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Seagrass light requirements using an algorithm for spatially-resolved depth of colonization

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1 Introduction

Issues related to excessive nutrient pollution have motivated a substantial amount of research to understand and address impacts on coastal waters. Eutrophication, defined as an increase in the rate of supply of organic matter to an ecosystem (Nixon 1995), is primarily caused by anthropogenic inputs of limiting nutrients that exceed background concentrations of receiving waters. Adverse impacts on aquatic resources are well-documented and have included increased occurrence in the frequency and severity of harmful algal blooms (Cloern 1996), reduction of dissolved oxygen necessary to support heterotrophic organisms (Justic et al. 1987, Diaz and Rosenberg 2008), and loss of ecosystem functioning through food web simplification (Tewfik et al. 2007). Although management activities have been successful in mitigating or reversing eutrophication impacts (e.g., Greening and Janicki 2006), the evaluation of response endpoints remains an important topic given that ecosystem changes in relation to different nutrient regimes are not fully understood nor anticipated (Duarte et al. 2009). The most appropriate indicators of ecosystem response may be those that exhibit clear biological linkages with water quality changes, such that the potential effects of management actions can be unambiguously characterized through known cause and effect pathways. Critical management decisions may be forced by tentative assessments, political or societal pressures, or qualitative criteria in the absence of empirical methods to identify adequate indicators of ecosystem response (Duarte et al. 2009).

The ecosystem services provided by seagrasses as well as their sensitivity to water quality changes has contributed to their proliferation as biological response endpoints for eutrophication. Seagrasses are ecosystem engineers (Jones et al. 1994, Koch 2001) that serve a structural and

26 functional role in altering aquatic habitat often through multiple feedback mechanisms with other
27 ecosystem components. For example, seagrass beds create habitat for juvenile fish and crabs by
28 reducing wave action and stabilizing sediment (Williams and Heck 2001, Hughes et al. 2009).
29 Seagrasses also respond to changes in water clarity through direct physiological linkages with
30 light availability. In short, increased nutrient loading contributes to reductions in water clarity
31 through increased algal concentrations, inhibiting the growth of seagrass through light limitation
32 (Duarte 1995). Empirical relationships between nutrient loading, water clarity, light requirements,
33 and the maximum depth of seagrass colonization have been identified (Duarte 1991, Kenworthy
34 and Fonseca 1996, Choice et al. 2014), such that quantitative standards can be developed to
35 maintain light regimes sufficient for seagrass growth targets (Steward et al. 2005). Conversely,
36 seagrass depth limits have formed the basis of quantitative criteria for nutrient load targets
37 (Janicki and Wade 1996). Contrasted with numeric standards for nutrients and phytoplankton,
38 seagrass-based criteria may be more practical for developing water quality standards given that
39 seagrasses are integrative of system-wide conditions over time and less variable with changes in
40 nutrient regimes (Duarte 1995).

41 The development of numeric criteria and standards for coastal waters has been a
42 management priority within the United States (USEPA, 1998) and internationally (WFD 2000).
43 Numerous agencies and management programs have developed a variety of techniques for
44 estimating seagrass depth limits as a basis for establishing numeric criteria, either as restoration
45 targets or for identifying critical load limits. Such efforts have been useful for site-specific
46 approaches where the analysis needs are driven by a particular management or research context
47 (e.g., Iverson and Bittaker 1986, Hale et al. 2004). However, a lack of standardization among
48 methods has prevented broad-scale comparisons between regions and has even contributed to

49 discrepancies between measures of depth limits based on the chosen technique. For example,
50 seagrass depth limits based on in situ techniques can vary with the sampling device (Spears et al.
51 2009). Despite the availability of data, techniques for estimating seagrass depth of colonization
52 using remotely sensed data have not been extensively developed. Such techniques have the
53 potential to facilitate broad-scale comparisons between regions given the spatial coverage and
54 annual availability of many products. For example, recent analyses by Hagy, In review have
55 shown that standardized techniques using seagrass coverage maps and bathymetric data can be
56 developed to compare growth patterns over time among different coastal regions of Florida. Such
57 methods show promise, although further development to improve the spatial resolution of the
58 analysis are needed. Specifically, methods for estimating seagrass depth limits should be
59 reproducible for broad-scale comparisons, while also maintaining flexibility for site-specific
60 estimates depending on management needs.

61 Reproducible and empirical approaches can be developed to provide more consistent
62 estimates of seagrass depth limits for restoration targets or criteria development. We describe a
63 method for estimating seagrass depth of colonization using information-rich datasets to create a
64 spatially explicit and repeatable estimate. In particular, methods described in Hagy, In review are
65 improved upon by creating a flexible and repeatable technique for estimating seagrass depth
66 limits from coverage maps and bathymetric data. The specific objectives are to 1) describe the
67 method for estimating seagrass depth limits within a relevant spatial context, 2) apply the
68 technique to four distinct regions of Florida to illustrate improved clarity of description for
69 seagrass growth patterns, and 3) develop a spatially coherent relationship between depth limits
70 and water clarity for the case studies. Overall, these methods are expected to inform the
71 development of water quality criteria based on empirical relationships of seagrass depth limits

72 with water clarity over time. The method is applied to data from Florida although the technique is
73 transferable to other regions with comparable data.

74 **2 Methods**

75 Development of a spatially-resolved approach to estimate seagrass depth of {acro:doc}
76 colonization (Z_c) relied extensively on data and partially on methods described in Hagy, In
77 review. The following is a summary of locations and data sources, methods and rationale for
78 incorporating spatial information in seagrass Z_c estimates, and evaluation of the approach
79 including relationships with water clarity.

80 **2.1 Locations and data sources**

81 Four unique locations were chosen for the analysis: Choctawatchee Bay (Panhandle), Big
82 Bend region (northeast Gulf of Mexico), Tampa Bay (central Gulf Coast of Florida), and Indian
83 River Lagoon (east coast) (Table 1 and Fig. 1). These locations represent different geographic
84 regions in the state, in addition to having available data and observed gradients in water clarity
85 that contribute to heterogeneity in seagrass growth patterns. For example, the Big Bend region
86 was chosen based on location near an outflow of the Steinhatchee River where higher
87 concentrations of dissolved organic matter are observed. Seagrasses near the outflow were
88 observed to grow at shallower depths as compared to locations far from the river source. Coastal
89 regions and estuaries in Florida are partitioned as distinct spatial units based on a segmentation
90 scheme developed by US Environmental Protection Agency (EPA) for the development of {acro:EPA}
91 numeric nutrient criteria. One segment from each geographic location was used to describe the
92 approach for estimating seagrass Z_c and to evaluate variation in growth patterns. The segments
93 included portions of Choctawatchee Bay (segment 303), the big bend region (820), Old Tampa

94 Bay (902), and Indian River Lagoon (1502). Each segment was a smaller unit within a larger
95 estuary or coastal region.

96 Data used to estimate seagrass Z_c were primarily obtained from publically available {acro:GIS}
97 Geographic Information System (GIS) products. At the most generic level, spatial data describing
98 seagrass aerial coverage combined with co-located bathymetric depth information were used to
99 estimate Z_c . These data products are available in coastal regions of Florida through the US
100 Geological Survey, Florida Department of Environmental Protection, and watershed management
101 districts. Data are generally more available in larger estuaries that are of specific management
102 concern. For example, seagrass coverage data are available from 1950 (Tampa Bay) to present day
103 (multiple estuaries), with more recent products available at annual or biennial intervals. Seagrass
104 coverage maps are less frequent in areas with lower population densities (e.g., Big Bend region)
105 or where seagrass is naturally absent (northeast Florida). Seagrass maps were produced using
106 photo-interpretations of aerial images to categorize coverage as absent, discontinuous (patchy), or
107 continuous. For this analysis, we considered seagrass coverage as being only present (continuous
108 and patchy) or absent since the former did not represent unequivocal categories between regions.

109 Seagrass coverage maps were combined with bathymetric depth layers to characterize
110 location and depth of growth in each location. Bathymetric depth layers for each location were
111 obtained from the National Oceanic and Atmospheric Administration's (NOAA) National
112 Geophysical Data Center as either Digital Elevation Models (DEMs) or raw sounding data from {acro:DEM}
113 hydroacoustic surveys. Tampa Bay data provided by the Tampa Bay National Estuary Program
114 are described in [Tyler et al. \(2007\)](#). Bathymetric data for the Indian River Lagoon were obtained
115 from the St. John's Water Management District ([Coastal Planning and Engineering 1997](#)). NOAA
116 products were referenced to mean lower low water, whereas Tampa Bay data were referenced to

117 the North American Vertical Datum of 1988 (NAVD88) and the Indian River Lagoon data were
118 referenced to mean sea level. Depth layers were combined with seagrass coverage layers using
119 standard union techniques for raster and vector layers in ArcMap 10.1 (Environmental Systems
120 Research Institute 2012). To reduce computation time, depth layers were first masked using a 1
121 km buffer of the seagrass coverage layer. The final layer used for analysis was a point layer with
122 attributes describing location (latitude, longitude, segment), depth (m), and seagrass (present,
123 absent). All spatial data were referenced to the North American Datum of 1983 as geographic
124 coordinates. Depth values in each seagrass layer were further adjusted from the relevant vertical
125 reference datum to local mean sea level (MSL) using the NOAA VDatum tool
126 (<http://vdatum.noaa.gov/>).
127

{acro:NAV}

{acro:MSL}

127 **2.2 Segment-based estimates of seagrass depth of colonization**

128 Hagy, In review describe an approach to estimate seagrass Z_c for individual coastal
129 segments. The approach described herein is theoretically similar to the initial method, although
130 the latter technique has a spatial resolution that uses segments as the smallest measurable unit.
131 Seagrass depth data described above are used to estimate maximum (Z_{cMax}) and median ($Z_{c50\%}$)
132 seagrass Z_c , where the maximum depth is defined as the deepest depth at which a “significant”
133 coverage of seagrasses occurred in a segment and the median depth is defined as the median depth
134 occurring at the deep water edge. The seagrass depth points are grouped into bins and the
135 proportion of points within each depth bin that contain seagrass are quantified. Both seagrass Z_c
136 estimates are obtained from a plot of proportion of points occupied at each depth bin. In general,
137 the plot is characterized by a decreasing trend such that the proportion of occupied points by
138 depth bin decreases and eventually flattens with increasing depth. A regression is fit on this

139 descending portion of the curve such that the intercept point on the x-axis is considered the
140 maximum depth of colonization. The median portion of this curve is considered the median depth
141 of the deepwater edge of seagrass.

142 Considerable spatial heterogeneity in the observed seagrass growth patterns suggests that
143 a segment-wide estimate of seagrass Z_c may be inadequate for fully characterizing growth
144 patterns, particularly for the examples in the current analysis. Fig. 2 illustrates spatial variation in
145 seagrass distribution for a location in the Big Bend region of Florida. Using methods in Hagy, In
146 review, the estimate for median seagrass Z_c for the segment is over- and under-estimated for
147 different locations. In particular, Z_c is greatly over-estimated at the outflow of the Steinhatchee
148 River where high concentrations of dissolved organic matter reduce water clarity and naturally
149 limit seagrass growth. This example suggests that estimates of Z_c may be needed at finer spatial
150 scales to provide a more robust determination of restoration targets and nutrient criteria. Although
151 the current example is immediately relevant for the Big Bend region of Florida, the remaining
152 examples discussed throughout also provide a justification for a more comprehensive assessment
153 of seagrass growth patterns.

154 **2.3 Estimating seagrass depth of colonization using spatial information**

155 The approach used to estimate seagrass Z_c with spatial information has several key
156 differences that make it distinct from the original method. As before, seagrass Z_c estimates are
157 based on empirical measures of the frequency occurrence of seagrass with increasing depth. The
158 first difference is that maximum Z_c is estimated using a logistic growth curve fit through the data,
159 as compared to a simple linear regression in the previous example. Second, a third measure
160 describing the minimum depth of colonization was defined, in addition to median and maximum

161 depth of growth. The third and most important difference is that the estimates are assigned to
162 discrete cartesian locations, using either a grid of points or as a single location of interest.

163 Methods and implications of these differences are described below.

164 The spatially-resolved approach for estimating Z_c begins by creating a grid of points
165 within the segment where the same process for estimating Z_c is used for each point. Alternatively,
166 a single location of interest can be chosen rather than a grid-based design. Seagrass depth data
167 (i.e., merged bathymetric and seagrass coverage data) that are located within a set radius from the
168 chosen locations are selected for estimating seagrass Z_c values (Fig. 3). The estimate for each
169 location is quantified from a plot of the proportion of bathymetric soundings that contain seagrass
170 at each depth bin (Fig. 4a). Although the chosen radius for selecting depth points is
171 problem-specific, the minimum radius must sample a sufficient number of points for estimating
172 Z_c . In general, an appropriate radius will produce a plot that indicates a decrease in the proportion
173 of points that are occupied by seagrass with increasing depth. An appropriate radius is also one
174 that creates a sample area around each point that has minimal overlap with the seagrass depth data
175 sampled by adjacent points.

176 A curve is fit to the sampled depth points using non-linear regression to characterize the
177 reduction in seagrass as a function of depth (Fig. 4b). Specifically, a decreasing logistic growth
178 curve is used with the assumption that seagrass decline with increasing depth is monotonic and
179 asymptotic at the maximum depth of colonization. The curve is fit by minimizing the residual
180 sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers 1992) and user-supplied
181 starting parameters that are an approximate estimate of the curve characteristics. The model has

182 the following form:

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

183 where the proportion of points occupied by seagrass at each depth is defined by a logistic curve

184 with an asymptote α , a midpoint inflection β , and a scale parameter γ . Starting values α , β , and γ

185 were estimated empirically from the observed data.

186 Finally, a simple linear curve is fit through the inflection point (β) of the logistic curve to

187 estimate the three measures of depth of colonization (Fig. 4c). The inflection point is considered

188 the depth at which seagrass are decreasing at a maximum rate and is used as the slope of the

189 linear curve. Three measures describing seagrass growth characteristics are obtained. The

190 maximum depth of seagrass colonization, $Z_{c, max}$, is the x-axis intercept of the linear curve. The

191 minimum depth of seagrass growth, $Z_{c, min}$, is the location where the linear curve intercepts the

192 asymptote of the logistic growth curve. This depth can be considered the start of the decline in

193 seagrass coverage with increasing depth. The median depth of seagrass colonization, $Z_{c, med}$, is

194 the depth halfway between $Z_{c, min}$ and $Z_{c, max}$. $Z_{c, med}$ was typically the inflection point of the

195 logistic growth curve. Functionally, each measure has specific ecological significance. The

196 median and maximum depth estimates describe the growth limitations of seagrasses as a function

197 of water clarity, whereas minimum depth of growth was often where the highest percentage of

198 seagrass coverage was observed in the sample. Median and maximum depth estimates differ in

199 that the former describes the median depth of the deep water edge, whereas the latter describes a

200 nominal characterization of maximum depth independent of outliers.

201 Estimates for each of the three Z_c measures are obtained only if specific criteria are met.

202 These criteria were implemented as a safety measure that ensures a sufficient amount and

appropriate quality of data were used. First, estimates were provided only if a sufficient number of seagrass depth points were present within the radius of the grid point to estimate a logistic growth curve. This criteria applies to the sample size as well as the number of points with seagrass in the sample. The curve could not be estimated for small samples or if an insufficient number of points contained seagrass regardless of sample size. Second, estimates were provided only if an inflection point was present on the logistic curve within the range of the sampled depth data. This criteria applied under two scenarios where the curve was estimated but a trend was not adequately described by the sampled data. That is, a curve could be estimated that described only the initial decrease in points occupied as a function of depth but the observed points do not occur at depths deeper than the predicted inflection point. The opposite scenario occurred when a curve was estimated but only the deeper locations beyond the inflection point were present in the sample. Third, the estimate for $Z_{c,min}$ was set to zero depth if the linear curve through the inflection point intercepted the asymptote at x-axis values less than zero. The estimate for $Z_{c,med}$ was also shifted to the depth value halfway between $Z_{c,min}$ and $Z_{c,max}$ if $Z_{c,min}$ was fixed at zero. Finally, estimates were considered invalid if the 95% confidence interval for $Z_{c,max}$ included zero. Methods used to determine confidence bounds on Z_c estimates are described below.

All estimates were obtained using custom-made functions in program R that were based on the `nls` and `SSlogis` functions to fit nonlinear least squares using a self-starting logistic growth model (Bates and Chambers 1992, R Development Core Team 2014). All seagrass depth shapefiles were imported and processed in R using functions in the `rgeos` and `sp` packages (Bivand et al. 2008, Bivand and Rundel 2014).

224 **2.4 Comparison with segment-based approach and sensitivity analysis**

225 Spatially-resolved estimates for seagrass Z_c were obtained for each of the four segments
226 described above. Segment-wide estimates obtained using methods in [Hagy, In review](#) were used
227 as a basis of comparison such that departures from these values were evidence of spatial
228 heterogeneity in seagrass growth patterns and improved clarity of description in depth estimates
229 using the new approach. A sampling grid of locations for estimating each of the three depth
230 values in Fig. 4 was created for each segment. The grid was masked by the segment boundaries,
231 whereas seagrass depth points used to estimate Z_c extended beyond the segment boundaries to
232 allow sampling by grid points that occurred near the edge of the segment. Initial spacing between
233 sample points was chosen arbitrarily as 0.02 decimal degrees, which is approximately 2 km at 30
234 degrees N latitude. The sampling radius around each sampling location in the grid was also
235 chosen as 0.02 decimal degrees to allow for complete coverage of seagrass within the segment
236 while also minimizing redundancy of information described by each location. In other words,
237 radii were chosen such that the seagrass depth points sampled by each grid location were only
238 partially overlapped by those sampled by neighboring points.

239 The ability to characterize heterogeneity in seagrass growth patterns using the grid-based
240 approach can be informed by evaluating the level of confidence associated with Z_c estimates.
241 Confidence intervals for non-linear regression can be estimated using a Monte Carlo simulation
242 approach that considers the variance and covariance between the model parameters and the depth
243 measurements ([Hilborn and Mangel 1997](#)). For simplicity, we assume that the variability
244 associated with parameter estimates is the dominant source of uncertainty. A 95% confidence
245 interval for each Z_c estimate was constructed by repeated sampling of a multivariate normal

246 distribution followed by prediction of the proportion of points occupied by seagrass as in eq. (1).

247 The sampling distribution assumes:

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

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

255 The uncertainty associated with the Z_c estimates were based on the upper and lower limits
256 of the estimated inflection point on the logistic growth curve. This approach was used because
257 uncertainty in the inflection point is directly related to uncertainty in each of the Z_c estimates that
258 are based on the linear curve fit through the inflection point. Specifically, linear curves were fit
259 through the upper and lower estimates of the depth value at the inflection point to identify upper
260 and lower limits for the estimates of $Z_{c,min}$, $Z_{c,med}$, and $Z_{c,max}$. These values were compared
261 with the initial estimates from the linear curve that was fit through the inflection point on the
262 predicted logistic curve (i.e., Fig. 4c). This approach provided an indication of uncertainty for
263 individual estimates for the chosen radius. Uncertainty estimates were obtained for each Z_c
264 estimate for the grids in each segment.

265 **2.5 Developing a spatially coherent relationship of water clarity with depth
266 of colonization**

267 Information describing seagrass light requirements can be obtained from the maximum
268 depth estimates by evaluating spatial relationships with water clarity. In particular, increased
269 resolution of seagrass depth estimates compared with measures of water clarity can potentially
270 improve the ability to empirically describe light requirements and areas where seagrasses are
271 growing at depths deeper or shallower than expected. Secchi measurements provide a precise
272 estimate of water clarity and have been obtained at numerous locations documented in the Florida

273 Department of Environmental Protection's Impaired Impaired Waters Rule (IWR) database.

{acro:IWR}

274 Secchi data for Florida coastal waters were obtained from update 40 of the IWR database for all
275 of Tampa Bay (2010 coverage) and the Indian River Lagoon (2009 coverage) given the spatial
276 extent of secchi observations for the two locations. Secchi data within the previous ten years of
277 the seagrass coverage data were evaluated to capture water quality trends from the most recent
278 decade (i.e., 1999–2009 for the Indian River Lagoon and 2000–2010 for Tampa Bay). Secchi data
279 were screened to exclude observations that were flagged indicating that the value was lower than
280 the maximum depth of the observation point. Secchi data were also compared with bathymetric
281 data to verify unflagged values were not missed by initial screening. Secchi observations that
282 were measured at the same geographic location were averaged across all dates. This approach
283 was preferred given that seagrass depth patterns are more representative of long-term trends in
284 water clarity as opposed to individual secchi measures that may be highly variable (Dennison
285 1987, Dennison et al. 1993).

286 The relationship between seagrass depth limits and secchi measurements were explored
287 using established light requirements and attenuation equations. The traditional Lambert-Beer

288 equation describes the exponential decrease of light availability with depth:

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

289 such that the irradiance of incident light at depth Z (I_Z) can be estimated from the irradiance at
290 the surface (I_O) and a light extinction coefficient (K_d). Duarte (1991) indicate that minimum light
291 requirements for seagrass are on average 11% of surface irradiance. Light requirements may also
292 be species-specific and variable by latitude such that value may range from less than 5% to
293 greater than 30% (Dennison et al. 1993). Light requirements of seagrass at a specific location can
294 be estimated by rearranging eq. (3):

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

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

$$Z_{c,max} = \frac{-\log(0.20)}{1.7} \cdot Z_d \quad (5) \quad \{\text{eqn:sgregression}\}$$

300 A regression of seagrass depth estimates against secchi measurements is expected to have a slope
301 corresponding to the constant in eq. (5). For the current analysis, 20% light requirements were
302 assumed to be an approximate median requirement for seagrasses in Florida. Scatter in the

regression through these points can be considered biologically meaningful, such that points below the curve are locations where seagrasses are observed at maximum depth with less irradiance than expected given eq. (5), whereas points above the curve are those where seagrasses are growing deeper than expected. The geographic coordinates for each secchi measurement in Tampa Bay and the Indian River Lagoon were used as locations for estimating $Z_{c,max}$. These estimates were compared with the averaged secchi estimates to identify light requirements at each location. However, the relationship is expected to vary depending on the specific radius around each sample point for estimating $Z_{c,max}$. An appropriate radius was chosen that minimized the difference between the empirically estimated slope and that in eq. (5). The estimated light requirements of each point were also plotted using the cartesian coordinates of each secchi observation to evaluate spatial variation in seagrass growth as a function of light-limitation. Light requirements were also summarized by individual segments in each bay to identify spatial trends for relevant management units.

3 Results

3.1 Segment characteristics and seagrass depth estimates

Each of the four segments varied by several key characteristics that potentially explain within-segment variation of seagrass growth patterns (Table 1). Mean surface area was 191.2 square kilometers, with area decreasing for the Big Bend (271.4 km), Indian River Lagoon (NA 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 Indian River Lagoon (NA %), Old Tampa Bay (11.9 %), and Choctawhatchee Bay (5.9 %).

325 %). Visual examination of the seagrass coverage maps for the respective year of each segment
326 suggested that seagrasses were not uniformly distributed (Fig. 1). Seagrasses in the
327 Choctawatchee Bay segments were generally sparse with the exception of a large patch located to
328 the west of the inlet connection with the Gulf of Mexico. Seagrasses in the Big Bend segment
329 were located throughout the segment with noticeable declines near the outflow of the
330 Steinhatchee River, whereas seagrasses in Old Tampa Bay and the Indian River Lagoon segment
331 were generally confined to shallow areas near the shore. Seagrass coverage showed a partial
332 decline toward the northern ends of both Old Tampa Bay and the Indian River Lagoon segments.
333 Mean depth was less than 5 meters for each segment, excluding Choctawatchee Bay which was
334 slightly deeper than the other segments on average (5.3 m). Maximum depths were considerably
335 deeper for Choctawatchee Bay (11.9 m) and Old Tampa Bay (10.4 m), as compared to the Big
336 Bend (3.6 m) and Indian River Lagoon (NA m) segments. Water clarity as indicated by average
337 secchi depths was similar between the segments (1.5 m), although Choctawatchee Bay had a
338 slightly higher average (2.1 m).

339 Estimates of seagrass Z_c using a segment-wide approach that did not consider spatially
340 explicit locations indicated that seagrasses generally did not grow deeper than three meters in any
341 of the segments (Table 2). Maximum and median depth of colonization were deepest for the Big
342 Bend segment (3.7 and 2.5 m, respectively) and shallowest for Old Tampa Bay (1.1 and 0.9 m),
343 whereas the minimum depth of colonization was deepest for Choctawatchee Bay (1.8 m) and
344 shallowest for Old Tampa Bay (0.6 m). Averages of all grid-based estimates for each segment
345 were different than the segment wide estimates, which suggests potential bias associated with
346 using a whole segment as a relevant spatial unit for estimating depth of colonization. In most
347 cases, the averages of all grid-based estimates were less than the whole segment estimates,

348 suggesting the latter provided an over-estimate of seagrass growth limits. For example, the
349 average of all grid estimates for $Z_{c,max}$ in the Big Bend region suggested seagrasses grew to
350 approximately 2 m, which was 1.6 m less than the whole segment estimate. This reduction is
351 likely related to improved resolution of seagrass depth limits near the outflow of the Steinhatchee
352 river. Although reductions were not as severe for the average grid estimates for the remaining
353 segments, considerable within-segment variation was observed depending on grid location. For
354 example, the deepest estimate for $Z_{c,min}$ (2 m) in the Indian River Lagoon exceeded the average
355 of all grid locations for $Z_{c,max}$ (1.7 m). $Z_{c,min}$ also had minimum values of zero meters for the
356 Big Bend and Old Tampa Bay segments, suggesting that seagrasses declined continuously from the
357 surface for several locations.

358 Visual interpretations of seagrass depth estimates using the grid-based approach provided
359 further information on the distribution of seagrasses in each segment (Fig. 5). Spatial
360 heterogeneity in depth limits was particularly apparent for the Big Bend and Indian River Lagoon
361 segments. As expected, depth estimates indicated that seagrasses grew deeper at locations far
362 from the outflow of the SteinHatchee River in the Big Bend segment. Similarly, seagrasses were
363 limited to shallower depths at the north end of the Indian River Lagoon segment near the Merrit
364 Island National Wildlife Refuge. Seagrasses were estimated to grow at maximum depths up to 2.1
365 m on the eastern portion of the Indian River Lagoon segment. Spatial heterogeneity was less
366 distinct for the remaining segments. Seagrasses in Old Tampa Bay grew deeper in the northeast
367 portion of the segment and declined to shallower depths near the inflow at the northern edge.
368 Spatial variation in the Choctowatchee Bay segment was not apparent, although the maximum Z_c
369 estimate was observed in the northeast portion of the segment. Z_c values were not available for all
370 grid locations givne the limitations imposed in the estimation method. Z_c could not be estimated

371 in locations where seagrasses were sparse or absent, nor where seagrasses were present but the
372 sampled points did not exhibit a sufficient decline with depth. The latter scenario was most
373 common in Old Tampa Bay and Choctawhatchee Bay where seagrasses were unevenly distributed
374 or confined to shallow areas near the shore. The former scenario was most common in the Big
375 Bend segment where seagrasses were abundant but locations near the shore were inestimable
376 given that seagrasses did not decline appreciably within the depths that were sampled.

377 Uncertainty for estimates of $Z_{c, max}$ indicated that confidence intervals were generally
378 acceptable (i.e., greater than zero), although the ability to discriminate between the three depth
379 estimates varied by segment (Fig. 6 and Table 3). Mean uncertainty for all estimates in each
380 segment measured as the width of a 95% confidence interval was 0.2 m. Greater uncertainty was
381 observed for Choctawhatchee Bay (mean width of all confidence intervals was 0.7 m) and Old
382 Tampa Bay (0.4 m), compared to the Big Bend (0.1 m) and Indian River Lagoon (0.1 m)
383 segments. The largest confidence interval for each segment was 1 m for Old Tampa Bay, 2.5 m for
384 Choctawhatchee Bay, 0.4 m for the Big Bend, and 0.3 m for the Indian River Lagoon segments.
385 However, most confidence intervals for the remaining grid locations were much smaller than the
386 maximum in each segment. A comparison of overlapping confidence intervals for $Z_{c, min}$, $Z_{c, med}$,
387 and $Z_{c, max}$ at each grid location indicated that not every measure was unique. Specifically, only
388 12.5% of grid points in Choctawhatchee Bay and 38.9% in Old Tampa Bay had significantly
389 different estimates, whereas 84% of grid points in the Indian River Lagoon and 94.1% of grid
390 points in the Big Bend segments had estimates that were significantly different. By contrast, all
391 grid estimates in Choctawhatchee Bay and Indian River Lagoon had $Z_{c, max}$ estimates that were
392 significantly greater than zero, whereas all but 10% of grid points in Old Tampa Bay and 5.6% of
393 grid points in the Big Bend segment had $Z_{c, max}$ estimates significantly greater than zero.

394 **3.2 Evaluation of seagrass light requirements**

395 Estimates of seagrass light requirements for all segments of Tampa Bay and the Indian
396 River Lagoon indicated substantial variation, both between and within the different bays (Table 4
397 and Figs. 7 and 8). Seagrass Z_c estimates were obtained for 38 locations in Tampa Bay and 68
398 locations in the Indian River Lagoon where secchi observations were available in the Florida IWR
399 database. Mean secchi depth for all recorded observations was 1.9 m ($n = 38$) for Tampa Bay and
400 1 m ($n = 68$) for Indian River Lagoon. Mean light requirements were significantly different
401 between the bays (two-sided t-test, $t = 6.3$, $df = 52.8$, $p < 0.001$) with a mean requirement of
402 26.2% for Tampa Bay and 11.2% for Indian River Lagoon. Within each bay, light requirements
403 were significantly different between segments (ANOVA, $F = 1.2$, $df = 3, 34$, $p = 0.34$ for Tampa
404 Bay, $F = 8.9$, $df = 5, 62$, $p = 0.000$ for Indian River Lagoon). However, post-hoc evaluation of
405 all pair-wise comparisons of mean light requirements indicated that significant differences were
406 only observed between a few segments within each bay. Significant differences in Tampa Bay
407 were observed between Old Tampa Bay and Hillsborough Bay (Tukey multiple comparisons, $p =$
408 0.498). Significant differences in the Indian River Lagoon were observed between the Upper
409 Indian River Lagoon and Banana River ($p = 0.000$), the Upper Indian River Lagoon and Lower
410 Indian River Lagoon ($p = 0.000$), and Upper Indian River Lagoon and Lower St. Lucie ($p = \text{NA}$)
411 segments. In general, spatial variation of light requirements in Tampa Bay suggested that
412 seagrasses were less light-limited (i.e., lower percent light requirements at $Z_{c, max}$) in
413 Hillsborough Bay and western areas of Lower Tampa Bay near the Gulf of Mexico (Fig. 7).
414 Seagrassess in the Indian River Lagoon were generally less light-limited towards the south and in
415 the Banana River segment (Fig. 8).

416 **4 Discussion**

417 **References**

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Table 1: Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates (see Fig. 1 for spatial distribution). 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), 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
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

Table 2: Summary of seagrass depth estimates (m) for each segment using all grid locations in Fig. 5. 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	1.33	0.82	0.00	2.64
$Z_{c, med}$	2.46	1.68	0.77	0.66	2.85
$Z_{c, max}$	3.66	2.03	0.80	0.86	3.31
CB					
$Z_{c, min}$	1.82	1.57	0.72	0.00	2.27
$Z_{c, med}$	2.16	1.98	0.46	1.19	2.48
$Z_{c, max}$	2.50	2.40	0.32	1.86	2.74
OTB					
$Z_{c, min}$	0.61	0.52	0.29	0.05	0.98
$Z_{c, med}$	0.88	0.85	0.27	0.30	1.24
$Z_{c, max}$	1.15	1.18	0.39	0.37	1.81
UIRL					
$Z_{c, min}$	1.25	1.32	0.23	1.00	2.02
$Z_{c, med}$	1.51	1.49	0.21	1.12	2.08
$Z_{c, max}$	1.77	1.66	0.21	1.23	2.14

^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. 6. 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	0.11	0.10	0.01	0.35
CB	0.72	0.74	0.22	2.52
OTB	0.36	0.28	0.11	1.04
UIRL	0.09	0.06	0.01	0.30

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

Table 4: Summary of water clarity data and estimated light requirements for all bay segments of 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_{Secchi}), sample size of seagrass depth estimates (n_Z) at each unique secchi location, mean values (m) of secchi data, mean $Z_{c,max}$, and estimated % light requirements for each segment. Summaries are based primarily on data in Figs. 7 and 8.^{tab:secch_summ}

Segment ^a	Min year	Max year	n_{Secchi}	n_Z	Secchi	$Z_{c,max}$	% light
Indian River Lagoon							
BR	2000	2009	909	21	1.06	1.49	8.04
LCIRL	2000	2009	656	19	1.03	1.42	10.90
LIRL	2000	2005	111	6	0.93	1.53	7.18
LML	2000	2009	239	13	1.11	1.32	10.04
LSL	2000	2005	52	3	0.94	NA	NA
UCIRL	2000	2009	1165	35	1.13	1.46	9.11
UIRL	2000	2009	599	15	1.30	1.10	24.20
UML	2000	2009	258	11	1.03	NA	NA
Tampa Bay							
HB	2001	2003	412	10	1.25	0.75	37.93
LTB	2001	2009	807	26	2.47	2.06	22.84
MTB	2001	2009	571	16	2.18	1.61	27.72
OTB	2001	2003	671	15	1.44	1.17	25.49

^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.

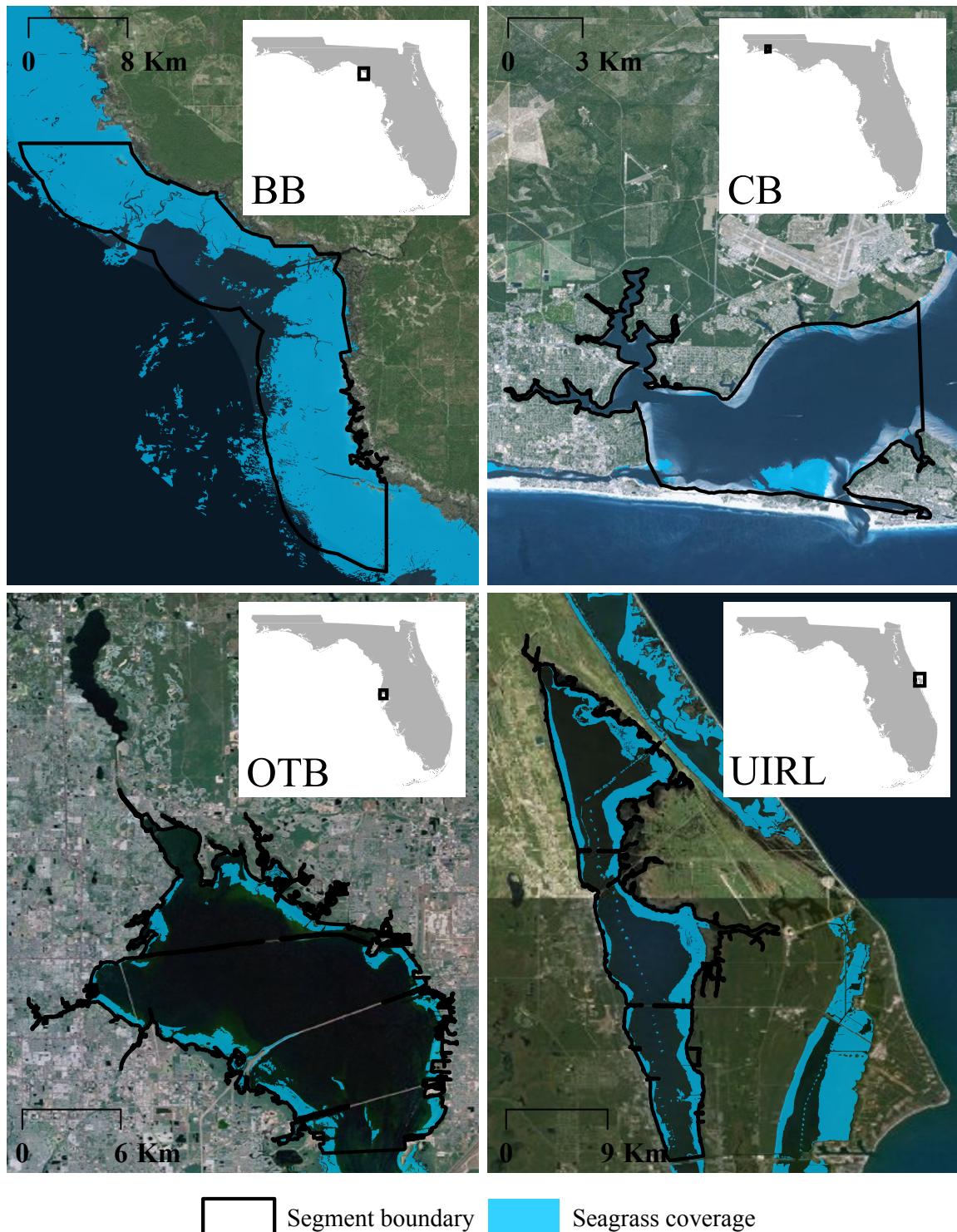


Fig. 1: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (CB: Choctawhatchee Bay), 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay), and 2009 (UIRL: Upper Indian R. Lagoon).

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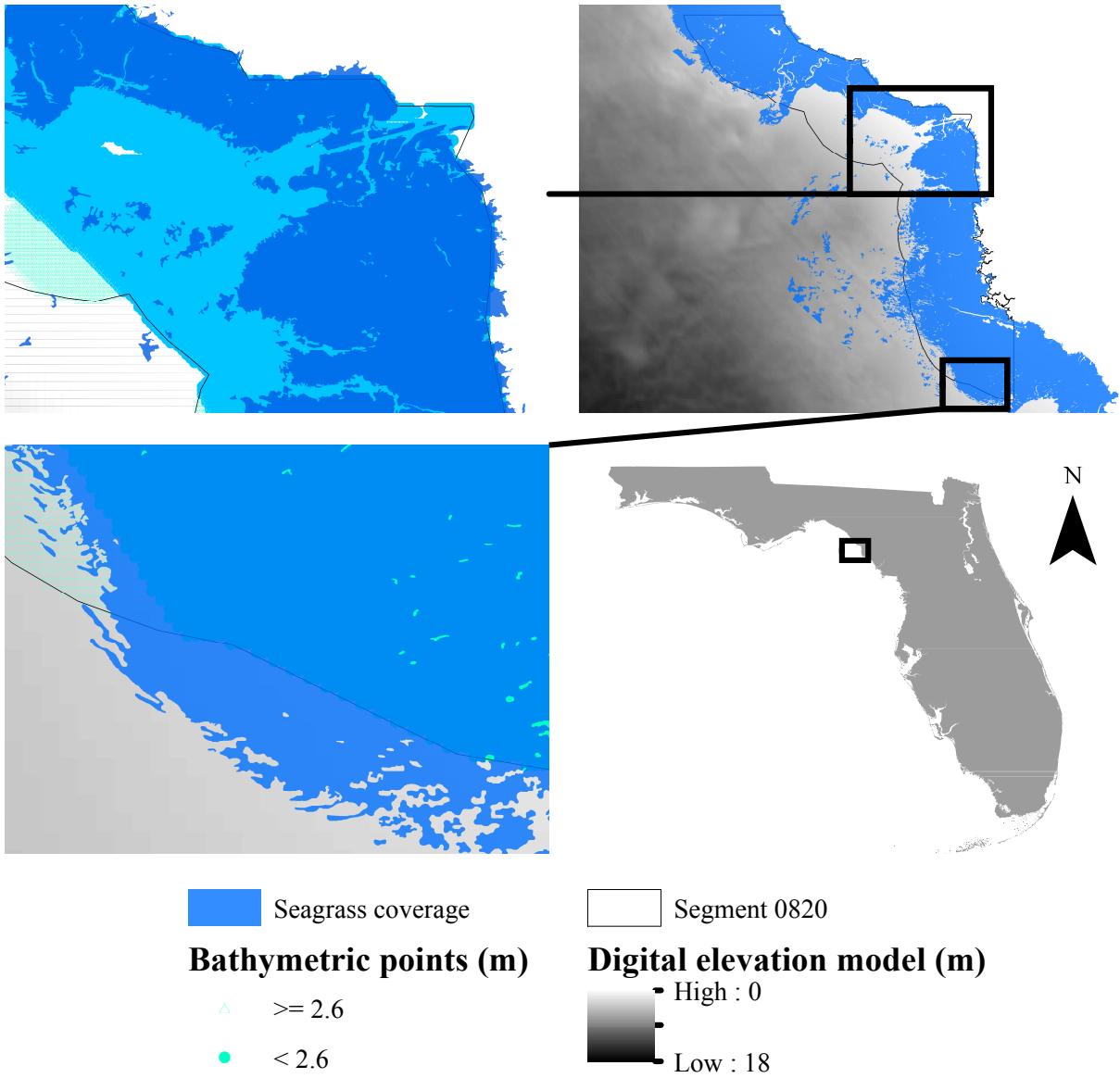
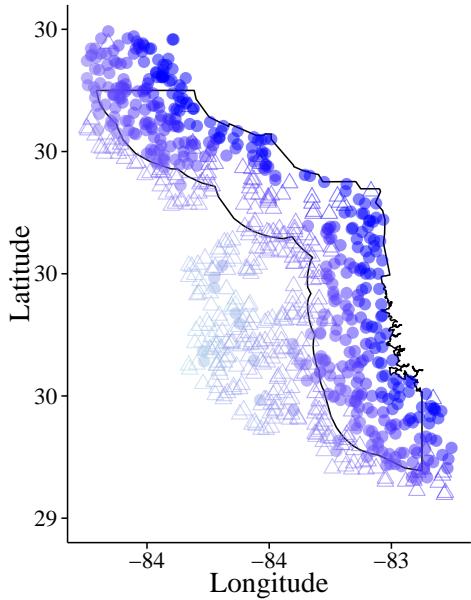


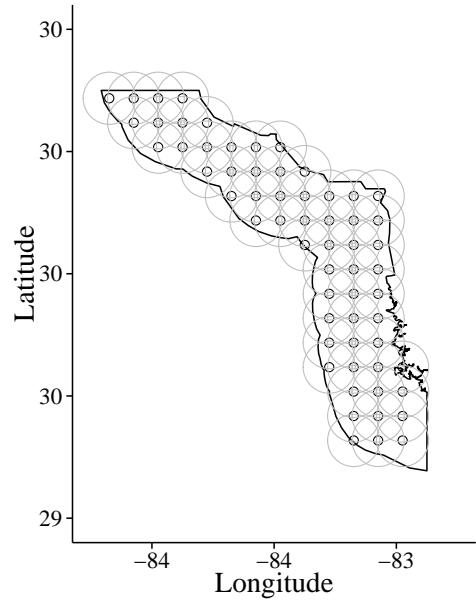
Fig. 2: Example of over- and under-estimates for seagrass depth of colonization for a segment in the Big Bend region, Florida. Layers include a seagrass coverage layer, bathymetric depth points, bathymetric digital elevation model, and spatial extents for the segment and Florida. The top-left figure indicates over-estimation and the bottom-left indicates under-estimation. Bathymetric points are color-coded by the median depth of colonization estimate for seagrass using data from the whole segment (2.6 m).

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(a) Seagrass depth points for the segment



(b) Grid of locations and sample areas for estimates



(c) Sampled observations for a test point

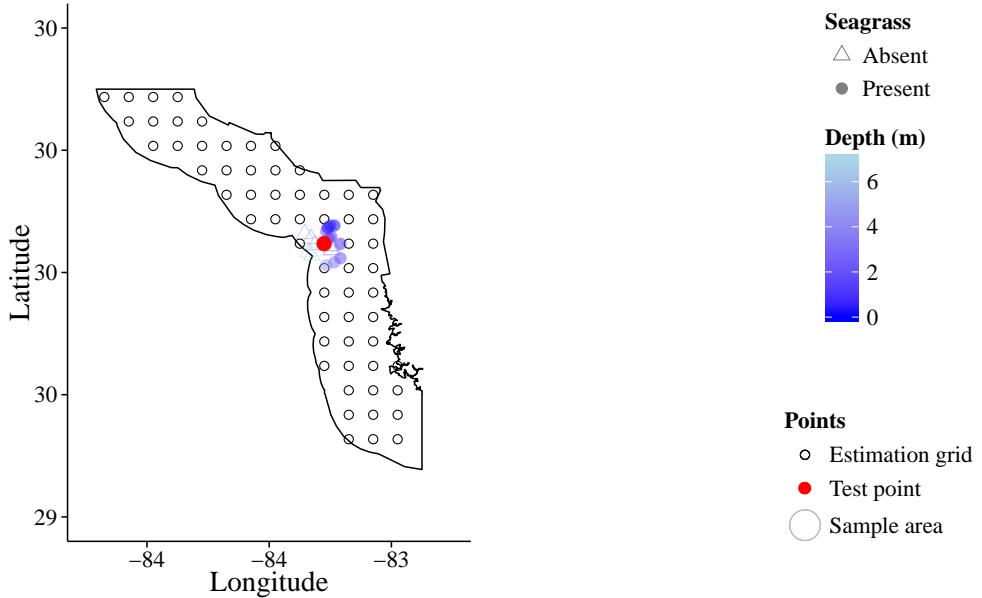
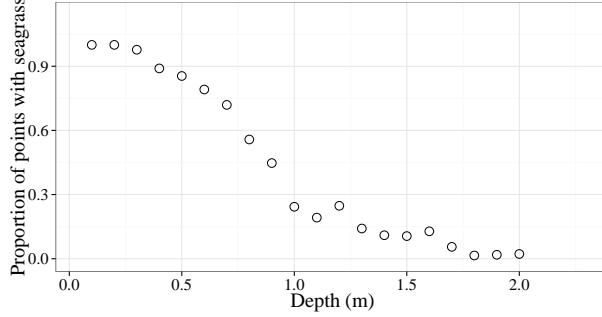


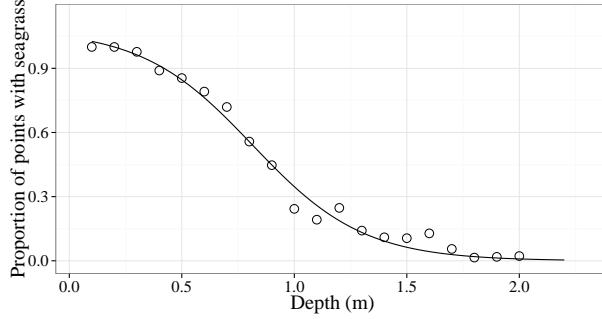
Fig. 3: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 3a shows the seagrass depth points that are used for sampling, Fig. 3b shows a grid of locations and sampling radii for estimating seagrass Z_c , and Fig. 3c shows an example of sampled seagrass depth points for a location. Estimates in Fig. 4 were obtained from the sampled location in Fig. 3c.

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(a) Proportion of points with seagrass by depth



(b) Logistic growth curve fit through points



(c) Depth estimates

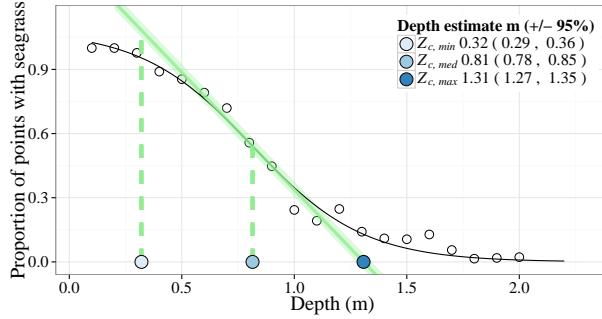


Fig. 4: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 4a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 3. Fig. 4b adds a decreasing logistic growth curve fit through the points. Fig. 4c shows three depth estimates based on a linear curve fit through the inflection point of logistic growth curve.

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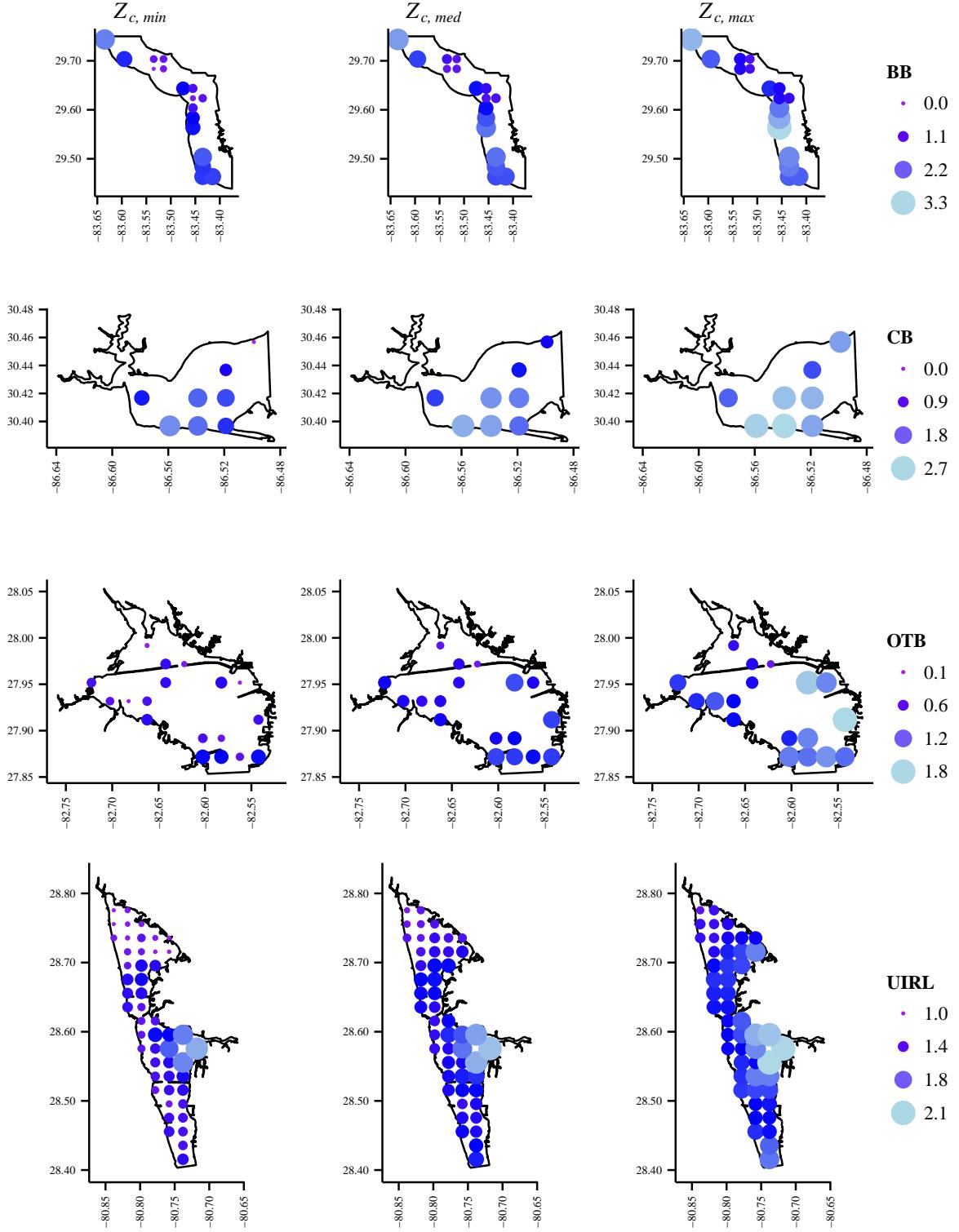


Fig. 5: Spatially-resolved estimates of seagrass depth limits (m) for four coastal segments of Florida. Estimates include minimum ($Z_{c, \text{min}}$), median ($Z_{c, \text{med}}$), and maximum depth of colonization ($Z_{c, \text{max}}$). Estimates are assigned to grid locations for each segment, where 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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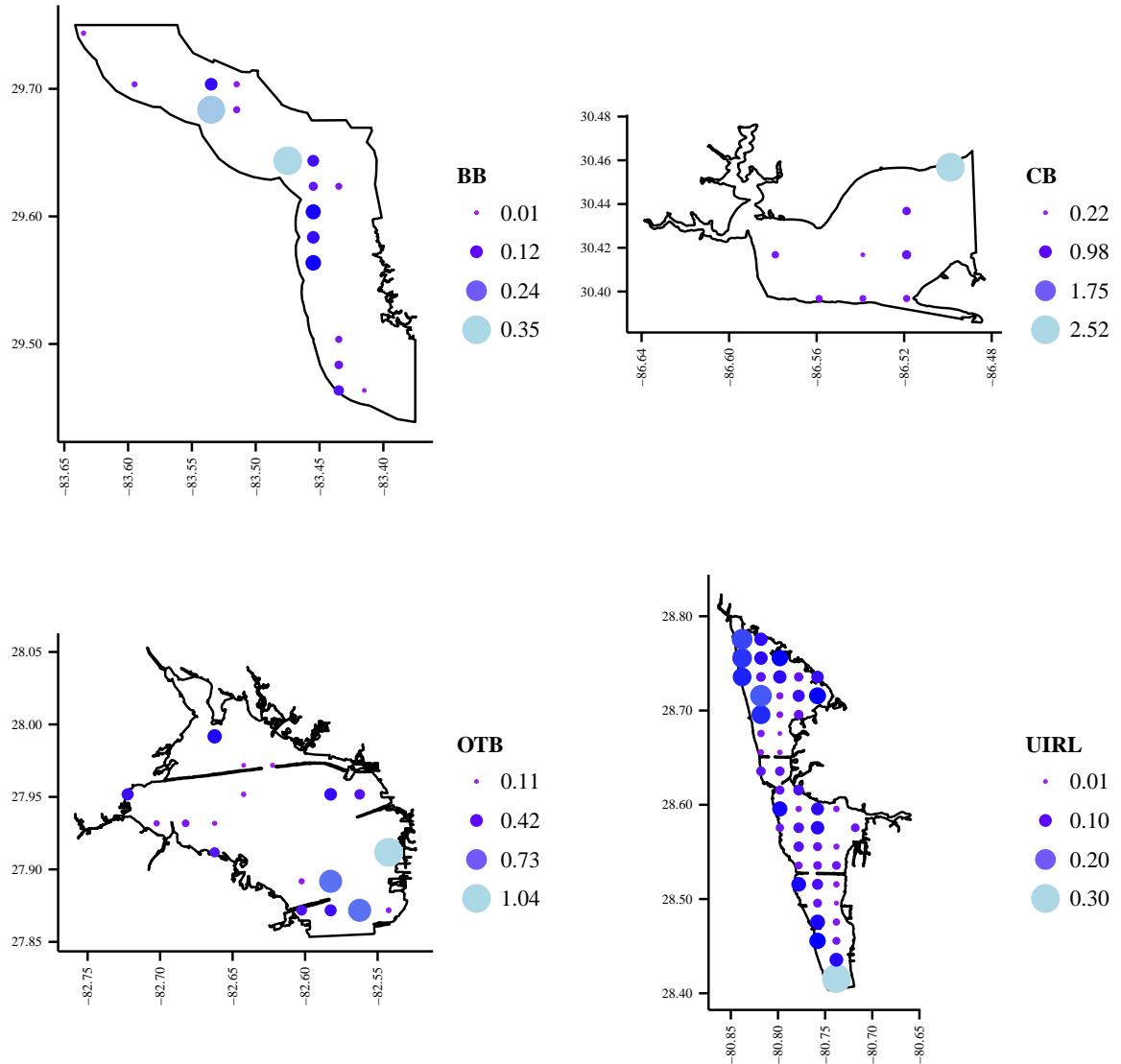


Fig. 6: Size of confidence intervals (m) for depth of colonization estimates in Fig. 5. Points are colored and sized based on the difference between the upper and lower bounds of a 95% confidence interval for all three Z_c estimates ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$). Bounds were obtained using Monte Carlo simulations to estimate uncertainty associated with the inflection point of the estimated logistic curve (Fig. 4) for each sample. BB: Big Bend, CB: Choctawhatchee Bay, OTB: Old Tampa Bay, UIRL: Upper Indian R. Lagoon.

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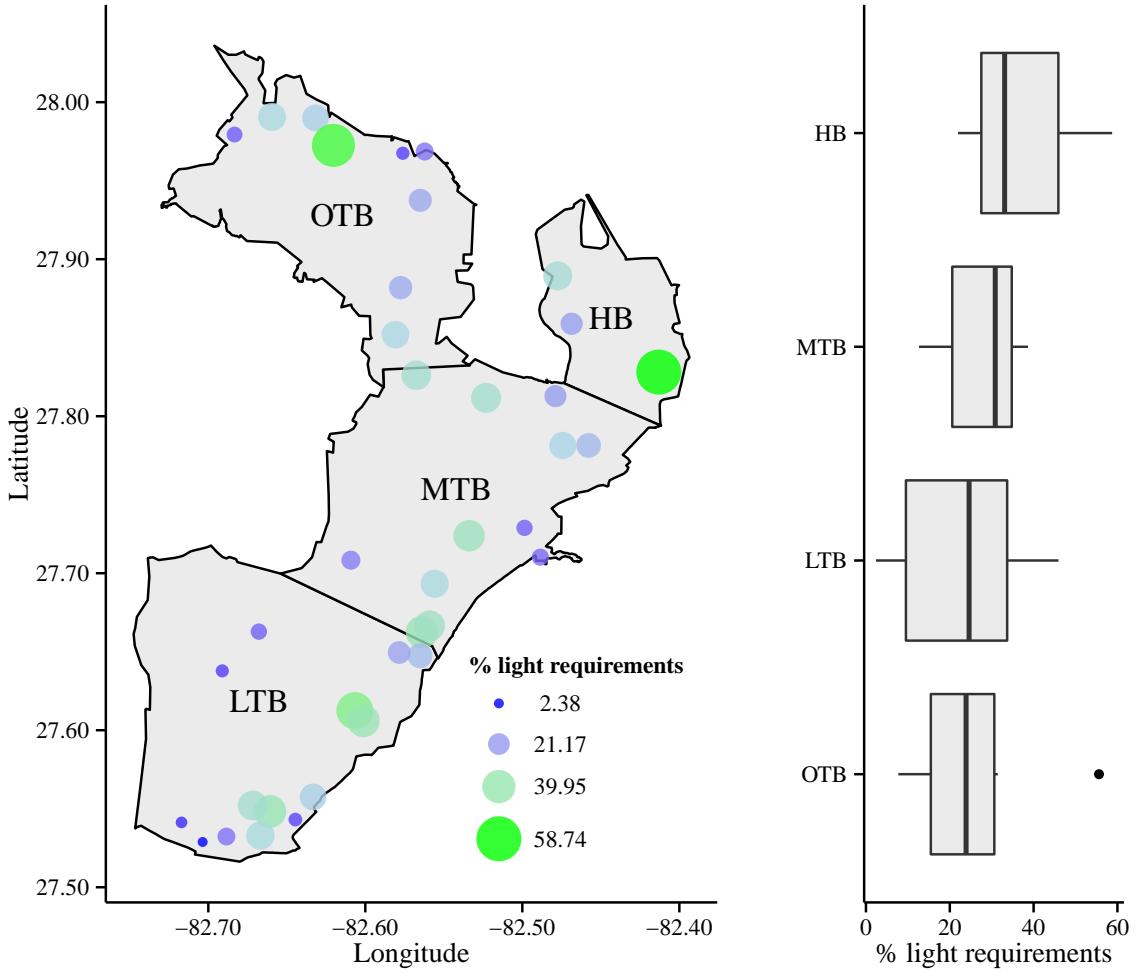


Fig. 7: Estimated light requirements of seagrass for multiple locations in Tampa Bay, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend beyond the boxes as 1.5 multiplied by the interquartile range. Light requirements are based on daily average secchi values for each location using all observations for Tampa Bay, estimated maximum depth of colonization using a radius of 0.7 decimal degrees for each secchi location to sample seagrass depth points for 2010 coverage data, and empirical relationships described by eq. (3). HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay.

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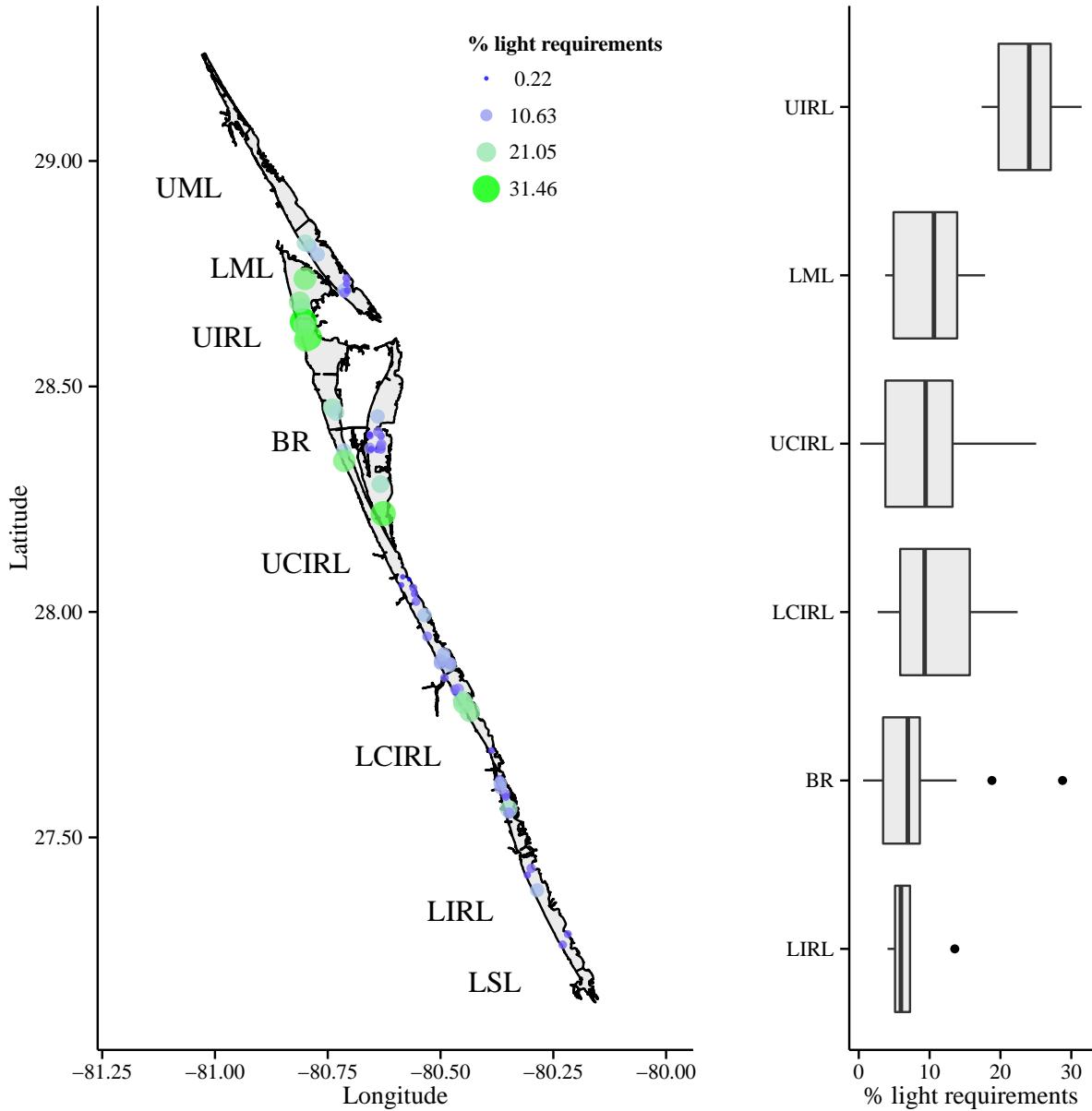


Fig. 8: Estimated light requirements of seagrass for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots as in Fig. 7. Light requirements are based on daily average secchi values for each location using all observations for Tampa Bay, estimated maximum depth of colonization using a radius of 0.02 decimal degrees for each secchi location to sample seagrass depth points for 2009 coverage data, and empirical relationships described by eq. (3). 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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