

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

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1 Introduction

Seagrasses are ecologically valuable components of aquatic systems that serve a structural and functional role in shaping aquatic habitat. These ‘ecosystem engineers’ often govern multiple characteristics of aquatic systems through direct and indirect interactions with additional components (Jones et al. 1994, Koch 2001). For example, seagrass beds create desirable habitat for juvenile fish and invertebrates by reducing wave action and stabilizing sediment (Williams and Heck 2001, Hughes et al. 2009). Seagrasses also respond to changes in water clarity through direct physiological linkages with light availability. Seagrass communities in highly productive aquatic systems may be light-limited as increased nutrient loading may contribute to reductions in water clarity through increased algal concentration (Duarte 1995). Empirical relationships between nutrient loading, water clarity, light requirements, and the maximum depth of seagrass colonization have been identified (Duarte 1991, Kenworthy and Fonseca 1996, Choice et al. 2014) and are often used to characterize light regimes sufficient to maintain habitat through increased seagrass coverage (Steward et al. 2005). Seagrass depth limits have also been used to establish quantitative criteria for nutrient load targets for the maintenance of water quality (Janicki and Wade 1996). Seagrasses are integrative of system-wide conditions over time in relation to changes in nutrient regimes (Duarte 1995) and are often preferred biological endpoints to describe ecosystem response to perturbations relative to more variable taxa (e.g., phytoplankton). Quantifying the relationship of seagrasses with water clarity is a viable means of understanding ecological characteristics of aquatic systems with potential insights into resilience and stability of system response to disturbance (Greve and Krause-Jensen 2005).

A variety of techniques have been developed for estimating seagrass depth limits as a basis for understanding water quality dynamics and developing a more robust description of aquatic habitat. Such efforts have been useful for site-specific approaches where the analysis needs are driven by a particular management or research question (e.g., Iverson and Bittaker 1986, Hale et al. 2004). However, a lack of standardization among methods has prevented broad-scale comparisons between regions and has even contributed to discrepancies between measures of depth limits based on the chosen technique. For example, seagrass depth limits based on in situ techniques can vary with the sampling device (Spears et al. 2009). Seagrass depth limits

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

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

63 factors that limit seagrass growth.

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

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

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

98 **2 Methods**

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

115 **2.1 Data sources**

116 **2.1.1 Study sites**

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

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

129 **2.1.2 Seagrass coverage and bathymetry**

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

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

{acro:EPA}

{sec:data}

{acro:DEM}

{acro:NAV}

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

156 **2.1.3 Water clarity**

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

178 **2.2 Flexible estimation of seagrass depth of colonization for finite areas**

179 The general approach to estimating seagrass depth of colonization uses combined seagrass
180 coverage maps and bathymetric depth data described above. The combined layer used for analysis
181 was a point shapefile with attributes describing location (latitude, longitude, segment), depth (m),

and seagrass (present, absent). Seagrass Z_c values are estimated from these data by quantifying the proportion of points with seagrass at each observed depth. Three unique measures describing seagrass depth limits obtained from these data are minimum ($Z_{c,min}$), median ($Z_{c,med}$), and maximum ($Z_{c,max}$) depth of colonization. Operationally, these terms describe characteristics of the seagrass coverage map with quantifiable significance. $Z_{c,max}$ is defined as the deepest depth at which a significant coverage of mappable seagrasses occurred independent of outliers, whereas $Z_{c,med}$ 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. Specific methods for estimating each Z_c value using spatially-resolved information are described below.

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 (Fig. 1). The estimate for each location is quantified from a plot of the proportion of sampled points that contain seagrass at decreasing 0.1 meter depth bins from the surface to the maximum observed depth in the sample (Fig. 3a). Although the chosen radius for selecting depth points is problem-specific, the minimum radius should be chosen to sample a sufficient number of points for estimating Z_c . In general, an appropriate radius will produce a plot that indicates a decrease in the proportion of points that are occupied by seagrass with increasing depth. If more than one location is used to estimate Z_c , appropriate radii for each point would have minimal overlap with the seagrass depth data sampled by neighboring points.

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 and asymptotic at the minimum and maximum depths of colonization. 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

210 characteristics. The model has the following form:

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

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

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

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

238 2.3 Estimating uncertainty in depth of colonization estimates

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

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

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

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

262 The algorithm for estimating Z_c was implemented custom-made and pre-existing
263 functions in program R. Nonlinear least squares models were based on the `nls` and `SSlogis`

264 functions that used a self-starting logistic growth model (Bates and Chambers 1992, R
265 Development Core Team 2014). Multivariate normal distributions used to evaluate uncertainty
266 were simulated using functions in the MASS package (Venables and Ripley 2002). Geospatial
267 data were imported and processed using functions in the rgeos and sp packages (Bivand et al.
268 2008, Bivand and Rundel 2014).

269 **2.4 Evaluation of spatial heterogeneity of seagrass depth limits**

270 Spatially-resolved estimates for seagrass Z_c were obtained for each of the four coastal
271 segments described above. Segment-wide estimates obtained using all data were used as a basis
272 of comparison such that departures from these values at smaller scales were evidence of spatial
273 heterogeneity in seagrass growth patterns and improved clarity of description in depth estimates.
274 A sampling grid of locations for estimating each of the three depth values in Fig. 3 was created
275 for each segment. The grid was masked by the segment boundaries, whereas seagrass depth
276 points used to estimate Z_c extended beyond the segment boundaries to allow sampling by grid
277 points that occurred near the edge of the segment. Initial spacing between sample points was
278 chosen arbitrarily as 0.01 decimal degrees, which is approximately 1 km at 30 degrees N latitude.
279 The sampling radius around each sampling location in the grid was also chosen as 0.02 decimal
280 degrees to allow for complete coverage of seagrass within the segment while also minimizing
281 redundancy of information described by each location. In other words, radii were chosen such
282 that the seagrass depth points sampled by each grid location were only partially overlapped by
283 those sampled by neighboring points, while also ensuring an adequate number of locations were
284 sampled that included seagrass.

285 **2.5 Developing a spatially coherent relationship of water clarity with depth 286 of colonization**

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

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

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

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

where the percent light requirements of seagrass at $Z_{c, max}$ are empirically related to light extinction. A conversion factor is often used to estimate the light extinction coefficient from secchi depth Z_{secchi} , such that $c = K_Z \cdot Z_{secchi}$, where c has been estimated as 1.7 (Poole and Atkins 1929, Idso and Gilbert 1974). Thus, K_Z can be replaced with the conversion factor and Z_{secchi} :

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

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

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

313 **3 Results**

314 **3.1 Segment characteristics and seagrass depth estimates**

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

336 Estimates of seagrass Z_c using a segment-wide approach that did not consider spatially
337 explicit locations indicated that seagrasses generally did not grow deeper than three meters in any
338 of the segments (Table 2). Maximum and median depth of colonization were deepest for the Big
339 Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old Tampa Bay (1.1 and 0.9 m),
340 whereas the minimum depth of colonization was deepest for Choctawhatchee Bay (1.8 m) and
341 shallowest for Old Tampa Bay (0.6 m). Averages of all grid-based estimates for each segment

were different than the segment wide estimates, which suggests potential bias associated with using a whole segment as a relevant spatial unit for estimating depth of colonization. In most cases, the averages of all grid-based estimates were less than the whole segment estimates, suggesting the latter provided an over-estimate of seagrass growth limits. For example, the average of all grid estimates for $Z_{c, max}$ in the Big Bend region suggested seagrasses grew to approximately 2.1 m, which was 1.6 m less than the whole segment estimate. This reduction is likely related to improved resolution of seagrass depth limits near the outflow of the Steinhatchee river. Although reductions were not as severe for the average grid estimates for the remaining segments, considerable within-segment variation was observed depending on grid location. For example, the deepest estimate for $Z_{c, min}$ (2 m) in the Indian River Lagoon exceeded the average of all grid locations for $Z_{c, max}$ (1.7 m). $Z_{c, min}$ also had minimum values of zero meters for the Big Bend and Old Tampa Bay segments, suggesting that seagrasses declined continuously from the surface for several locations.

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

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

374 Uncertainty for estimates of $Z_{c,max}$ indicated that confidence intervals were generally
375 acceptable (i.e., greater than zero), although the ability to discriminate between the three depth
376 estimates varied by segment (Fig. 5 and Table 3). Mean uncertainty for all estimates in each
377 segment measured as the width of a 95% confidence interval was 0.2 m. Greater uncertainty was
378 observed for Choctawhatchee Bay (mean width of all confidence intervals was 0.5 m) and Old
379 Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Indian River Lagoon (0.1 m)
380 segments. The largest confidence interval for each segment was 1.4 m for Old Tampa Bay, 1.6 m
381 for Choctawhatchee Bay, 1.8 m for the Big Bend, and 1.8 m for the Indian River Lagoon
382 segments. However, most confidence intervals for the remaining grid locations were much
383 smaller than the maximum in each segment. A comparison of overlapping confidence intervals for
384 $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$ at each grid location indicated that not every measure was unique.
385 Specifically, only 11.1% of grid points in Choctawhatchee Bay and 28.2% in Old Tampa Bay had
386 significantly different estimates, whereas 82% of grid points in the Indian River Lagoon and 95%
387 of grid points in the Big Bend segments had estimates that were significantly different. By
388 contrast, all grid estimates in Choctawhatchee Bay and Indian River Lagoon had $Z_{c,max}$ estimates
389 that were significantly greater than zero, whereas all but 12.4% of grid points in Old Tampa Bay
390 and 8% of grid points in the Big Bend segment had $Z_{c,max}$ estimates significantly greater than
391 zero.

392 3.2 Evaluation of seagrass light requirements

393 Estimates of seagrass depth limits and corresponding light requirements for all segments
394 of Tampa Bay and the Indian River Lagoon indicated substantial variation, both between and
395 within the different bays (Table 4 and Figs. 7 and 8). Seagrass Z_c estimates were obtained for 558
396 locations in Tampa Bay and 50 locations in the Indian River Lagoon where secchi observations
397 were available in the Florida IWR database. Mean secchi depth for all recorded observations was
398 2.3 m ($n = 558$) for Tampa Bay and 1 m ($n = 50$) for Indian River Lagoon. Mean light
399 requirements were significantly different between the bays (two-sided t-test, $t = 18.4$, $df = 62.6$,
400 $p < 0.001$) with a mean requirement of 29.8% for Tampa Bay and 10.6% for Indian River
401 Lagoon. Within each bay, light requirements were significantly different between segments

402 (ANOVA, $F = 104.4$, $df = 3, 554$, $p = 0.00$ for Tampa Bay, $F = 5.2$, $df = 7, 42$, $p = 0.000$ for
403 Indian River Lagoon). However, post-hoc evaluation of all pair-wise comparisons of mean light
404 requirements indicated that significant differences were only observed between a few segments
405 within each bay. Significant differences in Tampa Bay were observed between Old Tampa Bay
406 and Hillsborough Bay (Tukey multiple comparisons, $p = 0.001$). Significant differences in the
407 Indian River Lagoon were observed between the Upper Indian River Lagoon and Banana River
408 ($p = 0.915$), the Upper Indian River Lagoon and Lower Indian River Lagoon ($p = 0.140$), and
409 Upper Indian River Lagoon and Lower St. Lucie ($p = 0.103$) segments. In general, spatial
410 variation of light requirements in Tampa Bay suggested that seagrasses were less light-limited
411 (i.e., lower percent light requirements at $Z_{c, max}$) in Hillsborough Bay and western areas of Lower
412 Tampa Bay near the Gulf of Mexico (Fig. 7). Seagrassess in the Indian River Lagoon were
413 generally less light-limited towards the south and in the Banana River segment (Fig. 8).

414 **4 Discussion**

415 **References**

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

	Big Bend	Choctawhatchee Bay	Old Tampa Bay	Upper Indian R. Lagoon
Year ^a	2006	2007	2010	2009
Latitude	29.61	30.43	27.94	28.61
Longitude	-83.48	-86.54	-82.62	-80.77
Surface area	271.37	59.41	205.50	228.52
Seagrass area	203.02	3.51	24.48	74.89
Depth (mean)	1.41	5.31	2.56	1.40
Depth (max)	3.60	11.90	10.40	3.70
Secchi (mean)	1.34	2.14	1.41	1.30
Secchi (se)	0.19	0.08	0.02	0.02

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

Big Bend: http://atoll.floridamarine.org/Data/metadata/SDE_Current/seagrass_bigbend_2006_poly.htm

Choctawhatchee Bay: http://atoll.floridamarine.org/data/metadata/SDE_Current/seagrass_chotawhatchee_2007_poly.htm

Tampa Bay: http://www.swfwmd.state.fl.us/data/gis/layer_library/category/swim

Indian R. Lagoon: <http://www.sjrwmd.com/gisdevelopment/docs/themes.html>

Table 2: Summary of seagrass depth estimates (m) for each segment using all grid locations in Fig. 4. Whole segment estimates were obtained from all seagrass depth data for each segment.^{tab:est_summ}

Segment ^a	Whole segment	Mean	St. Dev.	Min	Max
BB					
$Z_{c,min}$	1.25	1.40	0.77	0.00	2.68
$Z_{c,med}$	2.46	1.75	0.76	0.47	2.90
$Z_{c,max}$	3.66	2.10	0.80	0.74	3.33
CB					
$Z_{c,min}$	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
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	0.26	0.47	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

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

Table 3: Summary of uncertainty for seagrass depth estimates (m) for each segment using all grid locations in Fig. 5. The uncertainty values are equally applicable to each seagrass depth measure ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$).^{tab:sens_summ}

Segment ^a	Mean	St. Dev	Min	Max
BB	0.12	0.21	0.01	1.75
CB	0.53	0.37	0.12	1.57
OTB	0.38	0.26	0.06	1.40
UIRL	0.10	0.16	0.00	1.83

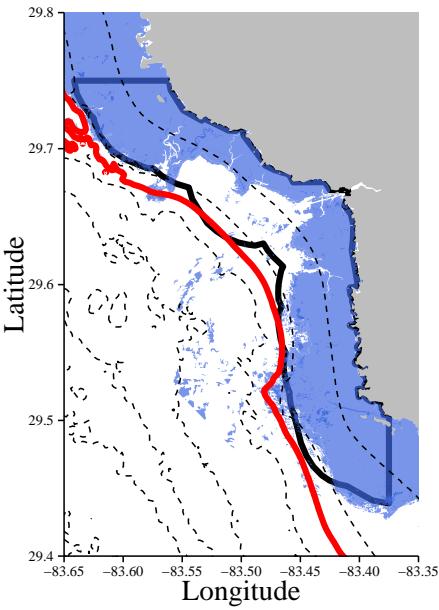
^aBB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon.

Table 4: Summary of water clarity data (Z_{secchi}), depth of colonization ($Z_{c,max}$), and estimated light requirements for bay segments with available data for the Indian River Lagoon and Tampa Bay. Water clarity data were obtained from secchi observations in the Florida Impaired Waters Rule database for all available locations and dates within ten years of the seagrass survey in each bay. Values are minimum and maximum years of secchi data, sample size of secchi data ($n_{Z_{secchi}}$), mean values (m) of secchi data, sample size of seagrass depth estimates ($n_{Z_{c,max}}$) at each unique secchi location, mean $Z_{c,max}$, and estimated % light requirements for each segment. See Figs. 7 and 8 for spatial distribution of the results.^a

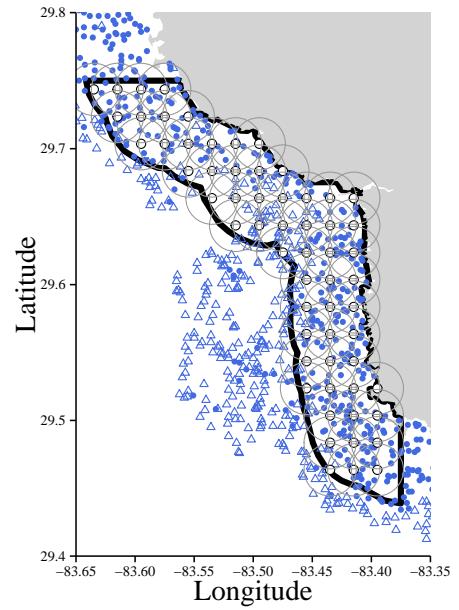
Segment ^a	Min year	Max year	$n_{Z_{secchi}}$	Z_{secchi}	$n_{Z_{c,max}}$	$Z_{c,max}$	% light
Indian River Lagoon							
BR	2000	2009	899	1.06	2	1.05	19.88
LCIRL	2000	2009	644	1.02	12	1.14	14.24
LIRL	2000	2005	111	0.93	6	1.48	7.38
LML	2000	2009	217	1.14	4	0.93	24.52
LSL	2000	2005	52	0.94	3	1.48	8.26
UCIRL	2000	2009	1148	1.14	18	0.89	18.10
UIRL	2000	2009	593	1.30	1	0.94	27.21
UML	2000	2009	258	1.03	4	0.84	28.80
Tampa Bay							
HB	2001	2003	412	1.25	52	1.05	39.61
LTB	2001	2009	807	2.47	152	1.49	36.48
MTB	2001	2009	570	2.19	216	1.30	38.68
OTB	2001	2003	671	1.44	152	0.78	51.36

^aBR: 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, HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

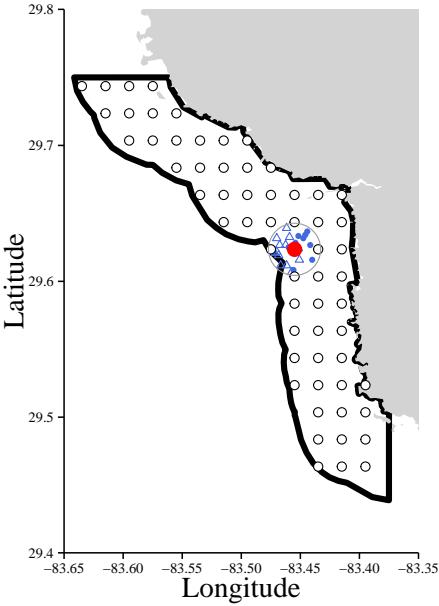
(a) Seagrass coverage and bathymetry for the segment



(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.

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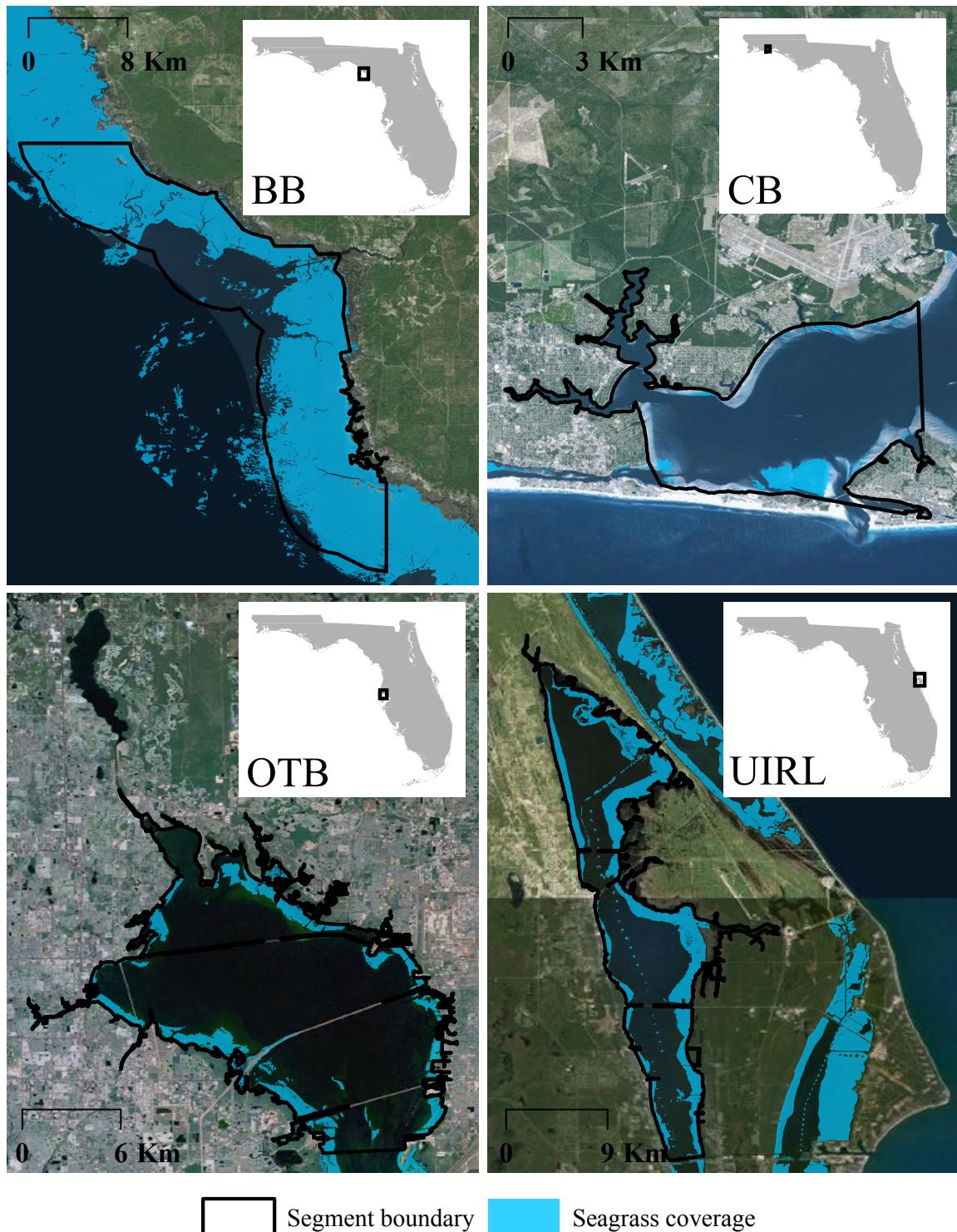
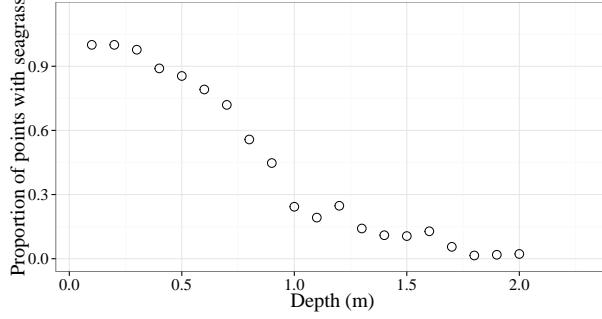


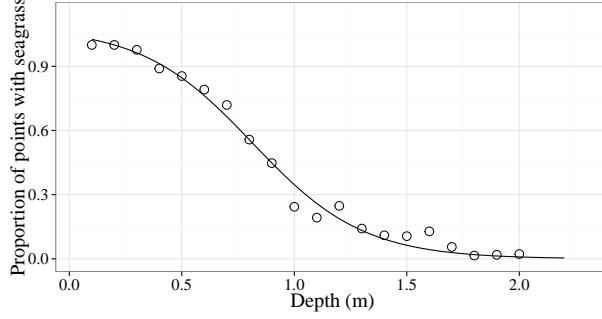
Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (CB: Choctawhatchee Bay), 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), and 2009 (UIRL: Upper Indian R. Lagoon).

{fig:seg_a}

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

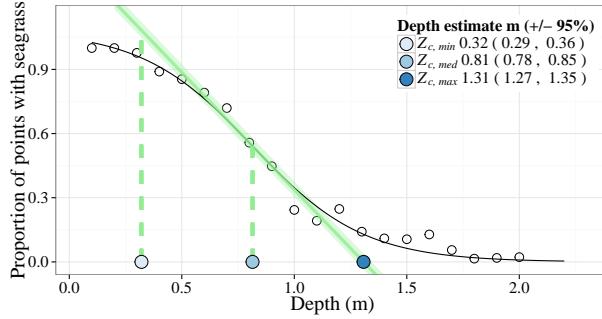


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit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

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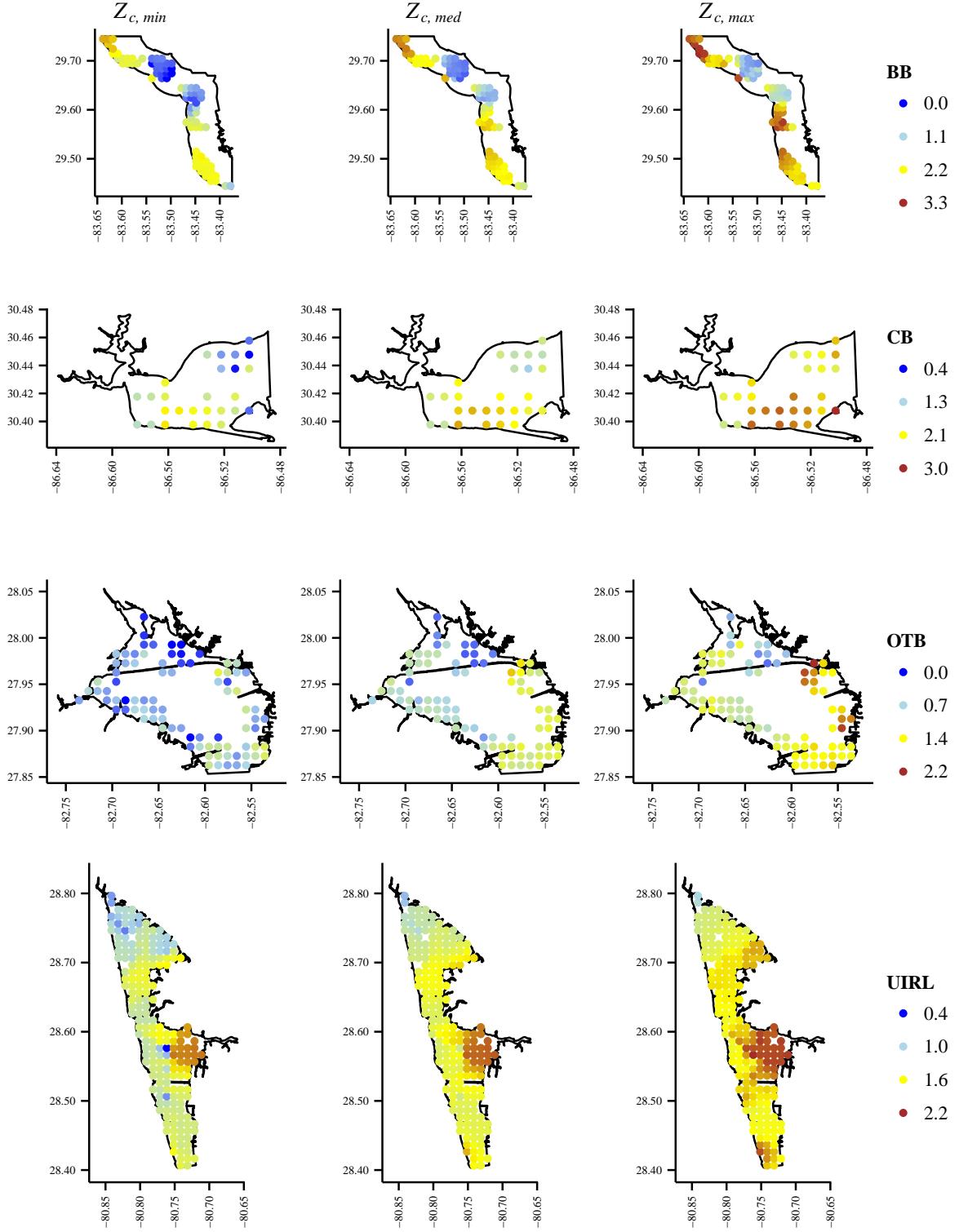


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Estimates include minimum ($Z_{c, \text{min}}$), median ($Z_{c, \text{med}}$), and maximum depth of colonization ($Z_{c, \text{max}}$). Estimates are assigned to grid locations for each segment, where 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. BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon.

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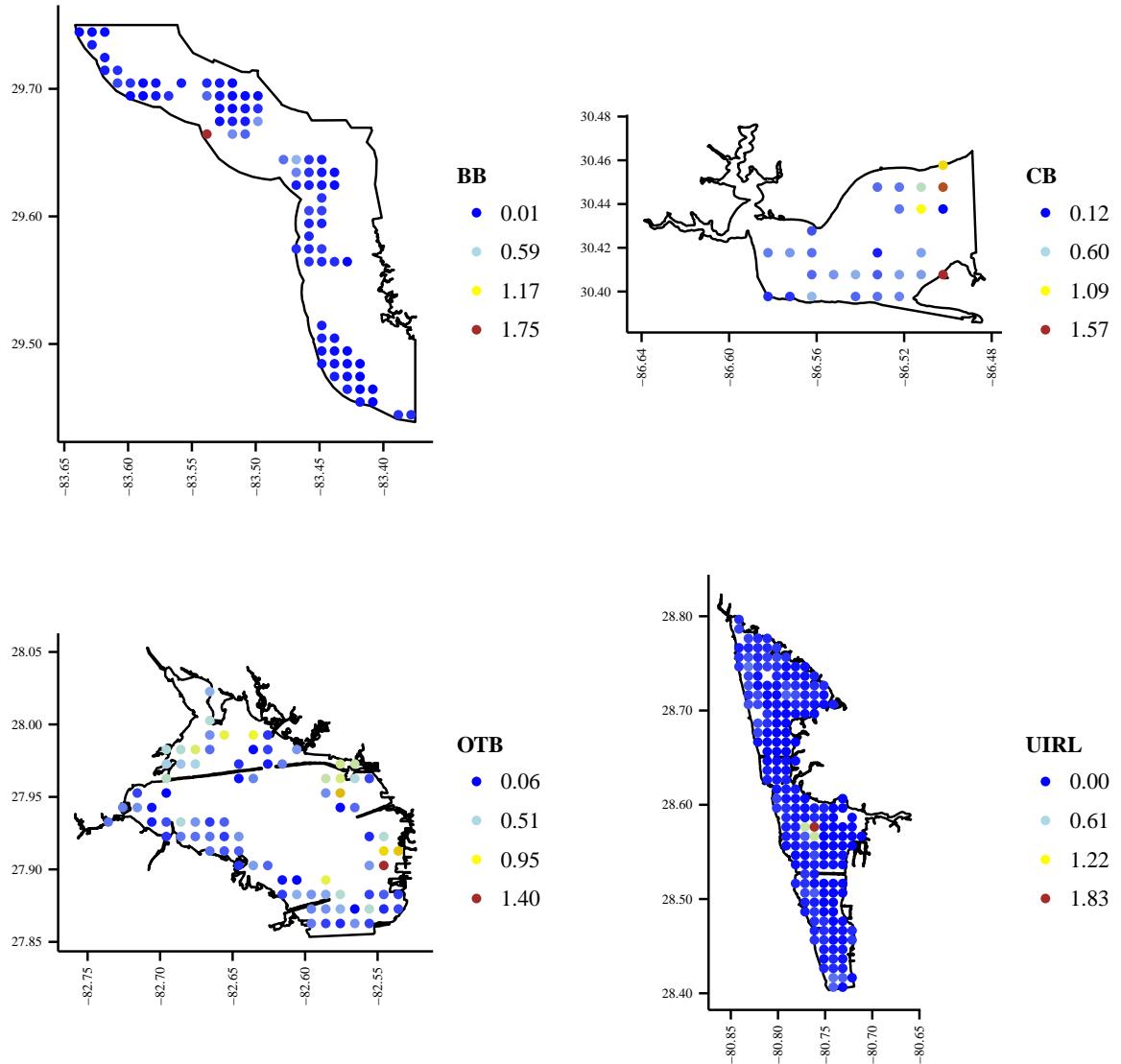


Fig. 5: Size of confidence intervals (m) for depth of colonization estimates in Fig. 4. Points are colored and sized based on the difference between the upper and lower bounds of a 95% confidence interval for all three Z_c estimates ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$). Bounds were obtained using Monte Carlo simulations to estimate uncertainty associated with the inflection point of the estimated logistic curve (Fig. 3) for each sample. BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon.

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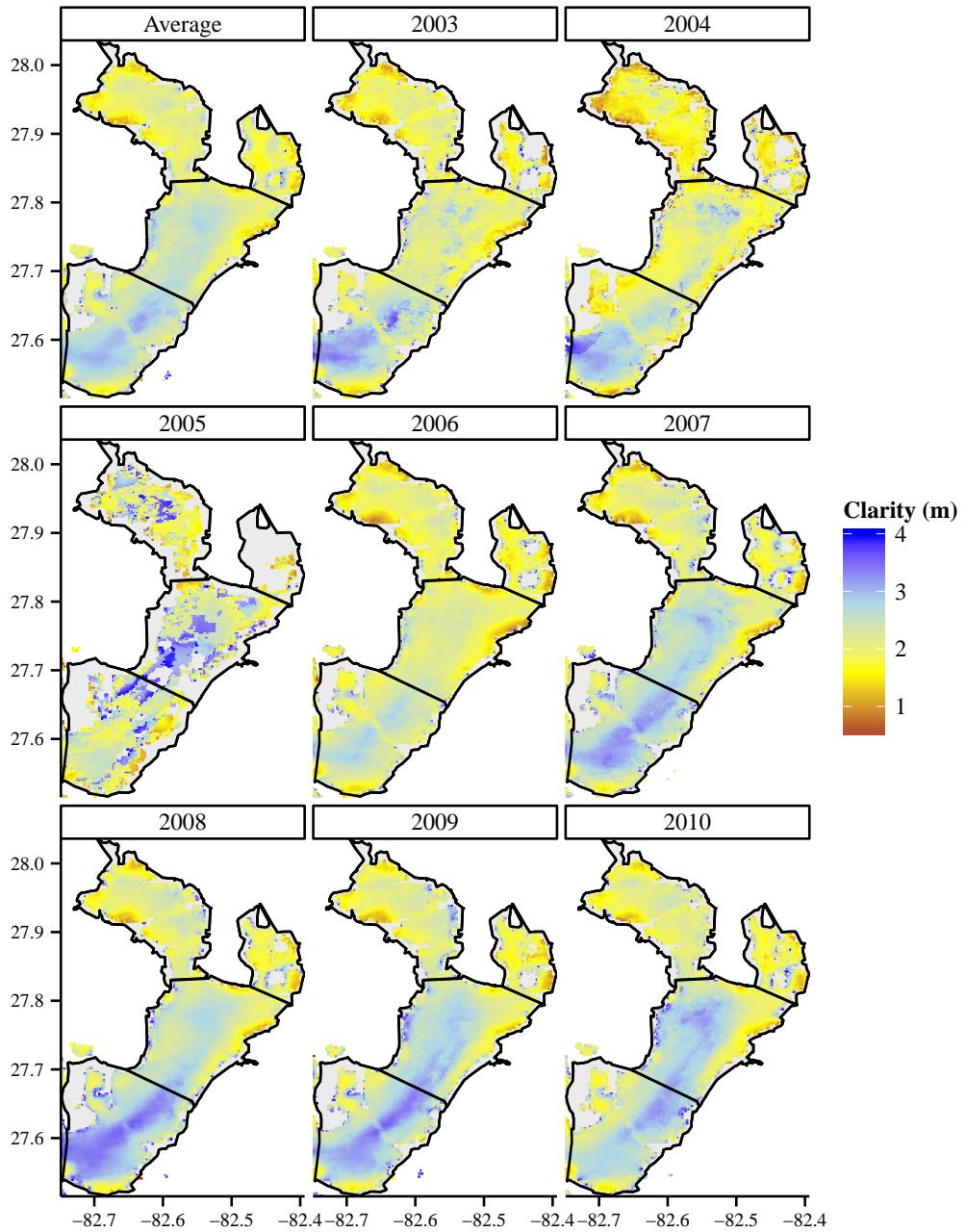


Fig. 6: Satellite estimated water clarity for Tampa Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 7 for segment identification.

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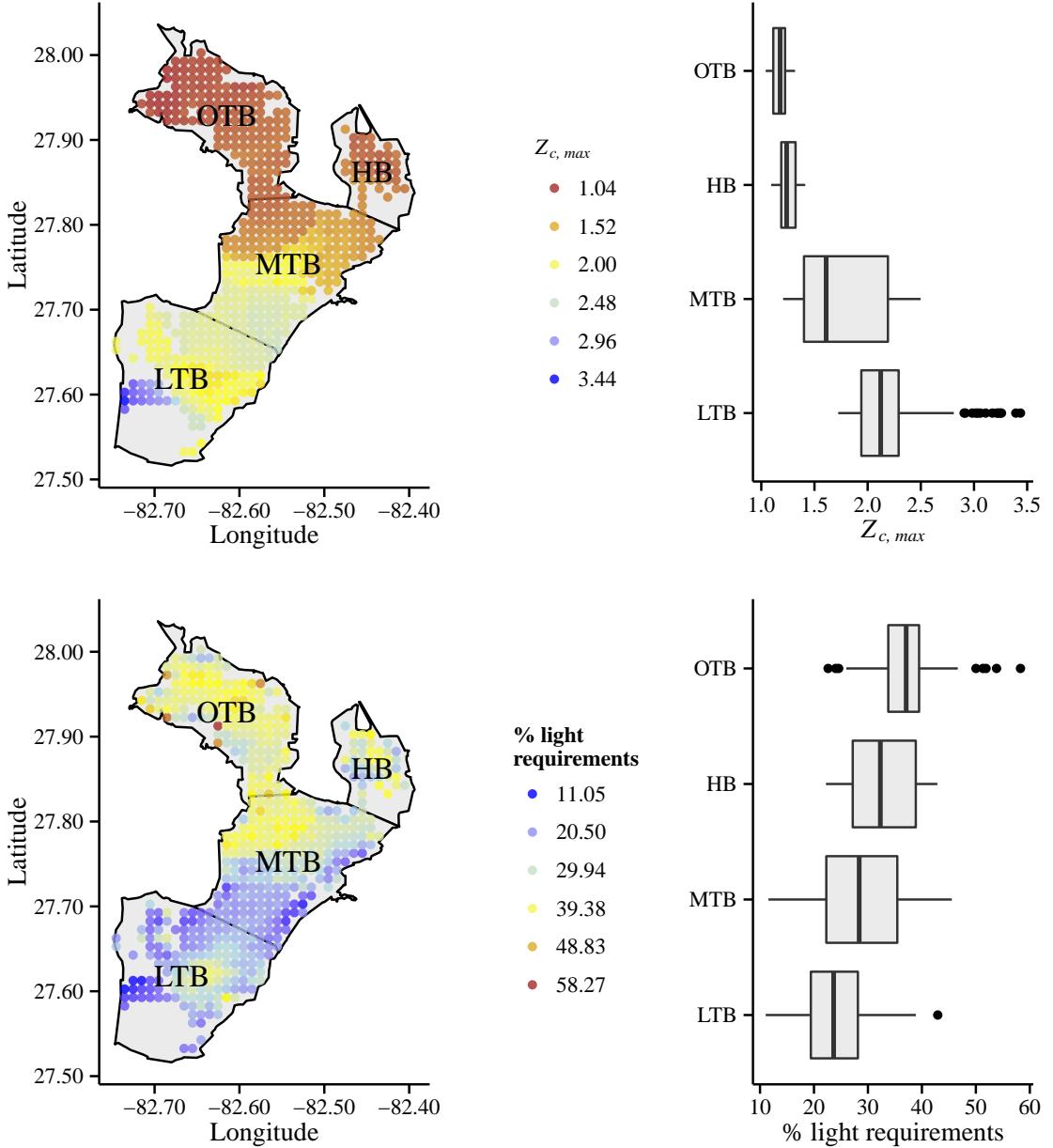


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees. Estimates are also summarized by bay segment as boxplots where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

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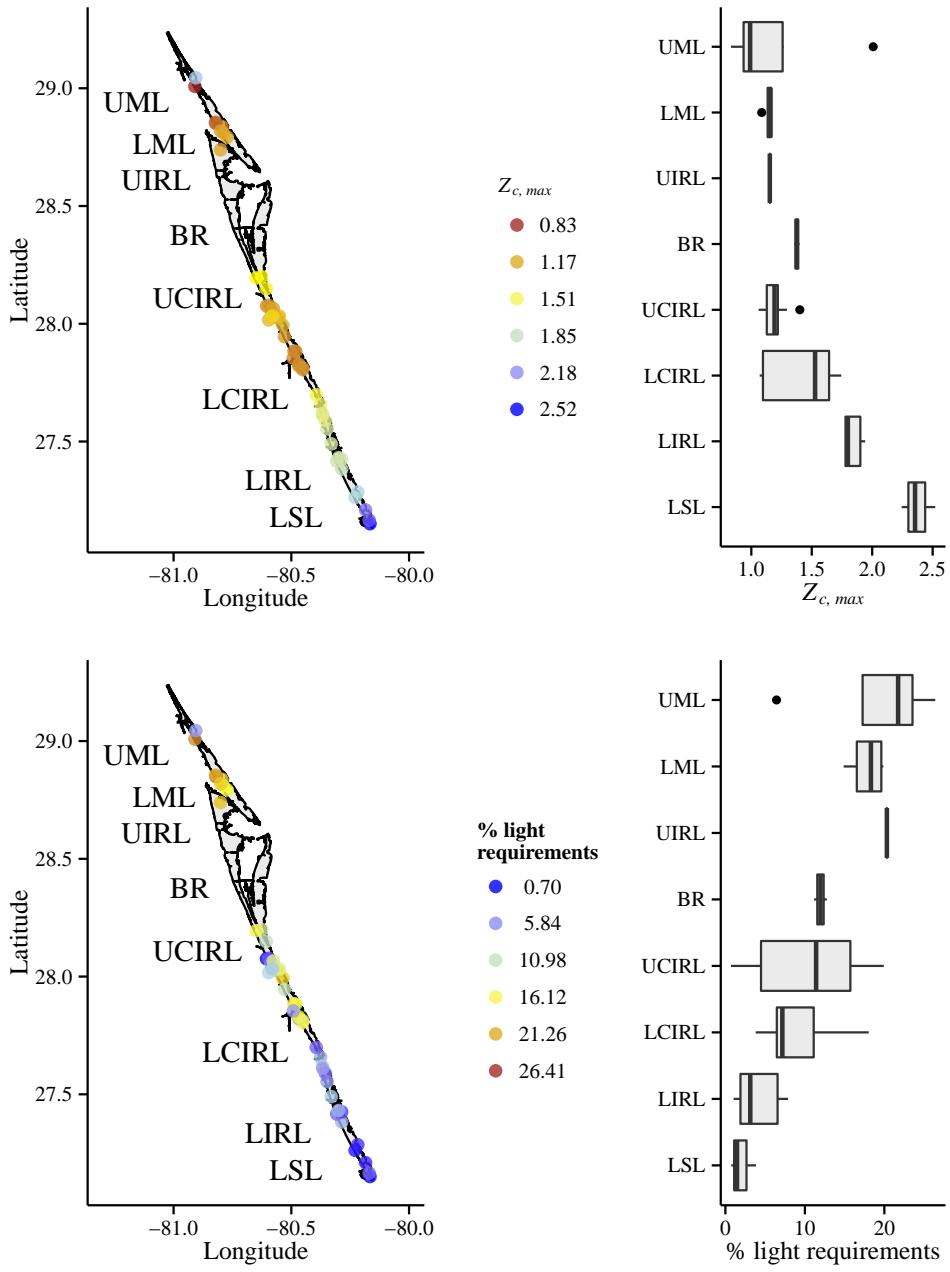


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment 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 0.02 decimal degrees for each secchi location to sample seagrass depth points. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon.

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