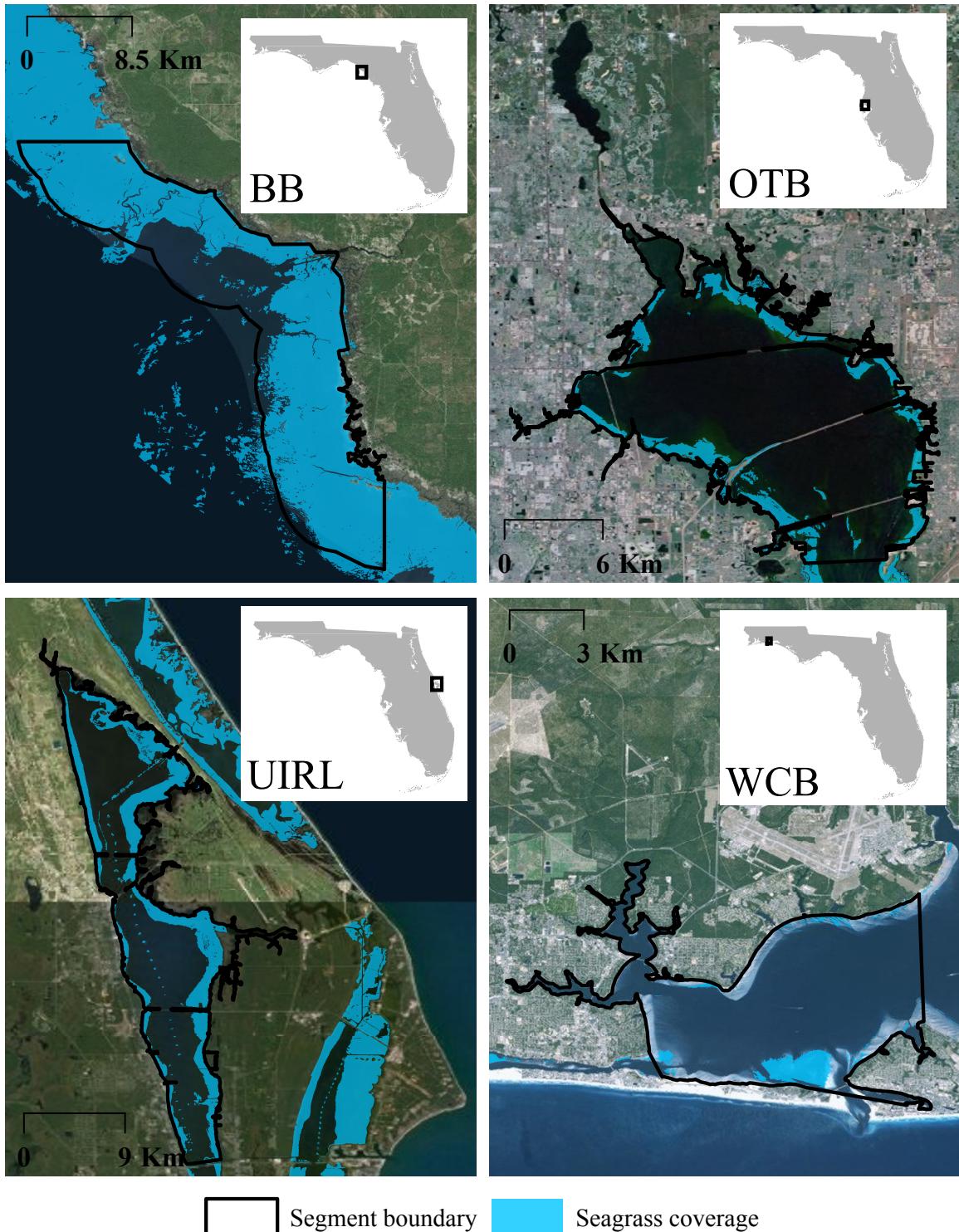
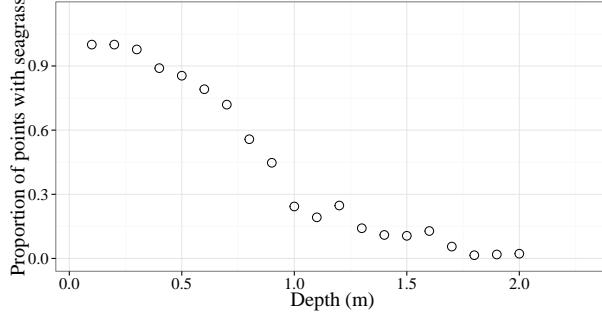
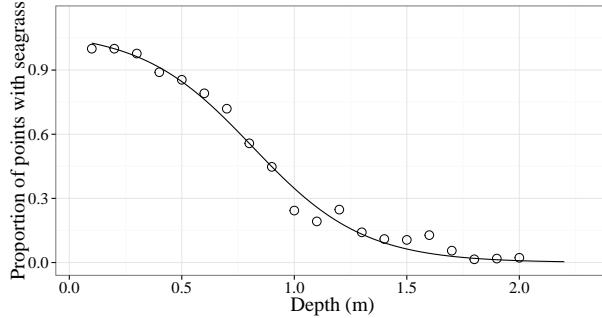


Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

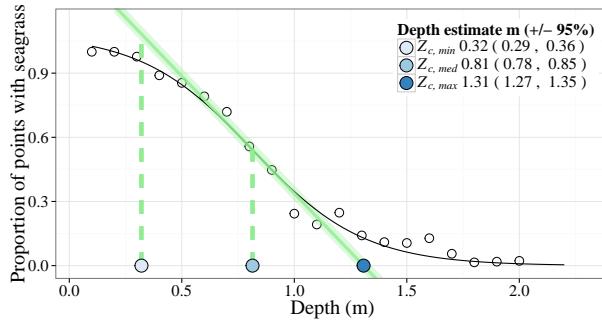


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test location in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit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

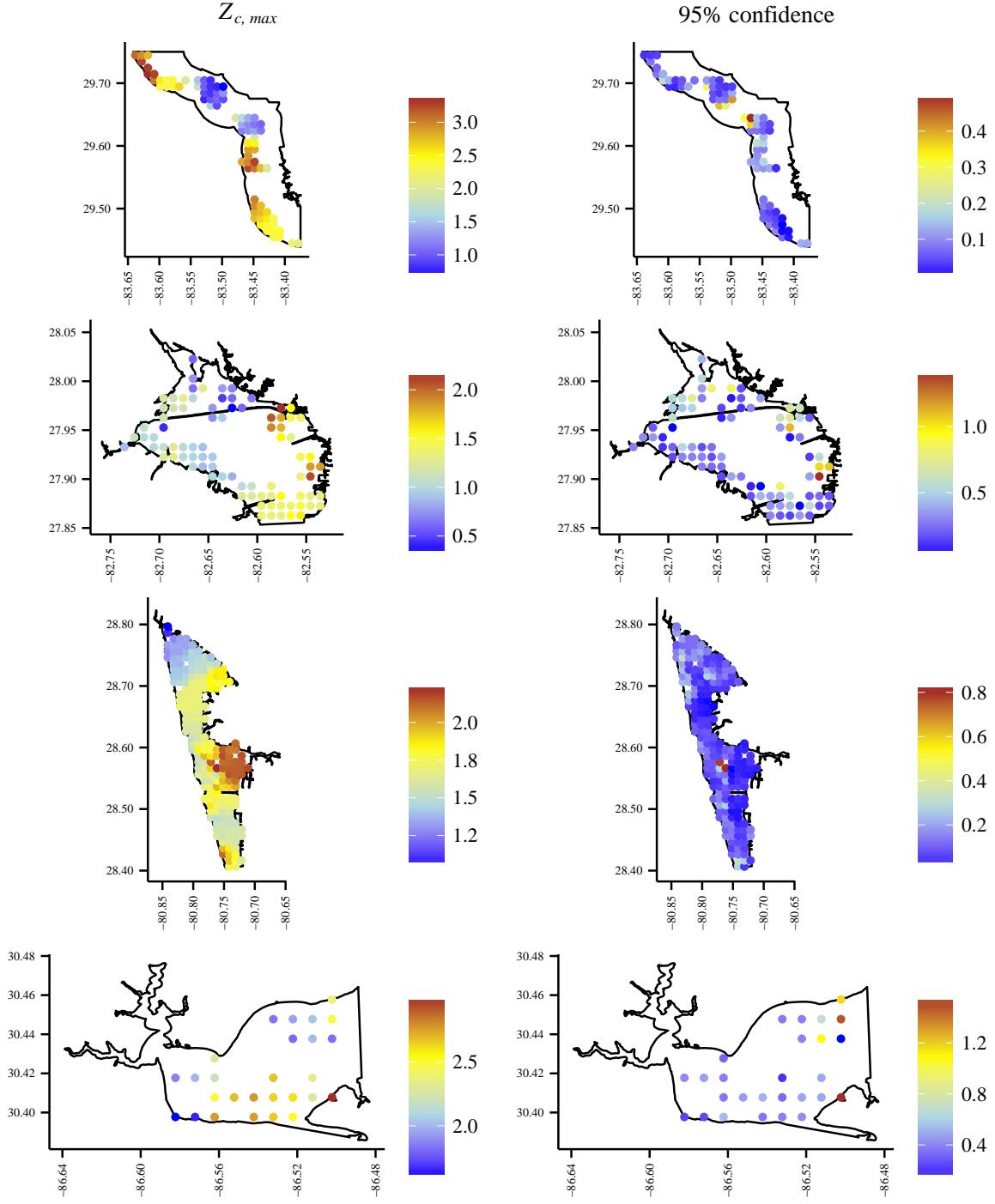


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ($Z_{c, max}$) estimates are on the left and corresponding widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each segment,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

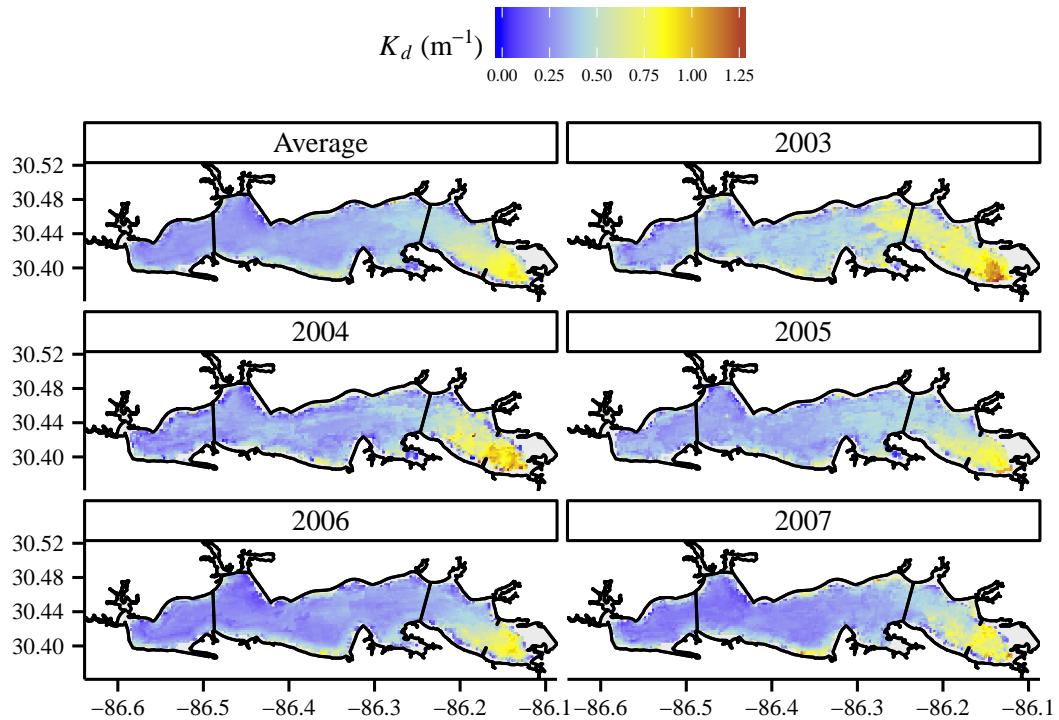


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment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

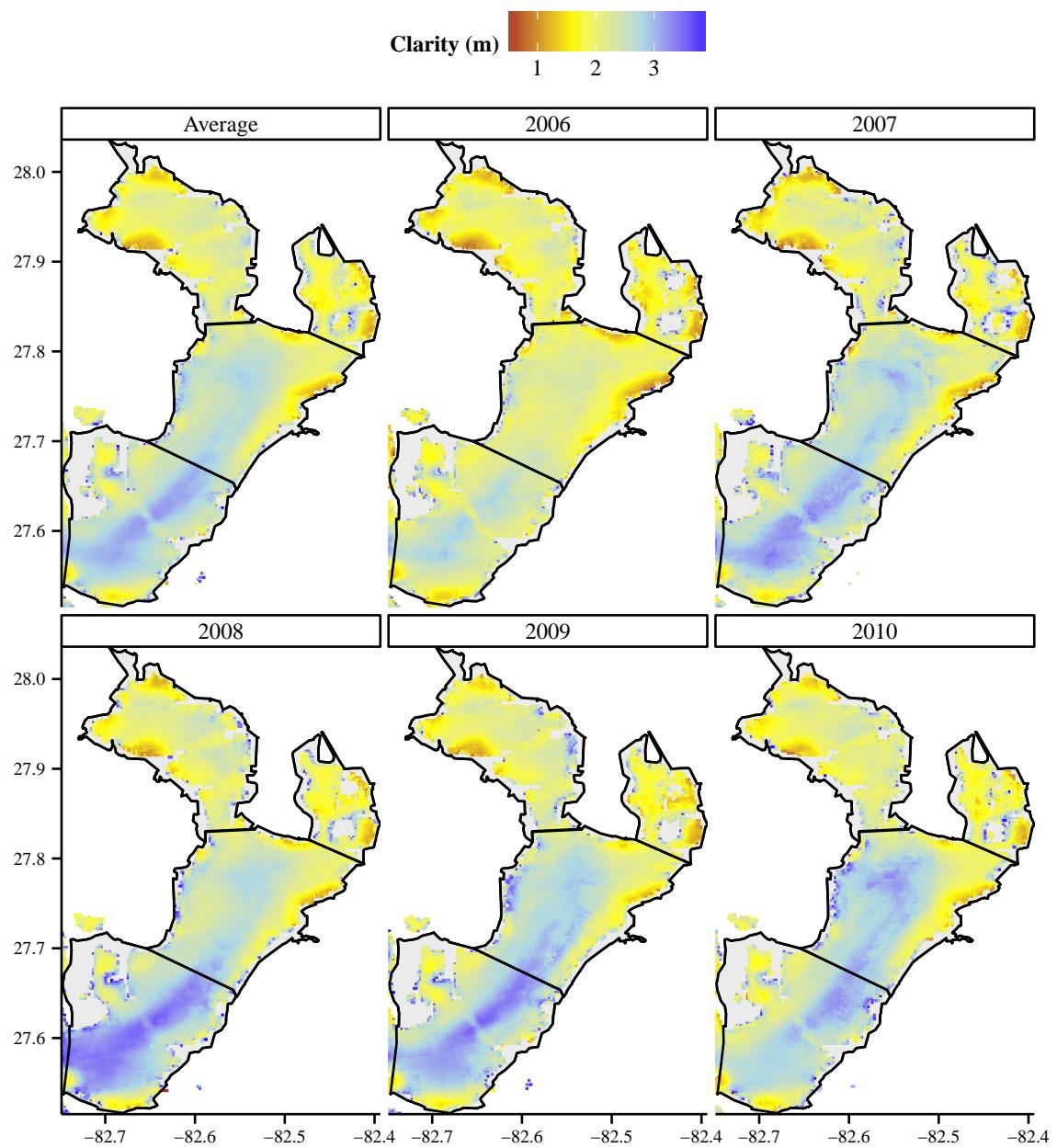


Fig. 6: Satellite estimated water clarity for Tampa Bay. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

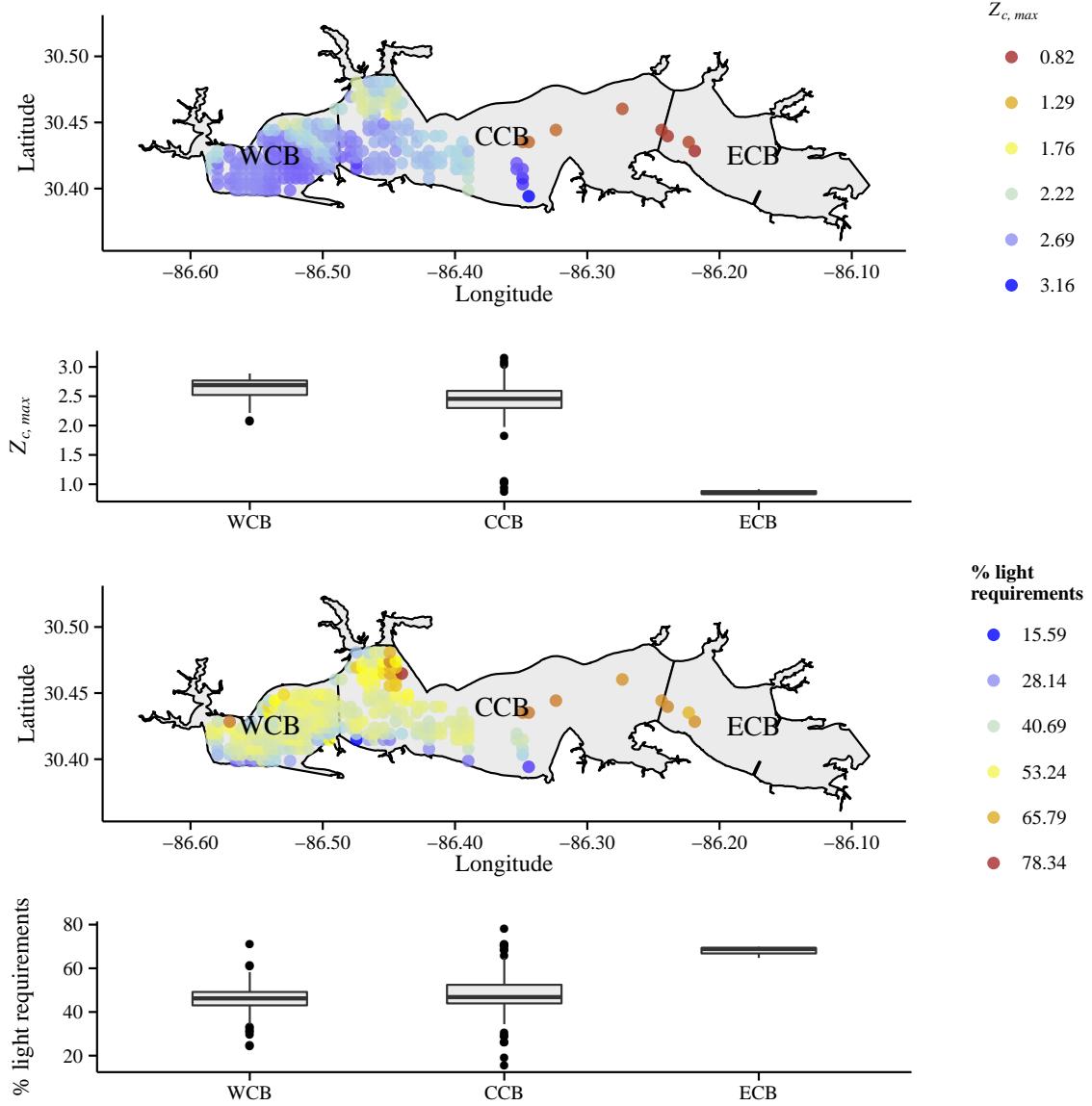


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.04 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 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.

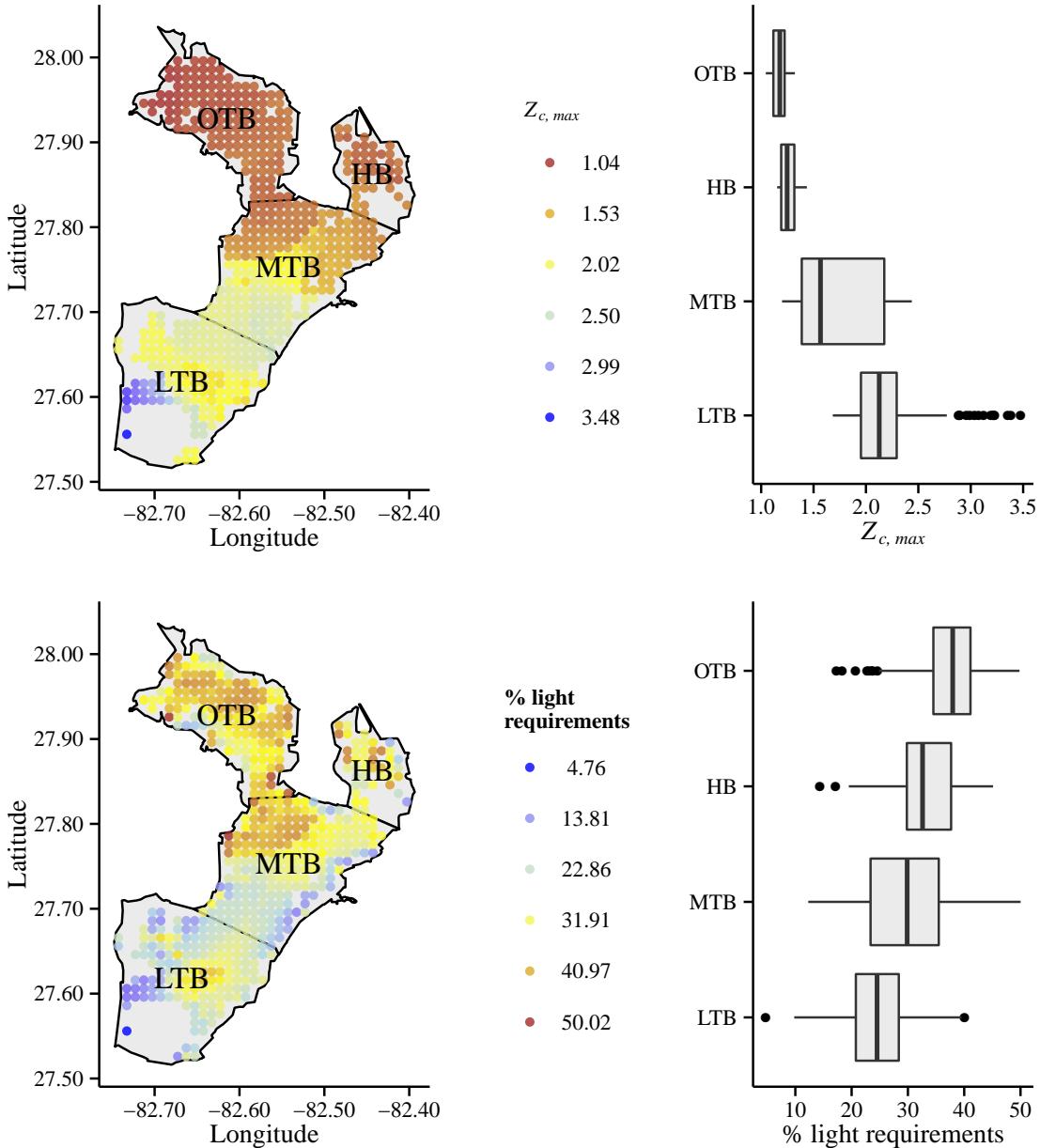


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. 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.

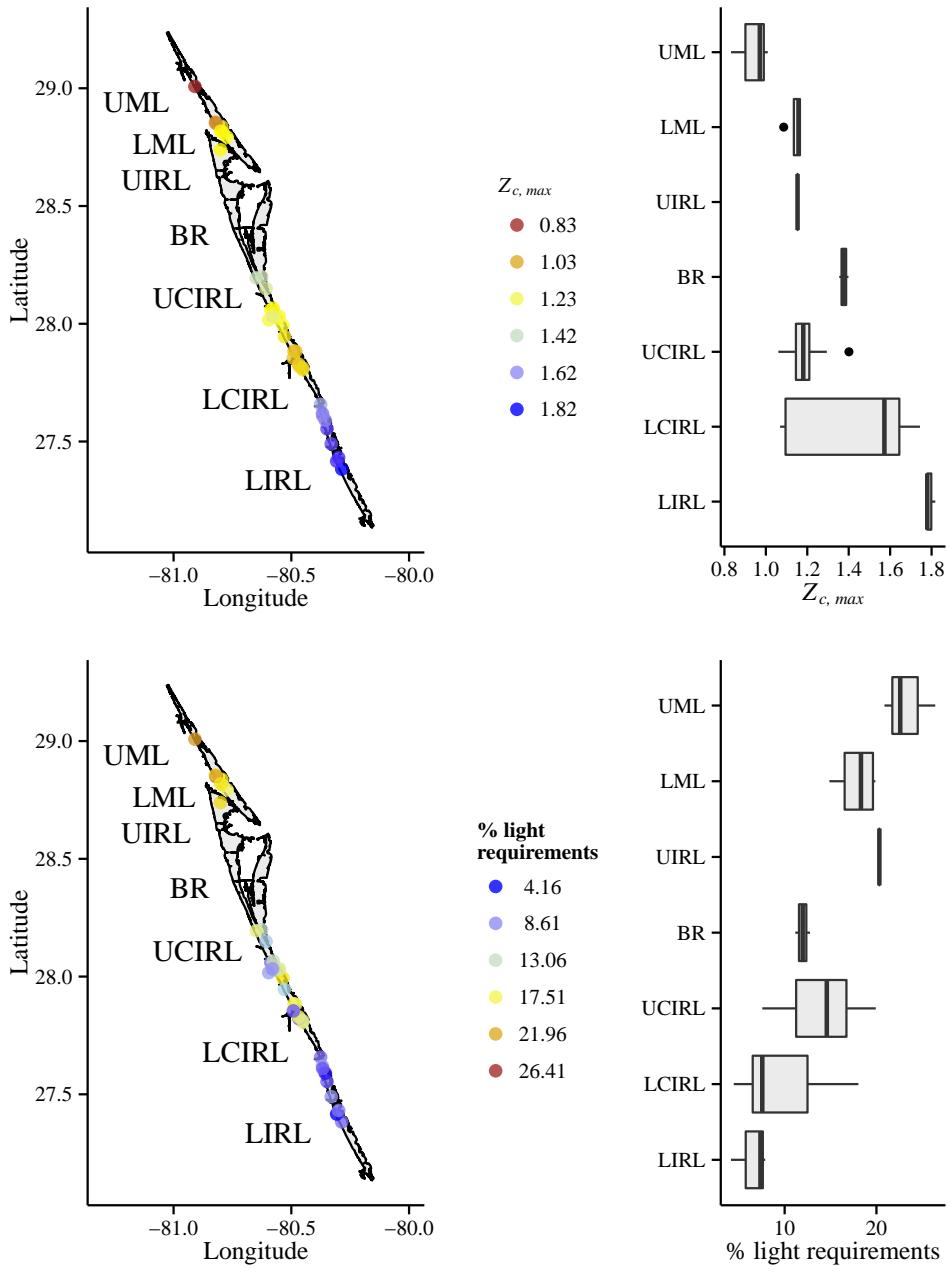


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment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