

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

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4 Abstract

5 The maximum depth of colonization (Z_c) is a useful measure of seagrass growth that
6 describes response to light attenuation in the water column. However, lack of standardization
7 among methods for estimating Z_c has limited the description of habitat requirements at spatial
8 scales most relevant for environmental management. An algorithm is presented for estimating
9 seagrass Z_c using geospatial datasets that are commonly available for coastal regions. A defining
10 characteristic of the algorithm is its ability to estimate Z_c using an adjustable spatial region such
11 that the estimated values can be interpreted for specific areas of interest. These spatially-resolved
12 estimates of Z_c can then be related to light attenuation to evaluate factors that affect seagrass
13 growth, such as light requirements. Four distinct coastal regions of Florida were evaluated,
14 describing seagrass growth patterns on relatively small spatial scales in each region. The analysis
15 was extended to entire bay systems using Z_c and estimates of light attenuation (K_d) to quantify
16 minimum light requirements derived from satellite remote sensing. Sensitivity analyses indicated
17 that estimates of Z_c were generally robust for each case study, although confidence intervals
18 varied with sample size and number of points containing seagrass. Z_c estimates also varied along
19 water quality gradients such that seagrass growth was more limited near locations with reduced
20 water clarity. Site-specific characteristics that contributed to variation in growth patterns were
21 easily distinguished using the algorithm as compared to less spatially-resolved estimates of Z_c .
22 Light requirements for the Indian River Lagoon (13.4%) on the Atlantic Coast were substantially
23 lower than those for Tampa Bay (30.6%) and Choctawhatchee Bay (46.9%) on the Gulf Coast.
24 More importantly, the algorithm characterized spatial variation in light requirements within bays,
25 with values ranging from 4.2 – 26.4% in the Indian River Lagoon, 10.6 – 86.2% in the
26 Choctawhatchee Bay, and 10.5 – 53.6% in Tampa Bay. Higher light requirements in Gulf Coast
27 estuaries may indicate regional differences in species composition or additional factors, such as
28 epiphyte growth, that further reduce light availability at the leaf surface. A spatially-resolved
29 characterization of seagrass Z_c is possible for other regions because the algorithm is transferable
30 with minimal effort to novel datasets.

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

32 1 Introduction

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

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

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

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

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

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

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

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

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

123 **2 Methods**

124 **2.1 Study sites and data sources**

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

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

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

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

158 **2.2 Quantifying water clarity**

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

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

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

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

188 **2.3 Estimating seagrass depth of colonization**

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

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

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

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

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

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

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

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

250 2.4 Estimating uncertainty

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

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

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

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

266 Nonlinear least squares models were based on the `nls` and `SSlogis` functions that used
267 a self-starting logistic growth model (Bates and Chambers 1992, RDCT (R Development Core
268 Team) 2015). Multivariate normal distributions were simulated using functions in the MASS
269 package (Venables and Ripley 2002). Geospatial data were imported and processed using
270 functions in the `rgeos` and `sp` packages (Bivand et al. 2008, Bivand and Rundel 2014).

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

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

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

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

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

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

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

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

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

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

314 **3 Results**

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

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

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

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

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

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

373 Bend (0.1 m) and Upper Indian River Lagoon (0 m) segments. The largest confidence interval for
374 each segment was 2.3 m for Old Tampa Bay, 1 m for Western Choctawhatchee Bay, 4 m for the
375 Big Bend, and 1 m for the Upper Indian River Lagoon segments. Most confidence intervals for
376 the remaining grid locations were much smaller than the maximum in each segment (e.g., an
377 extreme central location of the Upper Indian River Lagoon, Fig. 4). A comparison of overlapping
378 confidence intervals for $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$ at each grid location indicated that not every
379 measure was unique. Specifically, only 81.5% of grid points in Choctawhatchee Bay and 47.7%
380 in Old Tampa Bay had significantly different estimates, whereas 98.5% of grid points in the
381 Indian River Lagoon and 96.4% of grid points in the Big Bend segments had estimates that were
382 significantly different. By contrast, all grid estimates in Choctawhatchee Bay and Indian River
383 Lagoon had $Z_{c,max}$ estimates that were significantly greater than zero, whereas all but 11.3% of
384 grid points in Old Tampa Bay and 4.6% of grid points in the Big Bend segment had $Z_{c,max}$
385 estimates significantly greater than zero.

386 3.2 Evaluation of seagrass light requirements

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

401 Seagrass Z_c estimates were obtained for 267 locations in Choctawhatchee Bay, 553
402 locations in Tampa Bay, and 37 locations in the Indian River Lagoon (Table 4 and Figs. 7 to 9).

403 Mean $Z_{c,max}$ for each bay was 2.5, 1.7, and 1.3 m for Choctawhatchee Bay, Tampa Bay, and
404 Indian River Lagoon, respectively, with all values being significantly different between bays
405 (ANOVA, $F = 331.1$, $df = 2, 854$, $p < 0.001$, followed by Tukey multiple comparison,
406 $p < 0.001$ for all). Generally, spatial variation in $Z_{c,max}$ followed variation in light requirements
407 for broad spatial scales with more seaward segments or areas near inlets having lower light
408 requirements. Mean light requirements were significantly different between all bays (ANOVA,
409 $F = 451.6$, $df = 2, 854$, $p < 0.001$, Tukey $p < 0.001$ for all), with a mean requirement of 46.9%
410 for Choctawhatchee Bay, 30.6% for Tampa Bay, and 13.4% for Indian River Lagoon. Significant
411 differences in light requirements between segments within each bay were also observed
412 (ANOVA, $F = 29.9$, $df = 2, 264$, $p < 0.001$ for Choctawhatchee Bay, $F = 82.9$, $df = 3, 549$,
413 $p < 0.001$ for Tampa Bay, $F = 7.6$, $df = 6, 30$, $p < 0.001$ for Indian River Lagoon). Post-hoc
414 evaluation of all pair-wise comparisons of mean light requirements between segments within each
415 bay indicated that significant differences were apparent for several locations. Significant
416 differences were observed between all segments in Choctawhatchee Bay ($p < 0.001$ for all),
417 except the central and western segments (Fig. 7). Similarly, significant differences in Tampa Bay
418 were observed between all segments ($p < 0.05$ for all), except Middle Tampa Bay and Old Tampa
419 Bay (Fig. 8). Finally, for the Indian River Lagoon, significant differences were observed only
420 between the Lower Central Indian River Lagoon and the Upper ($p < 0.001$) and Lower Mosquito
421 Lagoons ($p = 0.023$), the Lower Indian River Lagoon and the Upper ($p < 0.001$) and Lower
422 Mosquito Lagoons ($p = 0.013$), and the Upper Central Indian River and the Upper Mosquito
423 Lagoon ($p = 0.018$) (Fig. 9). Small sample sizes likely reduced the ability to distinguish between
424 segments in the Indian River Lagoon.

425 **4 Discussion**

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

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

445 **4.1 Evaluation of the algorithm**

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

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

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

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

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 desiccation 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.

522 The use of light attenuation data, either as satellite-derived estimates or in situ secchi
523 observations, combined with Z_c estimates provided detailed and previously unavailable
524 characterizations of light requirements within the three estuaries. Requirements were lowest for
525 the Indian River Lagoon, whereas estimates were higher for Tampa Bay and highest for
526 Choctawhatchee Bay. Requirements for the Indian River Lagoon were generally in agreement
527 with other Atlantic coastal systems (Dennison et al. 1993, Kemp et al. 2004), such that
528 requirements typically did not exceed 25% with mean requirements for the whole bay estimated
529 at 13.4%. However, light requirements for Indian River Lagoon were based on secchi
530 observations with uneven spatial and temporal coverage, which potentially led to an incomplete
531 description of true variation in light attenuation. Alternative measures to estimate K_d (e.g.,
532 vertically-distributed PAR sensors) are required when bottom depth is shallower than maximum
533 water clarity, although scalability remains an issue. Conversely, satellite-derived estimates were
534 possible for Tampa and Choctawhatchee Bays where water column depth was sufficient and were
535 preferred over in situ data given more complete spatial coverage. Mean light requirements for
536 Tampa Bay were 30.6% of surface irradiance, which was in agreement with previously reported
537 values (Dixon and Leverone 1995). Light requirements in Lower Tampa Bay were further verified
538 using four locations from Dixon and Leverone (1995). Estimates using the current algorithm with
539 2010 data were within 0.1% of the previously estimated light requirements of 22.5%, although Z_c
540 estimates were deeper suggesting improvements in water clarity. Estimates for Choctawhatchee
541 Bay were substantially higher with a bay-wide average of 46.9%. The relatively higher light
542 requirements for Gulf Coast estuaries, particularly Choctawhatchee Bay, may reflect the need for
543 additional validation data for the conversion of satellite reflectance values to light attenuation.
544 However, estuaries in the northern Gulf of Mexico are typically shallow and highly productive
545 (Caffrey et al. 2013), such that high light requirements may in fact be related to the effects of high
546 nutrient loads on water clarity. Further evaluation of seagrass light requirements in the northern
547 Gulf of Mexico could clarify the extent to which our results reflect true differences relative to
548 other coastal regions.

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

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

570 4.3 Conclusions

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

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

587 Spatially-resolved Z_c estimates can be a preliminary source of information for developing a more
588 detailed characterization of seagrass habitat requirements and the potential to develop broad-scale
589 descriptions has been facilitated as a result. Specifically, ??? developed a more general approach
590 for estimating Z_c for each coastal segment of Florida such that data are available to apply the
591 current method on a much broader scale. Applications outside of Florida are also possible given
592 the minimal requirements for geospatial data products to estimate depth of 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. 2013. 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: refining
624 the way we consider, gather, and interpret patterns. Aquatic Biology, 5(2):157–166.
- 625 ESRI (Environmental Systems Research Institute). 2012. ArcGIS v10.1. ESRI, Redlands,
626 California.

- 627 (FLDEP) Florida Department of Environmental Protection. 2012. Site-specific information in
628 support of establishing numeric nutrient criteria for Choctawhatchee Bay. Technical report,
629 Florida Department of Environmental Protection, Tallahassee, Florida.
- 630 Greve T, Krause-Jensen D. 2005. Stability of eelgrass (*Zostera marina L.*) depth limits: influence
631 of habitat type. *Marine Biology*, 147(3):803–812.
- 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):1–15.

- 661 Lottig NR, Wagner T, Henry EN, Cheruvilil 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):1–8.
- 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 RDCT (R Development Core Team). 2015. R: A language and environment for statistical
668 computing, v3.2.0. R Foundation for Statistical Computing, Vienna, Austria.
669 <http://www.R-project.org>.
- 670 Søndergaard M, Phillips G, Hellsten S, Kolada A, Ecke F, Mäemets H, Mjelde M, Azzella MM,
671 Oggioni A. 2013. Maximum growing depth of submerged macrophytes in European lakes.
672 Hydrobiologia, 704(1):165–177.
- 673 Spears BM, Gunn IDM, Carvalho L, Winfield II, Dudley B, Murphy K, May L. 2009. An
674 evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven,
675 Scotland. Aquatic Botany, 91(2):75–81.
- 676 Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light
677 targets for the Indian River Lagoon system, Florida. Estuaries, 28(6):923–935.
- 678 Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007.
679 Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051
680 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.
- 681 USEPA (US Environmental Protection Agency). 2006. Volunteer estuary monitoring: A methods
682 manual, second edition. Technical Report EPA-842-B-06-003, Washington, DC.
- 683 Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Springer, New York, New
684 York, fourth edition.
- 685 Wagner T, Soranno PA, Cheruvilil KS, Renwick WH, Webster KE, Vaux P, Abbott RJ. 2008.
686 Quantifying sample biases of inland lake sampling programs in relation to lake surface area and
687 land use/cover. Environmental Monitoring and Assessment, 141(1-3):131–147.
- 688 Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay
689 ME, editors, Marine Community Ecology. Sinauer Associates, Sunderland, Massachusetts.
- 690 Woodruff DL, Stumpf RP, Scope JA, Paerl HW. 1999. Remote estimation of water clarity in
691 optically complex estuarine waters. Remote Sensing of Environment, 68(1):41–52.
- 692 Zhu B, Fitzgerald DG, Hoskins SB, Rudstam LG, Mayer CM, Mills EL. 2007. Quantification of
693 historical changes of submerged aquatic vegetation cover in two bays of Lake Ontario with
694 three complementary methods. Journal of Great Lakes Research, 33(1):122–135.

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	1.33	0.81	0.00	2.68
$Z_{c, med}$	2.46	1.71	0.75	0.47	2.90
$Z_{c, max}$	3.66	2.10	0.79	0.74	3.33
OTB					
$Z_{c, min}$	0.61	0.58	0.31	0.00	1.23
$Z_{c, med}$	0.88	0.89	0.29	0.30	1.64
$Z_{c, max}$	1.15	1.20	0.37	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	0.14	0.49	0.00	3.99
OTB	0.44	0.43	0.05	2.30
UIRL	0.04	0.08	0.00	0.98
WCB	0.20	0.20	0.06	0.99

^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	130	2.4	0.3	0.4	3.4	46.6	10.1	10.6	86.2
ECB	7	0.8	0.1	0.7	0.9	70.9	5.3	64.8	80.0
WCB	130	2.6	0.2	1.9	2.9	45.9	6.3	23.4	68.0
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	40	1.3	0.1	1.1	1.4	31.9	6.1	16.0	44.8
LTB	143	2.2	0.4	1.7	3.4	24.9	6.7	10.5	39.4
MTB	221	1.8	0.4	1.2	2.4	29.4	8.0	12.9	53.6
OTB	149	1.2	0.1	1.0	1.3	37.4	5.4	18.8	48.7

^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.

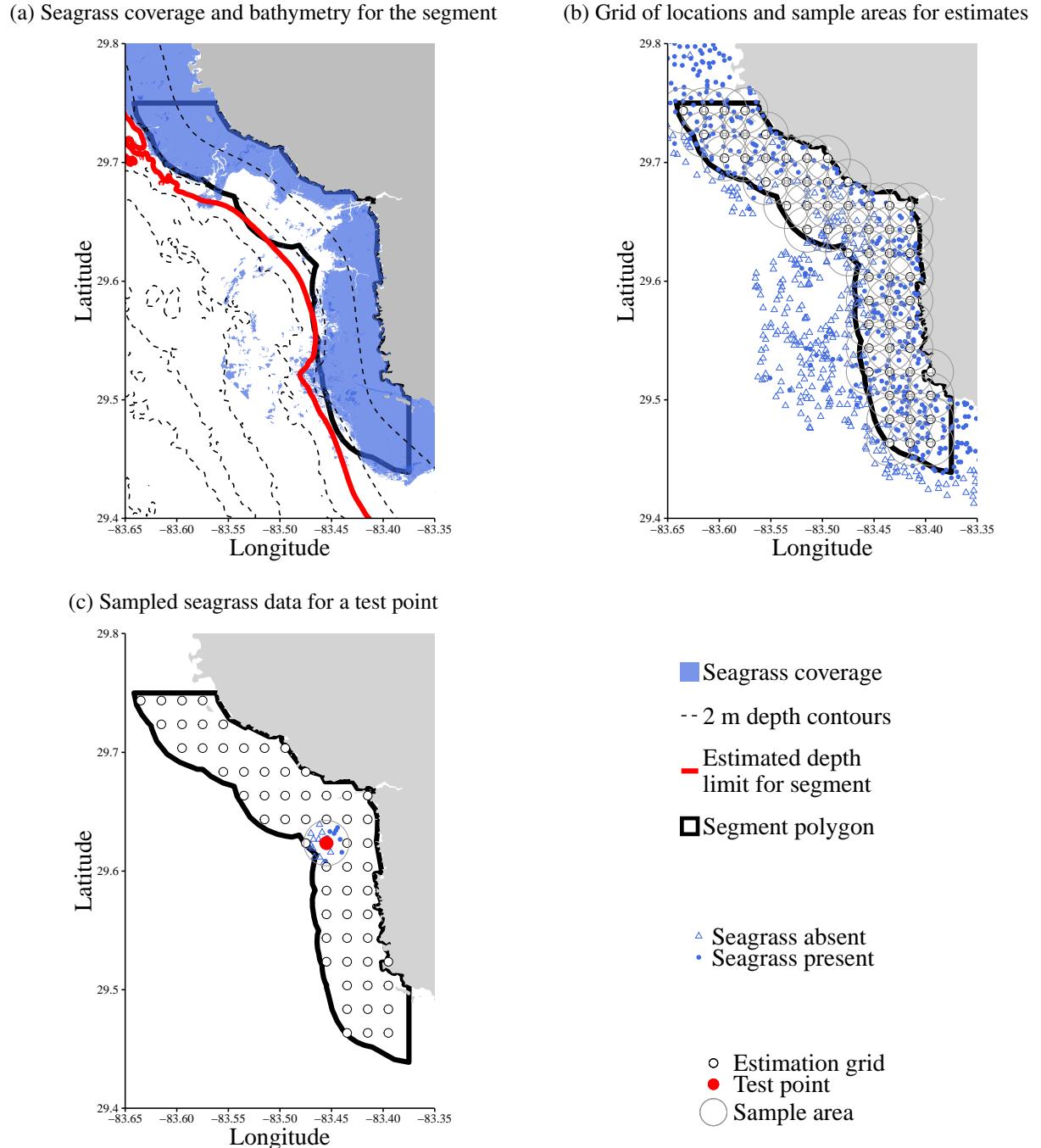


Fig. 1: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 1a shows the seagrass coverage and depth contours at 2 meter intervals, including the whole segment estimate for depth of colonization. Fig. 1b shows a grid of sampling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

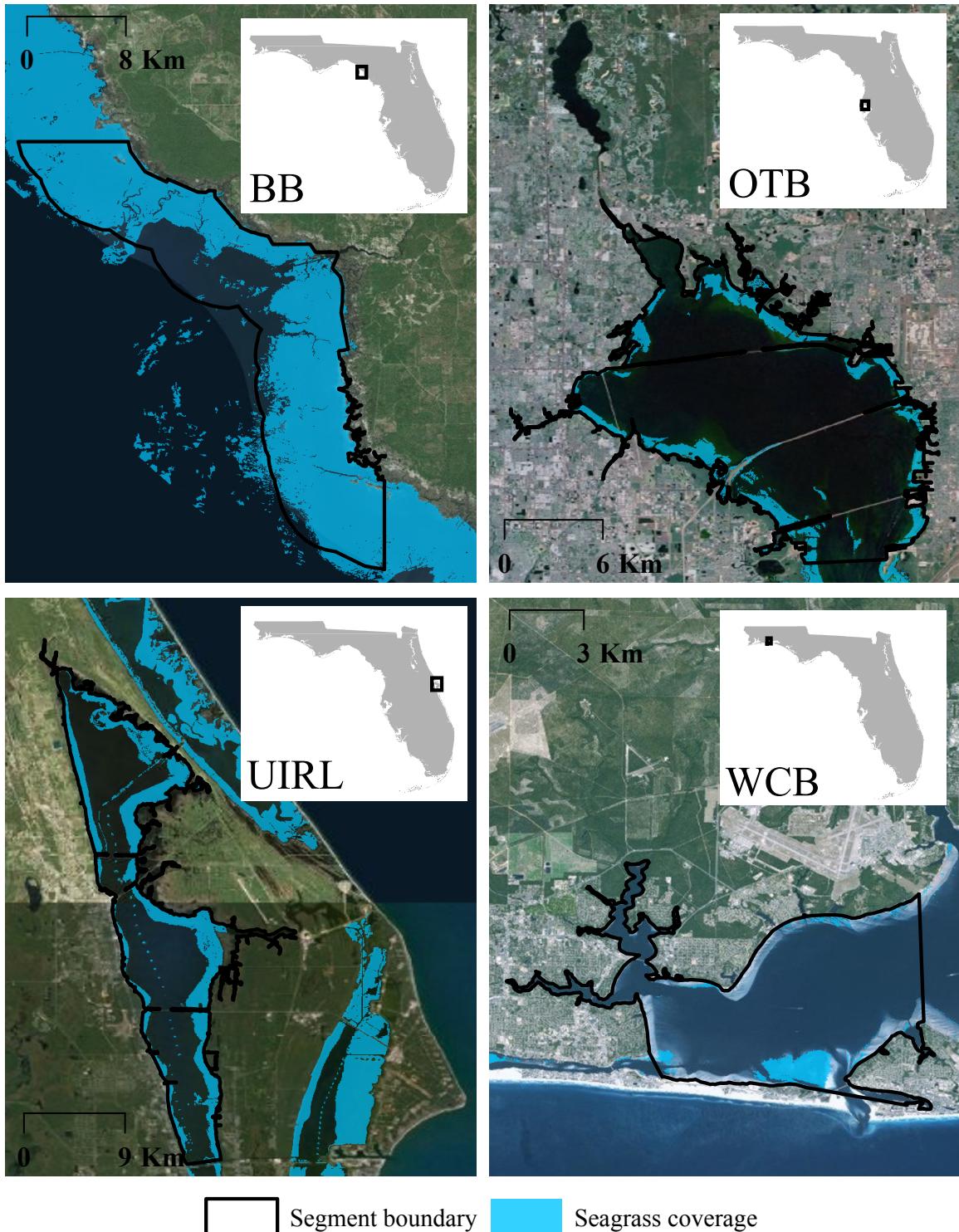


Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

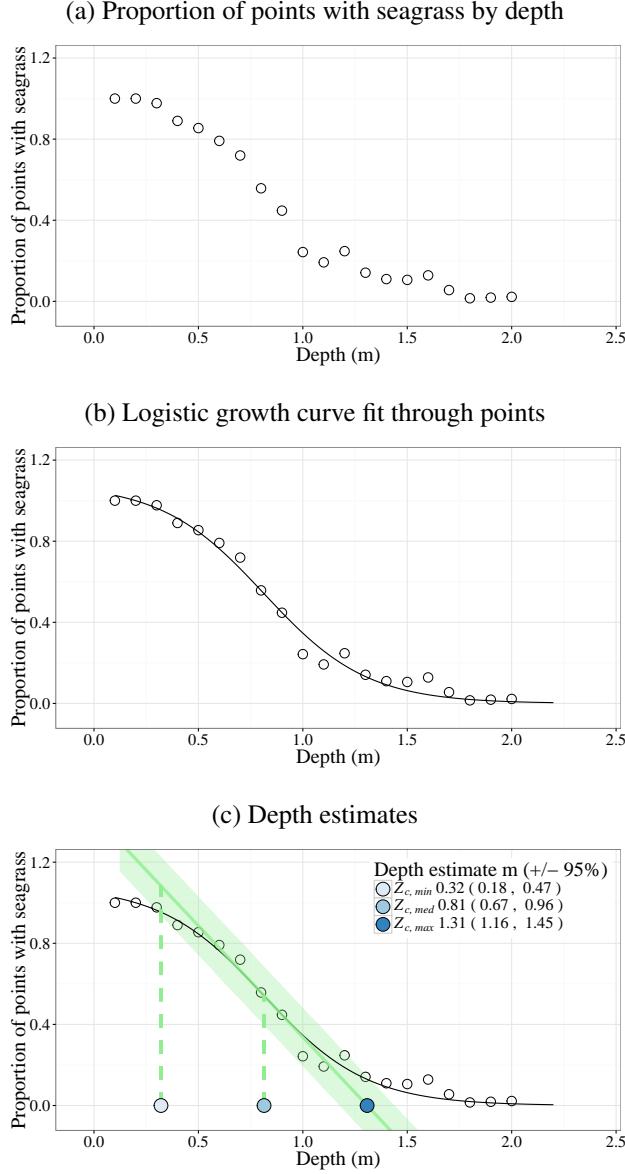


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test location in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit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

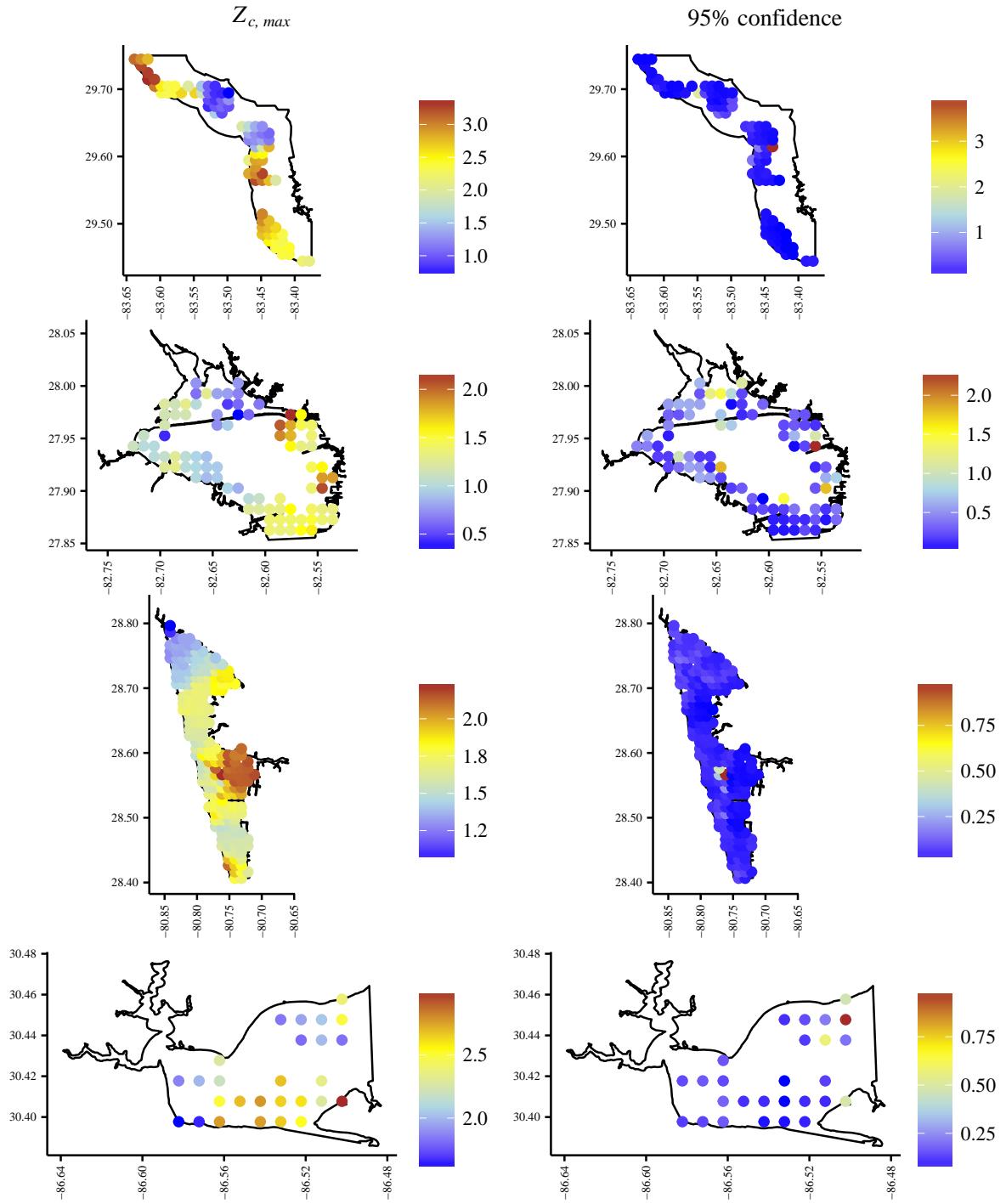


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ($Z_{c, max}$) estimates are on the left and corresponding widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each segment,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

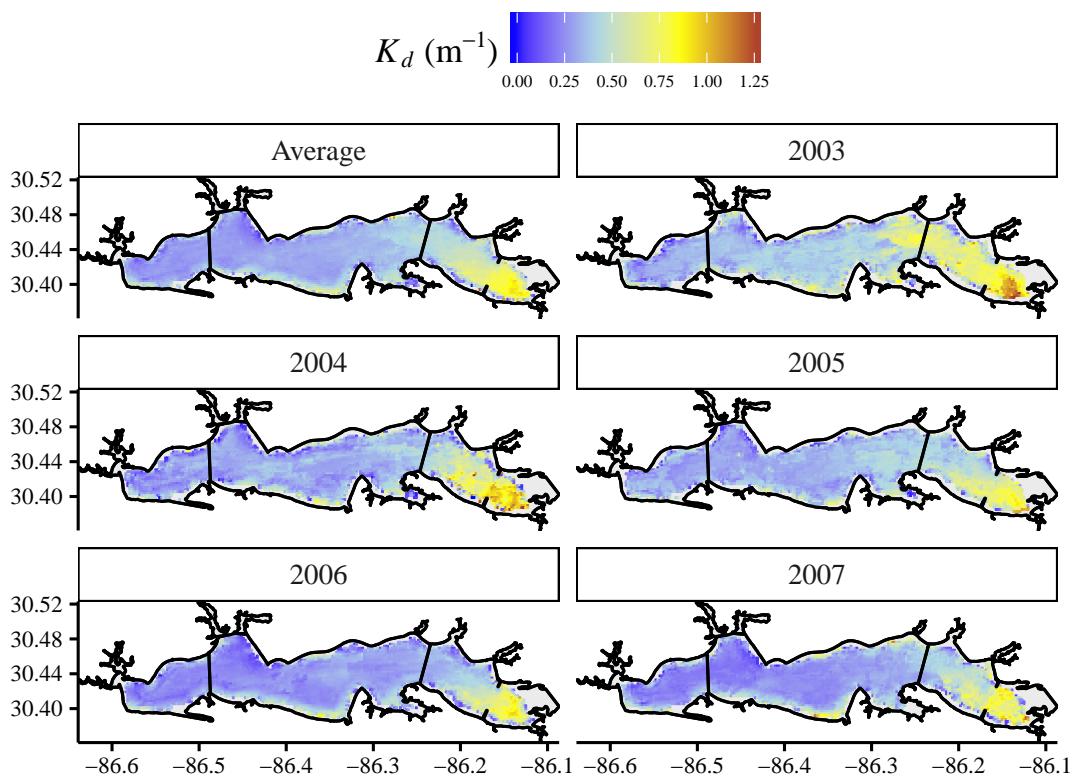


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment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

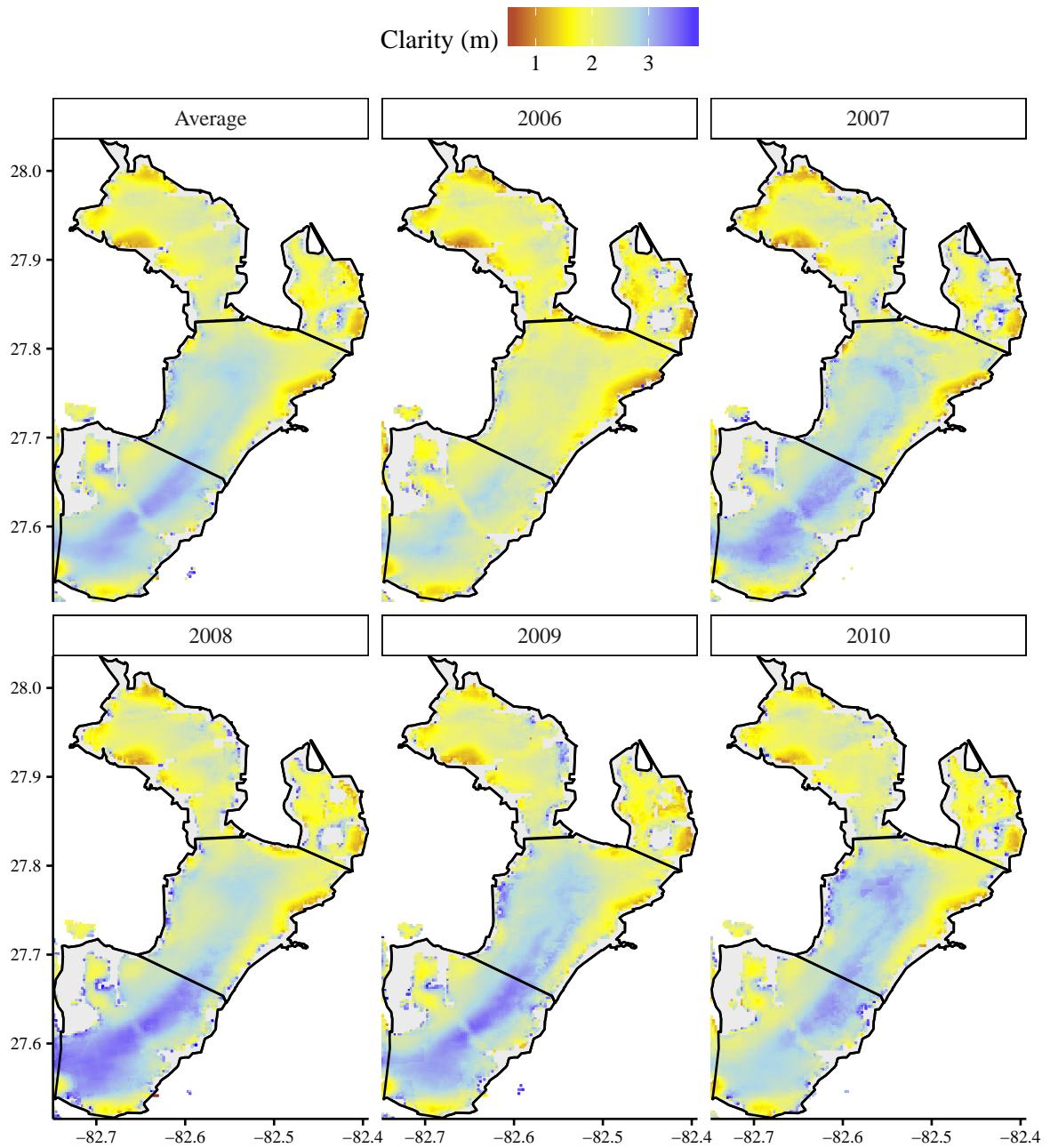


Fig. 6: Satellite estimated water clarity for Tampa Bay. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

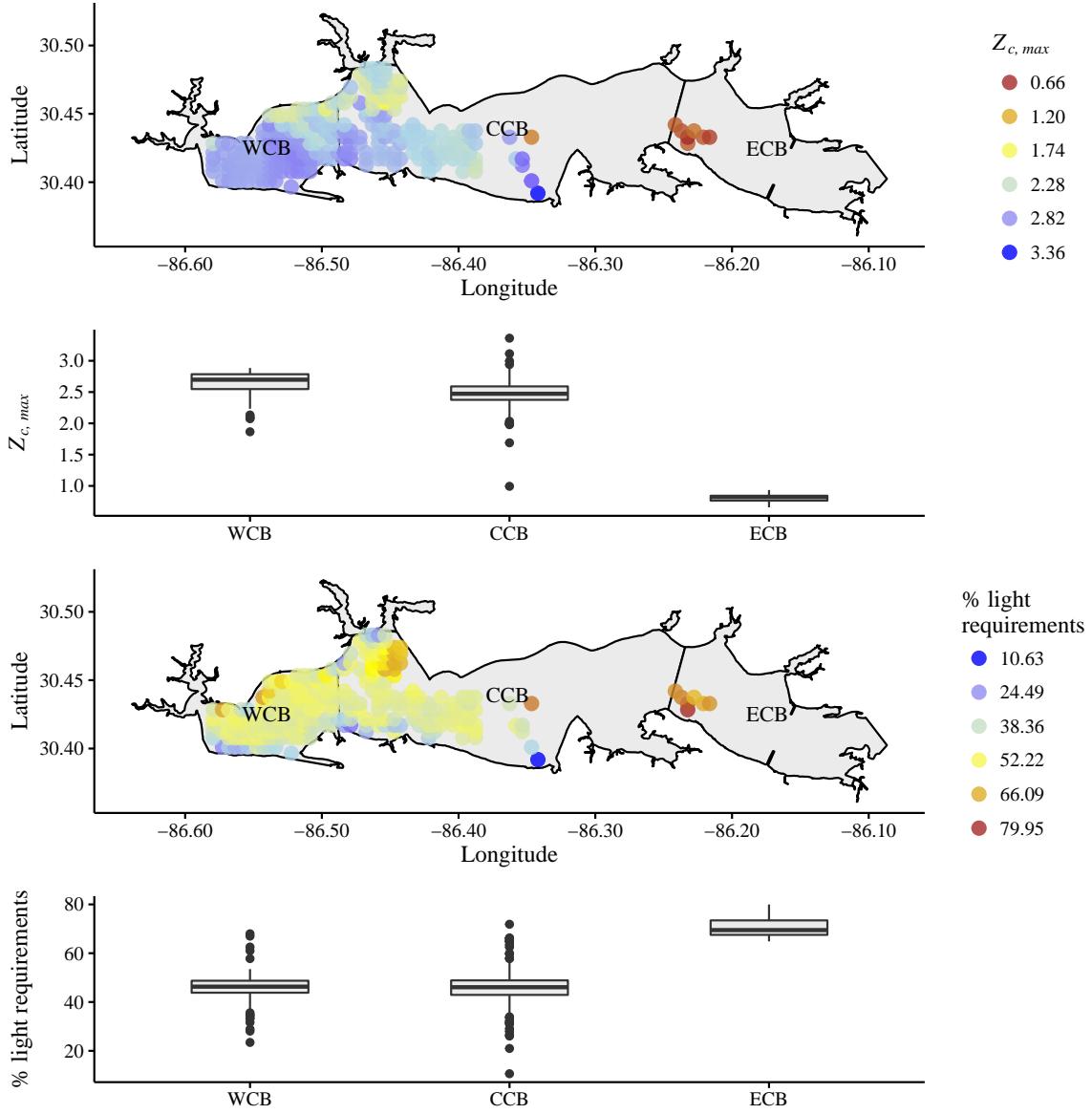


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.04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

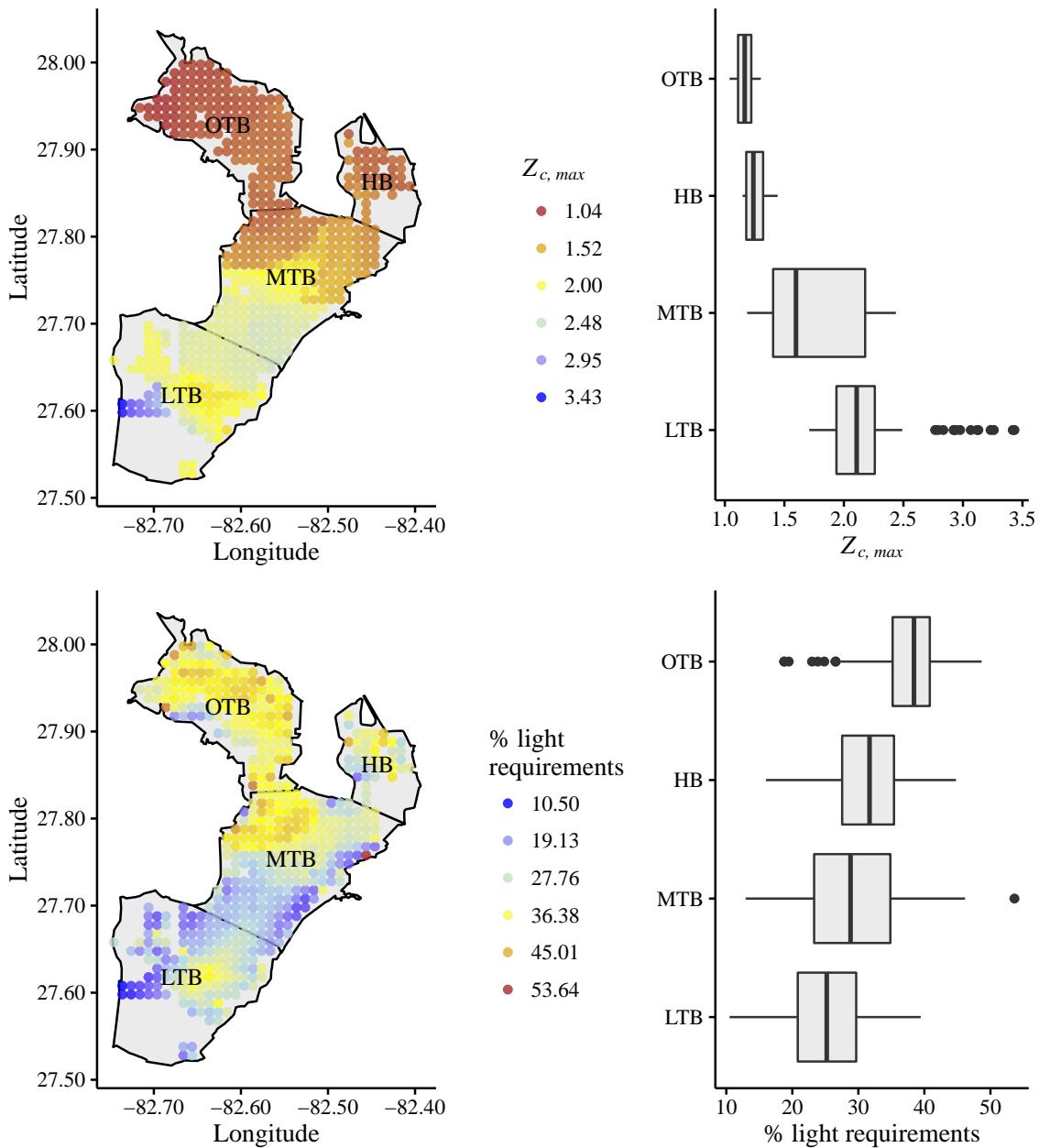


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees.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

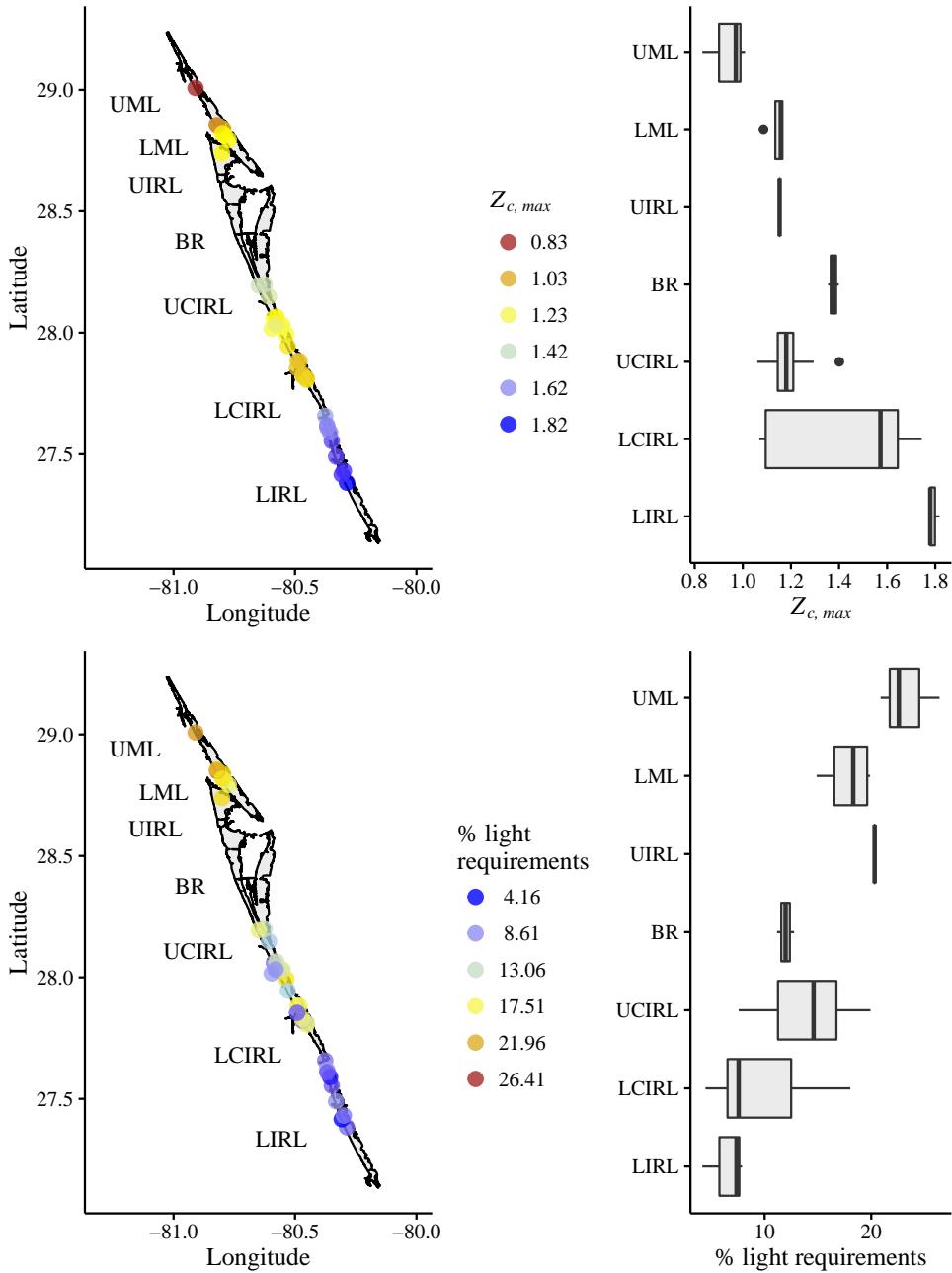


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment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