

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

93 description of depth limits, water clarity, and light requirements for the case studies. The method
94 is first illustrated using four relatively small areas of larger coastal regions followed by extension
95 to entire bay systems to characterize spatial variation in light requirements. Overall, these
96 methods are expected to inform the description of seagrass growth patterns to develop a more
97 ecologically relevant characterization of aquatic habitat. The method is applied to data from
98 Florida although the technique is easily transferable to other regions with comparable data.

99 **2 Methods**

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

116 **2.1 Data sources**

117 **2.1.1 Study sites**

118 Four locations in Florida were chosen for the analysis: the Big Bend region (northeast
119 Gulf of Mexico), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf Coast), and Indian
120 River Lagoon (east coast) (Table 1 and Fig. 2). These locations represent different geographic
121 regions in the state, in addition to having available data and observed gradients in water clarity

122 that contribute to heterogeneity in seagrass growth patterns. Coastal regions and estuaries in
123 Florida are partitioned into distinct spatial units based on a segmentation scheme developed by
124 US Environmental Protection Agency (EPA) for the development of numeric nutrient criteria. {acro:EPA}
125 Site-specific estimates of seagrass depth colonization and light requirements are the primary
126 focus of the analysis, with emphasis on improved clarity of description with changes in spatial
127 context. As such, estimates that use management segments as relevant spatial units are used as a
128 basis of comparison to evaluate variation in growth patterns at difference scales. The analysis
129 focuses on Choctawhatchee Bay (central panhandle), the big bend region (northeast
130 panhandle), Tampa Bay (west coast), and Indian River Lagoon (east coast). One segment within
131 each region is first evaluated to illustrate use of the method and variation at relatively small spatial
132 scales. The segments included a location near the outflow of the Steinhatchee River for the Big {acro:BB}
133 Bend (BB) region, Old Tampa Bay (OTB), Upper Indian River Lagoon (UIRL), and Western {acro:OTB}
134 Choctawhatchee Bay (WCB) Fig. 2). A second analysis focused on describing seagrass depth
135 limits for the entire area of each bay (Choctawhatchee Bay, Tampa Bay, and the Indian River
136 Lagoon) to develop a spatial description of light requirements.

137 **2.1.2 Seagrass coverage and bathymetry**

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

148 Bathymetric depth layers for each location were obtained from the National Oceanic and
149 Atmospheric Administration's (NOAA) National Geophysical Data Center
150 (<http://www.ngdc.noaa.gov/>) as either Digital Elevation Models (DEMs) or raw sounding data
151 from hydroacoustic surveys. Tampa Bay data provided by the Tampa Bay National Estuary {acro:DEM}

152 Program are described in [Tyler et al. \(2007\)](#). Bathymetric data for the Indian River Lagoon were
153 obtained from the St. John's Water Management District ([Coastal Planning and Engineering](#)
154 [1997](#)). NOAA products were referenced to mean lower low water, whereas Tampa Bay data were
155 referenced to the North American Vertical Datum of 1988 (NAVD88) and the Indian River
156 Lagoon data were referenced to mean sea level. Depth layers were combined with seagrass
157 coverage layers using standard union techniques for raster and vector layers in ArcMap 10.1
158 ([Environmental Systems Research Institute 2012](#)). To reduce computation time, depth layers were
159 first masked using a 1 km buffer of the seagrass coverage layer. Raster bathymetric layers were
160 converted to vector point layers to combine with seagrass coverage maps, described below. All
161 spatial data were referenced to the North American Datum of 1983 as geographic coordinates.
162 Depth values in each seagrass layer were further adjusted from the relevant vertical reference
163 datum to local mean sea level (MSL) using the NOAA VDatum tool (<http://vdatum.noaa.gov/>).
164 {acro:NAV}

2.1.3 Water clarity and light attenuation

165 Seagrass light requirements can be estimated by evaluating spatial relationships between
166 depth of colonization and water clarity. These relationships were explored using Z_c and water
167 clarity estimates for the entire areas of Choctawhatchee Bay, Tampa Bay, and the Indian River
168 Lagoon. Limited data describing water clarity in the Big Bend region prohibited analysis in this
169 location. Satellite images were used to create a gridded 1 km² map of light attenuation as either
170 estimated water clarity (m) or light extinction (K_d , m⁻¹) based on a previously-developed
171 algorithm for Tampa Bay ([Chen et al. 2007](#)). Daily MODIS (Aqua level-2) data for the preceding
172 five years from the seagrass coverage layer for each bay were downloaded from the NASA
173 website (<http://oceancolor.gsfc.nasa.gov/>). These images were reprocessed using the SeaWiFS
174 Data Analysis System software (SeaDAS, Version 7.0). The clarity algorithm proposed by [Chen](#)
175 [et al. \(2007\)](#) was used to derive monthly mean, then annual mean light attenuation coefficients for
176 Tampa Bay. Satellite-estimated water clarity was derived from the light attenuation estimates for
177 Tampa Bay using a conversion equation that was previously validated using in situ data. A single
178 layer for further analysis was created as the average of all five years.

179 Light attenuation data for Choctawhatchee Bay were similarly obtained using the clarity
180 algorithm developed for Tampa Bay. Satellite estimates were retained as light extinction
181 coefficients based on the availability of in situ data obtained from vertical profiles of
182 {acro:MSL}

photosynthetically active radiation. Light extinction estimates for 2010 were obtained at ten locations in Choctawhatchee Bay at monthly intervals that were used to correct the satellite K_d values. Monthly field estimates were averaged and compared to the annual mean estimates from the 2010 satellite data. An empirical correction equation was developed based on the difference between the cumulative distribution of the in situ K_d estimates and the satellite estimates at the same locations. The 2010 correction was applied to the all five years of annual mean satellite data prior to averaging all data to create a single layer for further analysis.

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

2.2 Estimation of seagrass depth of colonization

The approach to estimating seagrass depth of colonization uses combined seagrass coverage maps and bathymetric depth data described above. The combined layer used for analysis 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

{acro:IWR}

{sec:est_r}

212 spatially-resolved information are described below.

213 The spatially-resolved approach for estimating Z_c begins by choosing an explicit location
214 in cartesian coordinates within the general boundaries of the available data. Seagrass depth data
215 (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the
216 chosen location are selected for estimating seagrass Z_c values (Fig. 1). The estimate for each
217 location is quantified from a plot of the proportion of sampled points that contain seagrass at
218 decreasing 0.1 meter depth bins from the surface to the maximum observed depth in the sample
219 (Fig. 3a). Although the chosen radius for selecting depth points is problem-specific, the minimum
220 radius should be chosen to sample a sufficient number of points for estimating Z_c . In general, an
221 appropriate radius will produce a plot that indicates a decrease in the proportion of points that are
222 occupied by seagrass with increasing depth. If more than one location is used to estimate Z_c ,
223 appropriate radii for each point would have minimal overlap with the seagrass depth data sampled
224 by neighboring points.

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

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

232 where the proportion of points occupied by seagrass at each depth, Z , is defined by a logistic
233 curve with an asymptote α , a midpoint inflection β , and a scale parameter γ . Finally, a simple
234 linear curve is fit through the inflection point (β) of the logistic curve to estimate the three
235 measures of depth of colonization (Fig. 3c). The inflection point is considered the depth at which
236 seagrass are decreasing at a maximum rate and is used as the slope of the linear curve. The
237 maximum depth of seagrass colonization, $Z_{c,max}$, is the x-axis intercept of the linear curve. The
238 minimum depth of seagrass growth, $Z_{c,min}$, is the location where the linear curve intercepts the

239 upper asymptote of the logistic growth curve. The median depth of seagrass colonization, $Z_{c,med}$,
240 is the depth halfway between $Z_{c,min}$ and $Z_{c,max}$. $Z_{c,med}$ is typically the inflection point of the
241 logistic growth curve.

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

259 **2.3 Estimating uncertainty in depth of colonization estimates**

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

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

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

273 The uncertainty associated with the Z_c estimates was based on the upper and lower limits
274 of the estimated inflection point on the logistic growth curve. This approach was used because
275 uncertainty in the inflection point is directly related to uncertainty in each of the Z_c estimates that
276 are based on the linear curve fit through the inflection point. Specifically, linear curves were fit
277 through the upper and lower estimates of the depth value at the inflection point to identify upper
278 and lower limits for the estimates of $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$. These values were compared
279 with the initial estimates from the linear curve that was fit through the inflection point on the
280 predicted logistic curve (i.e., Fig. 3c). This approach provided an indication of uncertainty for
281 individual estimates for the chosen radius. Uncertainty estimates were obtained for each Z_c
282 estimate for the grids in each segment.

283 The algorithm for estimating Z_c was implemented custom-made and pre-existing
284 functions in program R. Nonlinear least squares models were based on the `nls` and `SSlogis`
285 functions that used a self-starting logistic growth model (Bates and Chambers 1992, R
286 Development Core Team 2014). Multivariate normal distributions used to evaluate uncertainty
287 were simulated using functions in the MASS package (Venables and Ripley 2002). Geospatial
288 data were imported and processed using functions in the `rgeos` and `sp` packages (Bivand et al.
289 2008, Bivand and Rundel 2014).

290 2.4 Evaluation of spatial heterogeneity of seagrass depth limits

291 Spatially-resolved estimates for seagrass Z_c were obtained for each of the four coastal
292 segments described above: BB, OTB, UIRL, and WCB. Segment-wide estimates obtained using
293 all data were used as a basis of comparison such that departures from these values at smaller
294 scales were evidence of spatial heterogeneity in seagrass growth patterns and improved clarity of
295 description in depth estimates. A sampling grid of locations for estimating each of the three depth

296 values in Fig. 3 was created for each segment. The grid was masked by the segment boundaries,
 297 whereas seagrass depth points used to estimate Z_c extended beyond the segment boundaries to
 298 allow sampling by grid points that occurred near the edge of the segment. Initial spacing between
 299 sample points was chosen arbitrarily as 0.01 decimal degrees, which is approximately 1 km at 30
 300 degrees N latitude. The sampling radius around each sampling location in the grid was also
 301 chosen as 0.02 decimal degrees to allow for complete coverage of seagrass within the segment
 302 while also minimizing redundancy of information described by each location. In other words,
 303 radii were chosen such that the seagrass depth points sampled by each grid location were only
 304 partially overlapped by those sampled by neighboring points, while also ensuring an adequate
 305 number of locations were sampled that included seagrass.

306 **2.5 Developing a spatially coherent relationship of water clarity with depth 307 of colonization**

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

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

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

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

317 where the percent light requirements of seagrass at $Z_{c, max}$ are empirically related to light
 318 extinction. A conversion factor is often used to estimate the light extinction coefficient from
 319 secchi depth Z_{secchi} , such that $c = K_d \cdot Z_{secchi}$, where c has been estimated as 1.7 (Poole and

320 Atkins 1929, Idso and Gilbert 1974):

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

321 such that K_d in eq. (4) is replaced by the ratio of the conversion factor and Z_{secchi} .

322 Two different approaches were used to estimate light requirements based on the
323 availability of satellite-based estimates or in situ observations of water clarity. For
324 Choctawhatchee and Tampa Bay, an evenly-spaced grid of sampling points was created that
325 covered each bay to estimate $Z_{c, \max}$ and sample the raster grid of satellite-derived water clarity.
326 Grid spacing was different in each bay (0.005 for Choctawhatchee Bay, 0.01 for Tampa Bay) to
327 account for variation in spatial scales of seagrass coverage. Equation (4) was used to estimate
328 light requirements at each point for Choctawhatchee Bay and eq. (5) was used for Tampa Bay.
329 Similarly, the geographic coordinates for each in situ secchi measurement in the Indian River
330 Lagoon were used as locations for estimating $Z_{c, \max}$ and light requirements using eq. (5).
331 Excessively small estimates for light requirements were removed for Indian River Lagoon which
332 were likely caused by shallow secchi observations that were not screened during initial data
333 processing. Sampling radii for locations in each bay were chosen to maximize the number of
334 points with estimable values for $Z_{c, \max}$ (as described in section 2.2), while limiting the upper
335 radius to adequately describe variation in seagrass growth patterns for emphasizing gradients in
336 light requirements. Radii were fixed at 0.04 decimal degrees for Choctawhatchee Bay, 0.1
337 decimal degrees for Tampa Bay, and 0.15 decimal degrees for Indian River Lagoon. The
338 estimated maximum depth values and light requirements of each point were plotted by location to
339 evaluate spatial variation in seagrass growth as a function of light-limitation.

340 **3 Results**

341 **3.1 Segment characteristics and seagrass depth estimates**

342 Each of the four segments varied by several key characteristics that potentially explain
343 within-segment variation of seagrass growth patterns (Table 1). Mean surface area was 191.2
344 square kilometers, with area decreasing for the Big Bend (271.4 km), Upper Indian River Lagoon
345 (228.5 km), Old Tampa Bay (205.5 km), and Choctawhatchee Bay (59.4 km) segments. Seagrass

coverage as a percentage of total surface area varied considerably by segment. Seagrasses covered a majority of the surface area for the Big Bend segment (74.8 %), whereas coverage was much less for Upper Indian River Lagoon (32.8 %), Old Tampa Bay (11.9 %), and Western Choctawhatchee Bay (5.9 %). Visual examination of the seagrass coverage maps for the respective year of each segment suggested that seagrasses were not uniformly distributed (Fig. 2). Seagrasses in the Choctawhatchee Bay segments were generally sparse with the exception of a large patch located to the west of the inlet connection with the Gulf of Mexico. Seagrasses in the Big Bend segment were located throughout the segment with noticeable declines near the outflow of the Steinhatchee River, whereas seagrasses in Old Tampa Bay and Upper Indian River Lagoon were generally confined to shallow areas near the shore. Seagrass coverage showed a partial decline toward the northern ends of both Old Tampa Bay and Upper Indian River Lagoon segments. Mean depth was less than 5 meters for each segment, excluding Western Choctawhatchee Bay which was slightly deeper than the other segments (5.3 m). Maximum depths were considerably deeper for Choctawhatchee Bay (11.9 m) and Old Tampa Bay (10.4 m), as compared to the Big Bend (3.6 m) and Indian River Lagoon (1.4 m) segments. Water clarity as indicated by average secchi depths was similar between the segments (1.5 m), although Choctawhatchee Bay had a slightly higher average (2.1 m).

Estimates of seagrass Z_c that did not consider spatially explicit locations (i.e., segment-wide) indicated that seagrasses generally did not grow deeper than three meters in any of the segments (Table 2). Maximum and median depth of colonization were deepest for the Big Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old Tampa Bay (1.1 and 0.9 m), whereas the minimum depth of colonization was deepest for Western Choctawhatchee Bay (1.8 m) and shallowest for Old Tampa Bay (0.6 m). In most cases, the averages of all grid-based estimates were less than the whole segment estimates, indicating 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 indicated seagrasses grew to approximately 2.1 m, which was 1.6 m less than the whole segment estimate. Although reductions were not as severe for the average grid estimates for the remaining segments, considerable within-segment variation was observed depending on grid location. For example, the deepest estimate for $Z_{c,min}$ (2 m) in the Upper Indian River Lagoon exceeded the average of all grid locations for $Z_{c,max}$ (1.7 m). $Z_{c,min}$ also

376 had minimum values of zero meters for the Big Bend and Old Tampa Bay segments, suggesting
377 that seagrasses declined continuously from the surface for several locations.

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

398 Uncertainty for estimates of $Z_{c,max}$ indicated that confidence intervals were generally
399 acceptable (i.e., greater than zero), although the ability to discriminate between the three depth
400 estimates varied by segment (Fig. 4 and Table 3). Mean uncertainty for all estimates in each
401 segment measured as the width of a 95% confidence interval was 0.2 m. Greater uncertainty was
402 observed for Western Choctawhatchee Bay (mean width of all confidence intervals was 0.5 m)
403 and Old Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Upper Indian River Lagoon
404 (0.1 m) segments. The largest confidence interval for each segment was 1.4 m for Old Tampa
405 Bay, 1.6 m for Western Choctawhatchee Bay, 0.5 m for the Big Bend, and 0.8 m for the Upper

406 Indian River Lagoon segments. Most confidence intervals for the remaining grid locations were
407 much smaller than the maximum in each segment (e.g., central location of the Upper Indian River
408 Lagoon, Fig. 4). A comparison of overlapping confidence intervals for $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$
409 at each grid location indicated that not every measure was unique. Specifically, only 11.1% of
410 grid points in Choctawhatchee Bay and 28.2% in Old Tampa Bay had significantly different
411 estimates, whereas 82.4% of grid points in the Indian River Lagoon and 96.2% of grid points in
412 the Big Bend segments had estimates that were significantly different. By contrast, all grid
413 estimates in Choctawhatchee Bay and Indian River Lagoon had $Z_{c,max}$ estimates that were
414 significantly greater than zero, whereas all but 12.4% of grid points in Old Tampa Bay and 8% of
415 grid points in the Big Bend segment had $Z_{c,max}$ estimates significantly greater than zero.

416 3.2 Evaluation of seagrass light requirements

417 Estimates of water clarity, seagrass depth limits and corresponding light requirements for
418 all segments of Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon indicated
419 substantial variation, both between and within the different bays. Satellite-derived estimates of
420 light attenuation for Choctawhatchee Bay (as K_d , Fig. 5) and Tampa Bay (as clarity, Fig. 6)
421 indicated variation between years and along major longitudinal and lateral axes. For
422 Choctawhatchee Bay, K_d estimates for western and central segments were substantially lower
423 than those for the more shallow, eastern segment. Maximum K_d values were also observed in
424 earlier years (e.g., 2003, 2004). Clarity estimates for Tampa Bay also showed an increase towards
425 more seaward segments, with particularly higher clarity along the mainstem. Clarity in 2006 was
426 relatively lower than other years, with noticeable increases in 2007 and 2008. In situ secchi
427 observations for the Indian River Lagoon followed a clear latitudinal gradient with higher values
428 in more southern segments Fig. 9. Very few measurements were available for the Upper Indian
429 River Lagoon and Banana River segments, likely due to water clarity exceeding the maximum
430 depth.

431 Seagrass Z_c estimates were obtained for 271 locations in Choctawhatchee Bay, 566
432 locations in Tampa Bay, and 37 locations in the Indian River Lagoon (Table 4 and Figs. 7 to 9).
433 Mean $Z_{c,max}$ for each bay was 2.5, 1.7, and 1.3 m for Choctawhatchee Bay, Tampa Bay, and
434 Indian River Lagoon, respectively, with all values being significantly different between bays
435 (ANOVA, $F = 352.8$, $df = 2, 871$, $p < 0.001$, followed by Tukey multiple comparison,

⁴³⁶ $p < 0.001$ for all). Generally, spatial variation in $Z_{c, max}$ followed variation in light requirements
⁴³⁷ for broad spatial scales with more seaward segments within each bay having lower light
⁴³⁸ requirements. Mean light requirements were significantly different between all bays (ANOVA,
⁴³⁹ $F = 464.3$, $df = 2, 871$, $p < 0.001$, Tukey $p < 0.001$ for all), with a mean requirement of 46.4%
⁴⁴⁰ for Choctawhatchee Bay, 30.4% for Tampa Bay, and 13.4% for Indian River Lagoon. Significant
⁴⁴¹ differences in light requirements between segments within each bay varied. All segments in
⁴⁴² Tampa Bay were significantly different except Middle Tampa Bay and Hillsborough Bay. Within
⁴⁴³ each bay, light requirements were significantly different between segments (ANOVA, $F = 29.8$,
⁴⁴⁴ $df = 2, 268$, $p < 0.001$ for Choctawhatchee Bay, $F = 84.6$, $df = 3, 562$, $p < 0.001$ for Tampa
⁴⁴⁵ Bay, $F = 7.6$, $df = 6, 30$, $p < 0.001$ for Indian River Lagoon). Post-hoc evaluation of all
⁴⁴⁶ pair-wise comparisons of mean light requirements indicated that significant differences varied
⁴⁴⁷ between segments within each bay. Significant differences were observed between all segments in
⁴⁴⁸ Choctawhatchee Bay, except the central and western segments (Fig. 7). Similarly, significant
⁴⁴⁹ differences in Tampa Bay were observed between all segments, except Middle Tampa Bay and
⁴⁵⁰ Old Tampa Bay (Fig. 8). Finally, for the Indian River Lagoon, significant differences were
⁴⁵¹ observed between the Lower Central Indian River Lagoon and the Upper ($p < 0.001$) and Lower
⁴⁵² Mosquito Lagoons ($p = 0.023$), the Lower Indian River and the Upper ($p < 0.001$) and Lower
⁴⁵³ Mosquito Lagoons ($p = 0.013$), and the Upper Central Indian River and the Upper Mosquito
⁴⁵⁴ Lagoon ($p = 0.018$) (Fig. 9).

⁴⁵⁵ **4 Discussion**

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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}

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

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

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

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

W. 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

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

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

Table 3: Summary of uncertainty for seagrass depth estimates (m) for each segment using all grid locations in Fig. 4. 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	0.10	0.09	0.01	0.49
OTB	0.38	0.26	0.06	1.40
UIRL	0.10	0.10	0.00	0.81
WCB	0.53	0.37	0.12	1.57

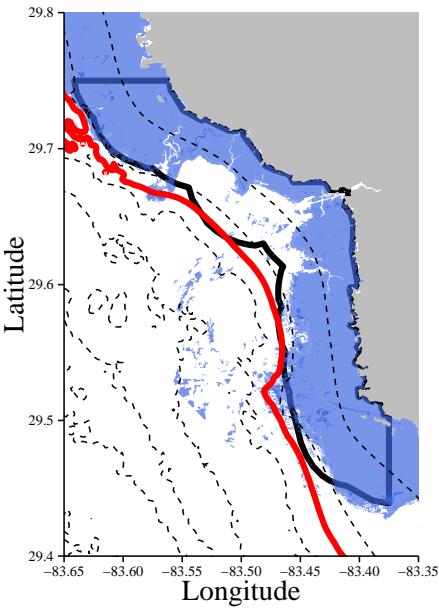
^aBB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Choctawhatchee Bay.

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

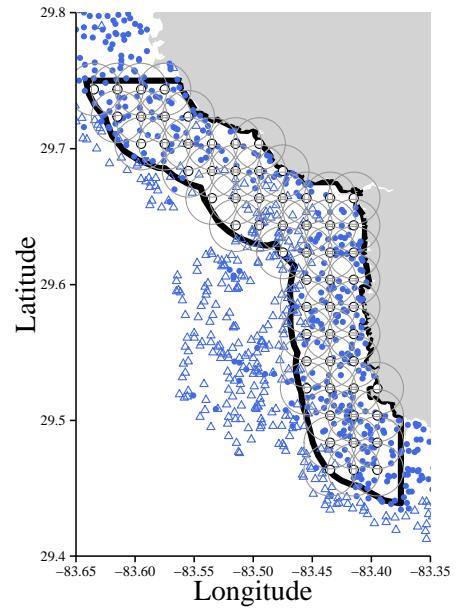
Segment ^a	n	$Z_{c,max}$				% light			
		Mean	St. Dev.	Min	Max	Mean	St. Dev.	Min	Max
Choctawhatchee Bay									
CCB	130	2.5	0.3	1.0	3.1	46.7	8.7	23.3	82.6
ECB	5	0.8	0.1	0.6	0.9	71.8	7.7	65.7	85.2
WCB	136	2.6	0.2	2.1	2.9	45.3	6.3	24.4	64.4
Indian River Lagoon									
BR	2	1.4	0.0	1.4	1.4	12.0	1.1	11.2	12.8
LCIRL	11	1.4	0.3	1.1	1.7	9.7	4.7	4.5	18.0
LIRL	3	1.8	0.0	1.8	1.8	6.5	2.0	4.2	7.9
LML	4	1.1	0.0	1.1	1.2	17.8	2.3	14.9	19.9
UCIRL	13	1.2	0.1	1.1	1.4	14.1	4.2	7.6	19.9
UIRL	1	1.2		1.2	1.2	20.3		20.3	20.3
UML	3	0.9	0.1	0.8	1.0	23.3	2.8	20.9	26.4
Tampa Bay									
HB	43	1.3	0.1	1.2	1.4	32.7	7.4	14.3	45.1
LTB	158	2.2	0.4	1.7	3.5	24.3	6.7	4.8	40.0
MTB	215	1.7	0.4	1.2	2.4	29.8	8.0	12.3	50.0
OTB	150	1.2	0.1	1.0	1.3	37.0	5.8	17.3	49.8

^aCCB: Central Choctawhatchee Bay, ECB: Eastern Choctawhatchee Bay, WCB: Western Choctawhatchee Bay, BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, UCIRL: Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon, HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

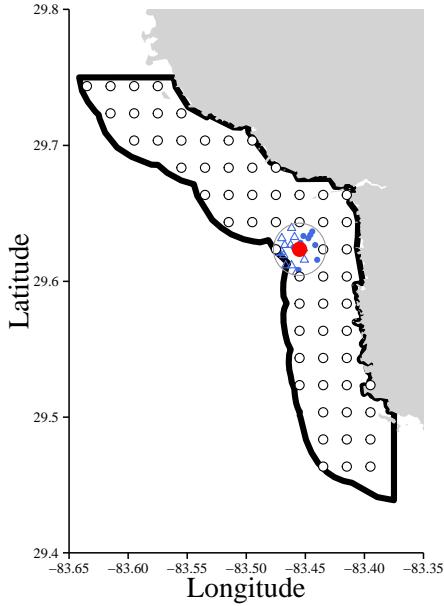
(a) Seagrass coverage and bathymetry for the segment



(b) Grid of locations and sample areas for estimates



(c) Sampled seagrass data for a test point



- Seagrass coverage
- 2 m depth contours
- Estimated depth limit for segment
- ▨ Segment polygon

- △ Seagrass absent
- Seagrass present

- Estimation grid
- Test point
- Sample area

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

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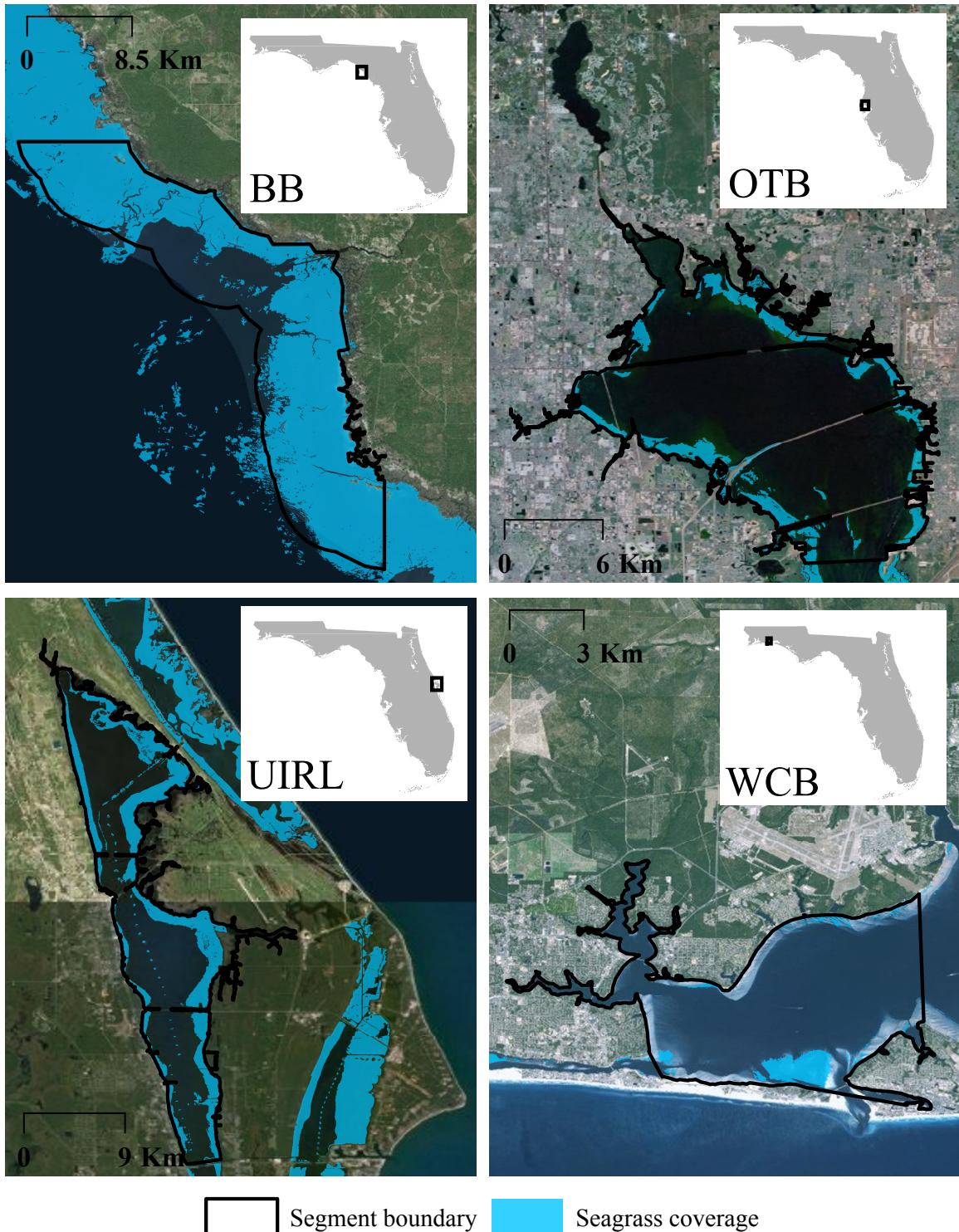
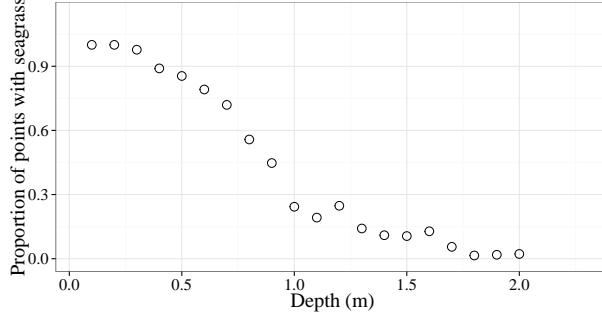


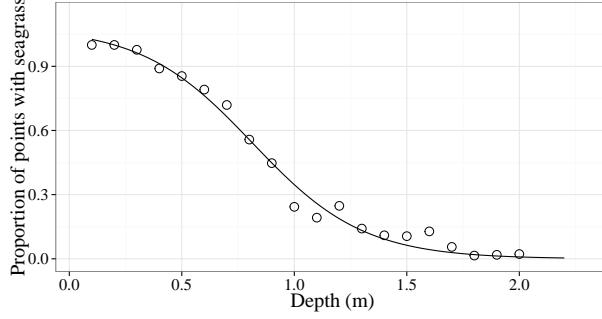
Fig. 2: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay).

{fig:seg_a}

(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

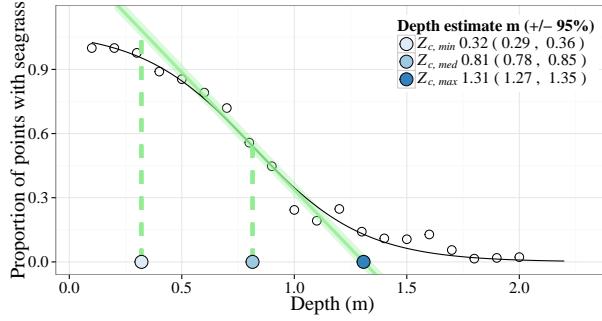


Fig. 3: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 3a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 1. Fig. 3b adds a decreasing logistic growth curve fit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

{fig:est_e}

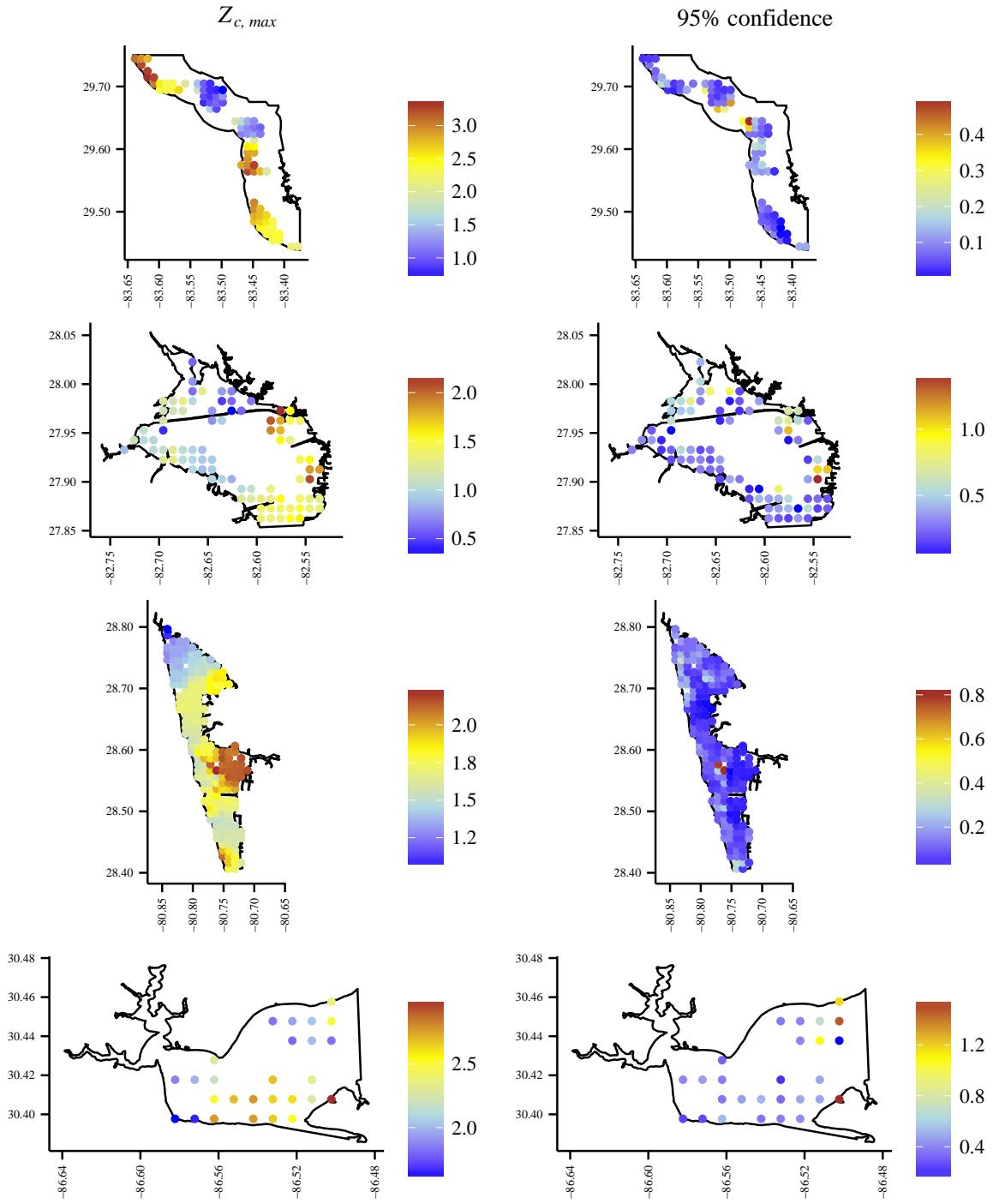


Fig. 4: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Maximum depth of colonization ($Z_{c, max}$) estimates are on the left and correspondings widths of the 95% confidence intervals are on the right. Estimates are assigned to grid locations for each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

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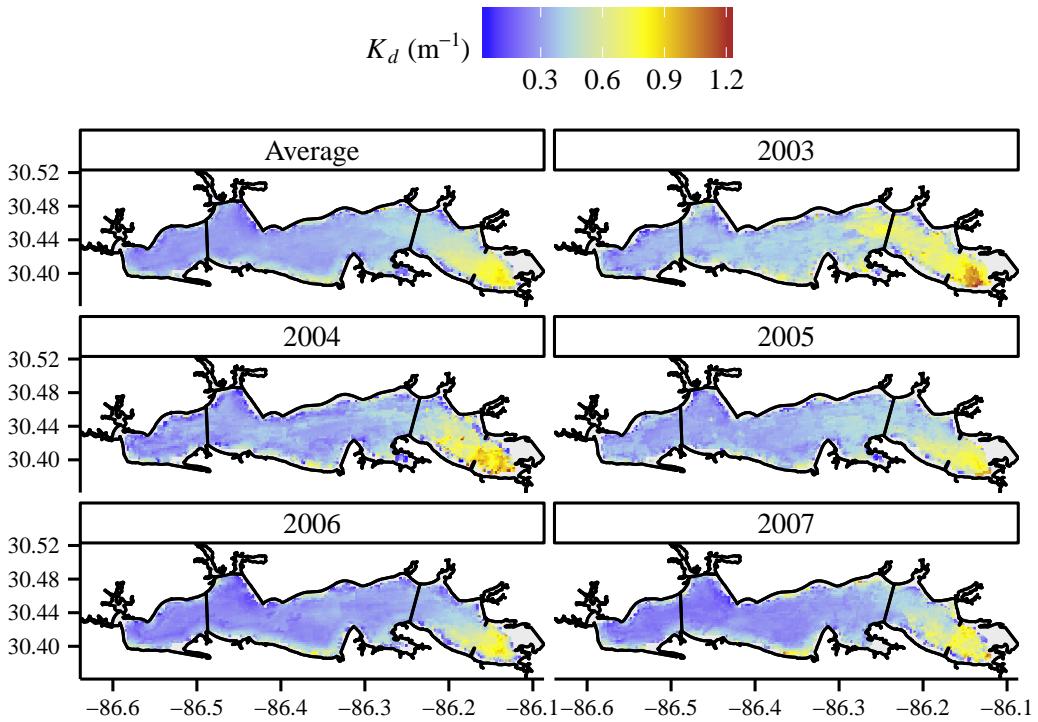


Fig. 5: Satellite estimated light attenuation for Choctawhatchee Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of light attenuation for available years of satellite data up to the year of seagrass coverage used to estimate depth of colonization. The first facet is an average of all years. See Fig. 7 for segment identification.

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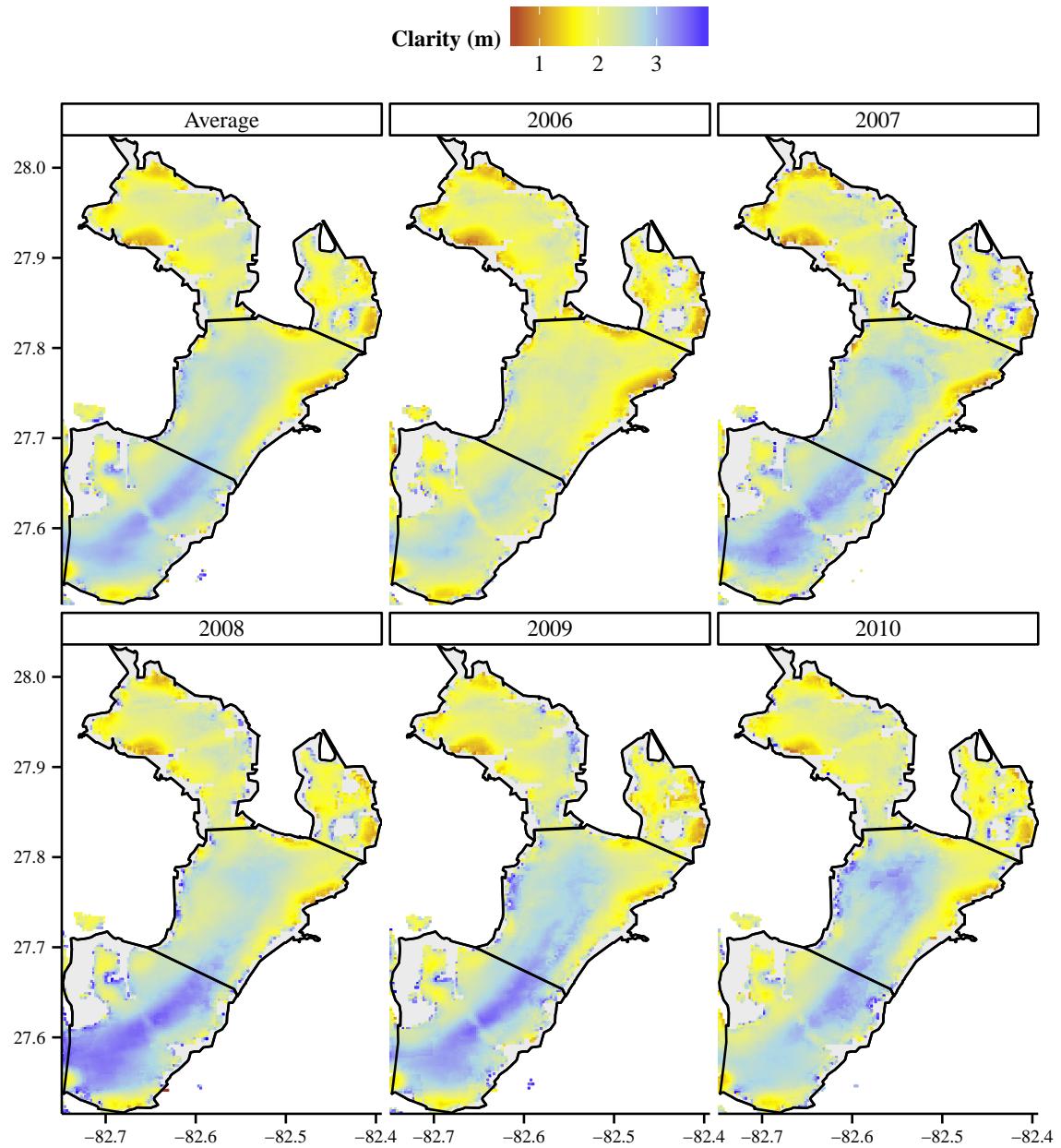


Fig. 6: Satellite estimated water clarity for Tampa Bay based on empirical relationships between *in situ* secchi observations and surface reflectance. Each facet is an annual average of water clarity for available years of satellite data. The first facet is an average of all years. See Fig. 8 for segment identification.

{fig:clar}

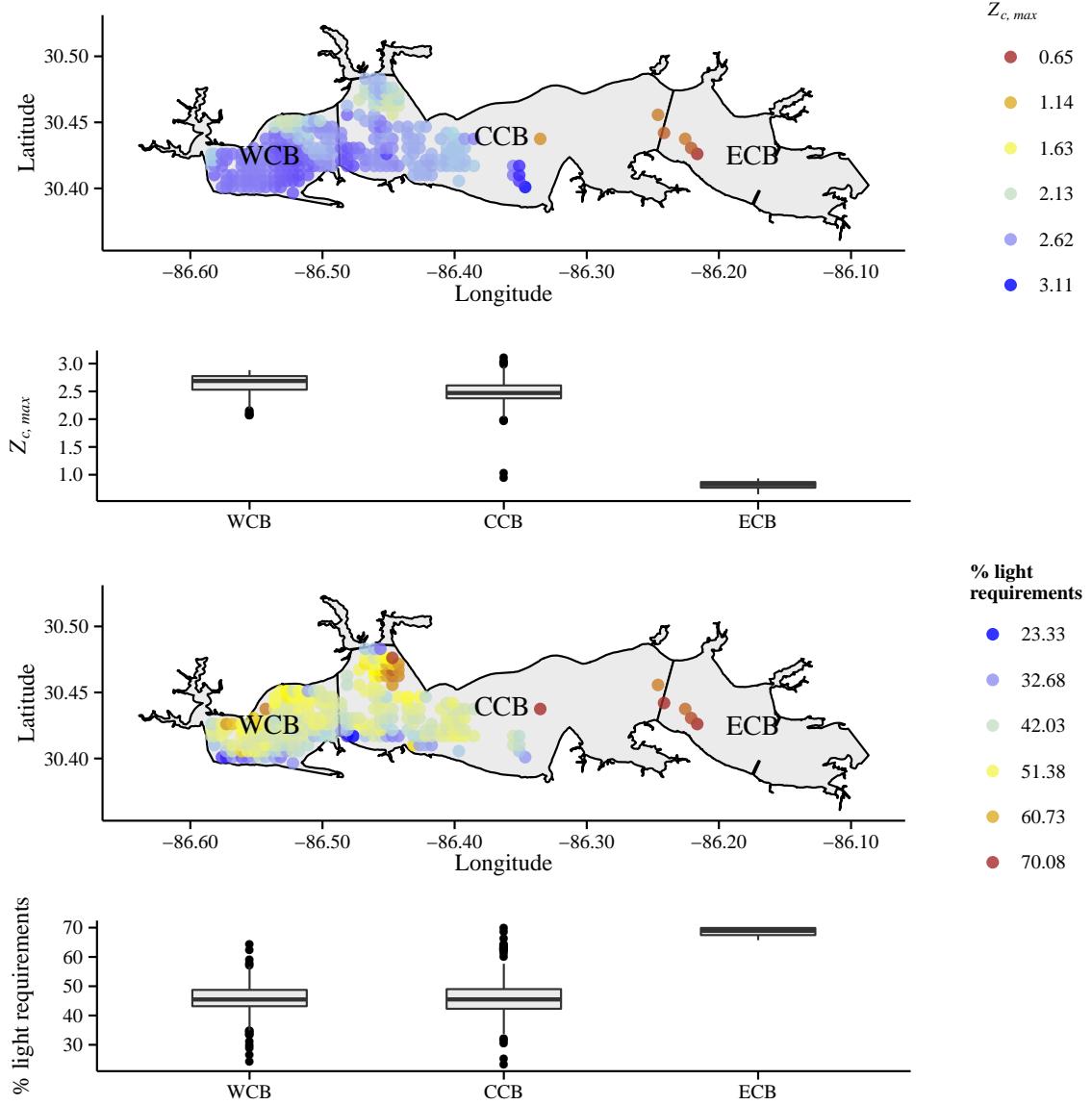


Fig. 7: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Choctawhatchee Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal 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. CCB: Central Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay.

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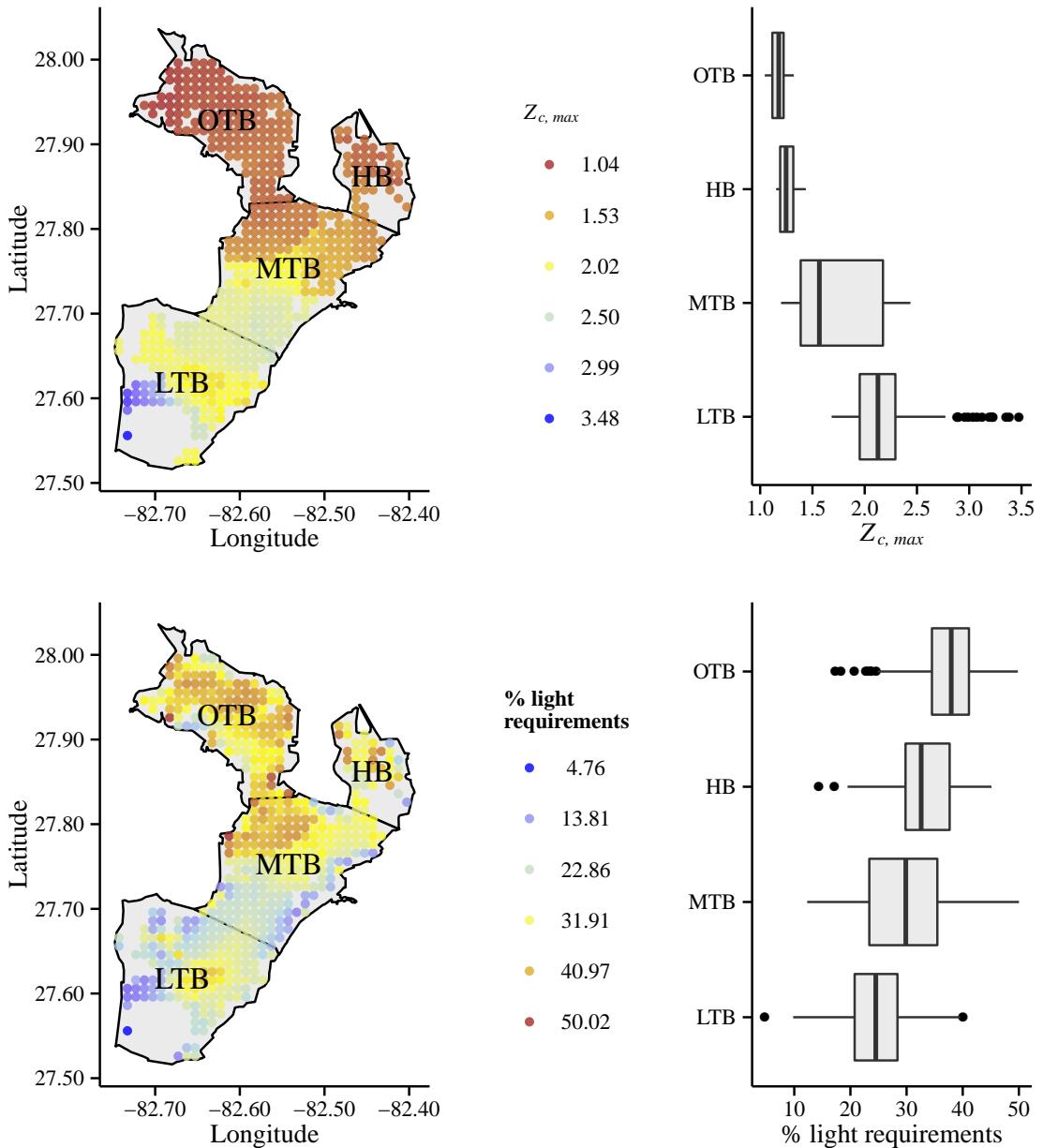


Fig. 8: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Tampa Bay, Florida. Locations are those where water clarity estimates were available from satellite observations and seagrass depth of colonization was estimable using a radius of 0.1 decimal degrees.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

{fig:light}

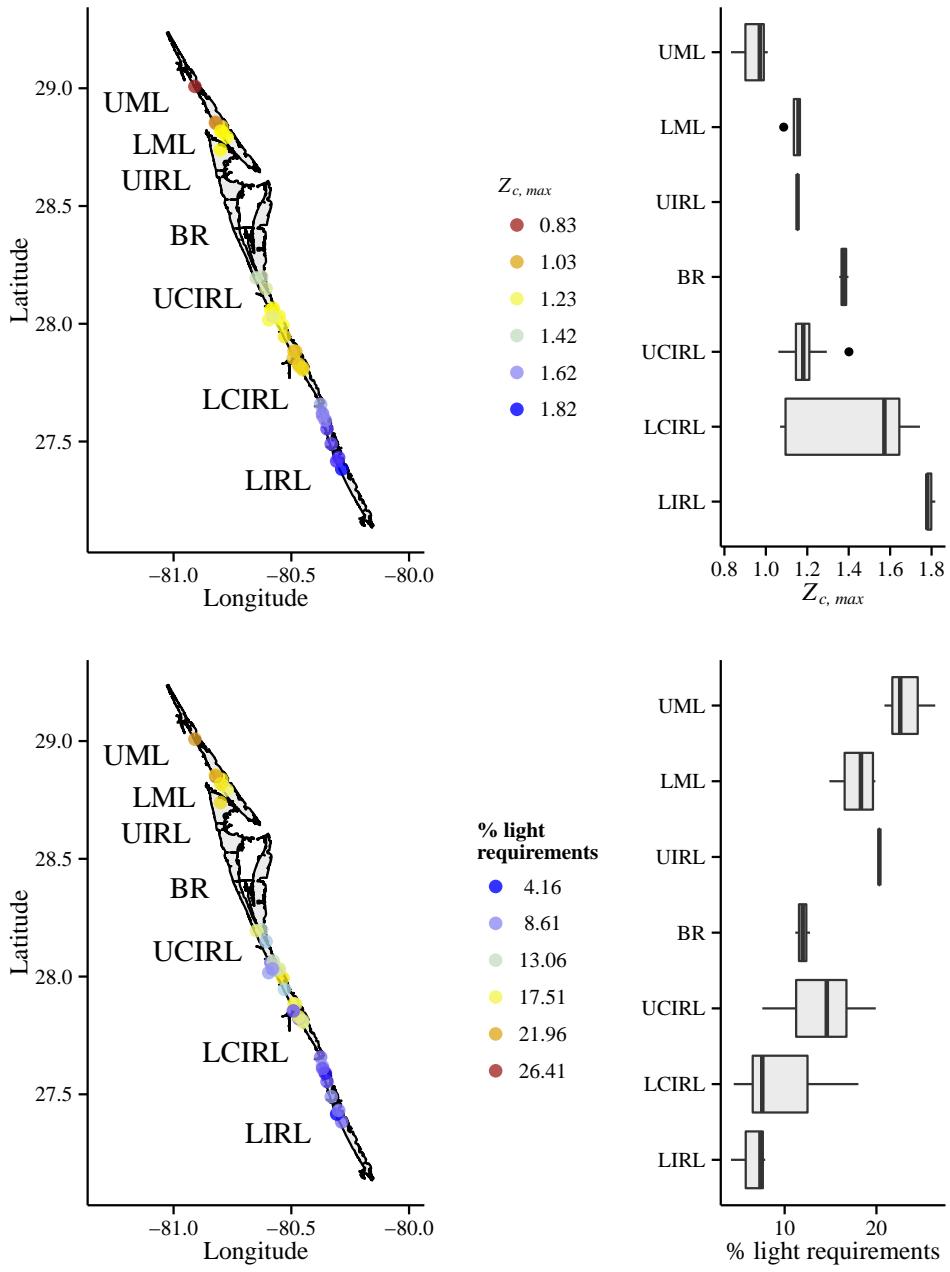


Fig. 9: Estimated maximum depths of seagrass colonization and light requirements for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity in the Florida Impaired Waters Rule database, update 40. Estimates are also summarized by bay segment as boxplots as in Fig. 8. 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.

{fig:light}