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Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization
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Abstract:	Depth of colonization (Zc) is a useful seagrass growth metric that describes seagrass response to light attenuation. Similarly, percent surface irradiance (% SI) at Zc is a measure of seagrass light requirements with applications in seagrass ecology and management. Methods for estimating Zc and % SI, and the resulting estimates are highly variable making meaningful comparisons among estimates difficult. A new algorithm is presented to compute maps of median and maximum Zc, Zc, med and Zc,max, respectively, for four Florida coastal areas (Big Bend, Tampa Bay, Choctawhatchee Bay, Indian River Lagoon). Maps of light attenuation (Kd) based on SeaWiFS satellite imagery, PAR profiles, and Secchi depth measurements were combined to produce maps of % SI at Zc,med and Zc,max. Among estuary segments, mean Zc,med varied from (±s.e.) 0.86±0.08 m for Old Tampa Bay to 1.96±0.10 m for Western Choctawhatchee Bay. Coefficients of variation for Zc,med were 1-10%. Percent SI at Zc,med averaged 19% for Indian River Lagoon (range = 9-24%), 42% for Tampa Bay (37-49%) and 56% for Choctawhatchee Bay (51-67%). Estimated light requirements were significantly lower in Indian River Lagoon than in the other estuaries, while estimates for Tampa Bay and Choctawhatchee Bay were higher than the often cited estimate of 20%. Spatial gradients in depth of colonization and % SI were apparent in all estuaries. The analytical approach, implemented in R, could be applied easily to new data from these estuaries or to other estuaries and could be incorporated routinely in assessments of seagrass status and condition.
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RESEARCH AND DEVELOPMENT

July 25, 2016

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Co-Editors-In-Chief
Estuaries and Coasts

I am pleased to submit our manuscript, "Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization," for publication as an original research article in Estuaries and Coasts.

Seagrass depth limits have been used for decades to characterize light regimes and water quality requirements that maintain critical habitat in coastal waters. Several methods have been developed and applied in different contexts that complicate meaningful comparisons between systems, including methods that link depth limits and water clarity to estimate light requirements. In this manuscript, we present a novel method to estimate seagrass depth of colonization and light requirements that incorporates seagrass coverage maps and estimates of water clarity from remote sensing products. Our method is novel and useful because it documents spatial variation in a way that has not been achieved previously, thereby improving our understanding of relationships between water quality and seagrass. We are also able to separate "uncertainty" and "variability" to an extent not previously attempted, which is invaluable in both scientific and management applications. Our spatially resolved estimates provide a viable alternative to broad application of a single rule of thumb for light requirements. Both the questions that we address and our methods should be of broad interest in seagrass ecology and to those interested in managing coastal ecosystems.

Please feel free to contact me with any questions or concerns about our submission. I can be reached at (850) 934-2480 and beck.marcus@epa.gov. We appreciate the opportunity to publish our work with Estuaries and Coasts.

Sincerely,

Marcus W. Beck, PhD

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

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32   **Abstract**

33   Depth of colonization (Z_c) is a useful seagrass growth metric that describes seagrass response to

34   light attenuation. Similarly, percent surface irradiance (% SI) at Z_c is a measure of seagrass light

35   requirements with applications in seagrass ecology and management. Methods for estimating Z_c

36   and % SI, and the resulting estimates are highly variable making meaningful comparisons among

37   estimates difficult. A new algorithm is presented to compute maps of median and maximum Z_c, $Z_{c,med}$

38   and $Z_{c,max}$, respectively, for four Florida coastal areas (Big Bend, Tampa Bay, Choctawhatchee

39   Bay, Indian River Lagoon). Maps of light attenuation (K_d) based on SeaWiFS satellite imagery,

40   PAR profiles, and Secchi depth measurements were combined to produce maps of % SI at $Z_{c,med}$

41   and $Z_{c,max}$. Among estuary segments, mean $Z_{c,med}$ varied from (±s.e.) 0.86±0.08 m for Old Tampa

42   Bay to 1.96±0.10 m for Western Choctawhatchee Bay. Coefficients of variation for $Z_{c,med}$ were 1-

43   10%. Percent SI at $Z_{c,med}$ averaged 19% for Indian River Lagoon (range = 9-24%), 42% for Tampa

44   Bay (37-49%) and 56% for Choctawhatchee Bay (51-67%). Estimated light requirements were

45   significantly lower in Indian River Lagoon than in the other estuaries, while estimates for Tampa

46   Bay and Choctawhatchee Bay were higher than the often cited estimate of 20%. Spatial gradients

47   in depth of colonization and % SI were apparent in all estuaries. The analytical approach,

48   implemented in R, could be applied easily to new data from these estuaries or to other estuaries and

49   could be incorporated routinely in assessments of seagrass status and condition.

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51   **Key words**: seagrass, depth of colonization, light requirements, remote sensing

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Introduction

Seagrasses are ecologically valuable components of aquatic ecosystems that have a critical role in shaping aquatic habitat. These 'ecosystem engineers' influence multiple characteristics of aquatic systems through interactions with many biological and abiotic components (Jones *et al*. 1994; Koch 2001). For example, seagrasses reduce wave action, stabilize sediments, and provide habitat and refuge for invertebrates and juvenile fish (Williams and Heck 2001; Hughes *et al*. 2009). Seagrasses also respond to changes in water clarity via physiological linkages with light availability. Seagrass coverage declines with water depth due to light attenuation, and declines more rapidly in productive aquatic systems where light attenuation is relatively high (Duarte 1995). The light-limited maximum depth to which seagrass grows is variously called "depth limits" or "depth of colonization." Empirical relationships between nutrient loading, water clarity, light requirements, and depth of colonization have been identified (Duarte 1991; Kenworthy and Fonseca 1996; Choice *et al*. 2014) and have been used to characterize light regimes and other water quality requirements to maintain seagrass habitat (Janicki and Wade 1996; Steward *et al*. 2005). Seagrasses may be particularly useful in this respect because they respond to water quality over relatively long time scales, "integrating" their exposure to stress. Thus, time scales of seagrass response better match time scales for monitoring, assessment and nutrient management (Duarte 1995; Burkholder *et al*. 2007).

A variety of approaches have been used to estimate seagrass depth of colonization. A common *in situ* approach is to sample seagrass along depth transects until the maximum depth is adequately characterized (e.g., Spears *et al*. 2009; Choice *et al*. 2014). Alternative techniques include underwater photos or videos, aquascope identification, or hydroacoustic assessments (Zhu *et al*. 2007; Søndergaard *et al*. 2013). These are especially useful for site-specific evaluations where the analysis needs are driven by local questions (e.g., Iverson and Bittaker 1986; Hale *et al*. 2004). Availability of estuary-scale geospatial data for seagrass coverage, based on photo-interpretation of aerial imagery, suggests that standardized techniques can be applied at similarly large spatial scales and would be valuable for a variety of scientific and policy applications. For such large scale analysis, it is often useful to subdivide water bodies into segments for the purpose of analysis and policy development (e.g., Steward *et al*. 2005; Schaeffer *et al*. 2012; US EPA 2012). One challenge in doing so is that estuaries are often characterized by gradients in water

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82 quality, such that any segmentation scheme is likely to include within-segment gradients in water

83 quality and associated seagrass depth of colonization.

84   An example from the Big Bend region of Florida illustrates the issue of scale in analyzing

85 seagrass depth of colonization (Fig. 1a). In a segment from this region, the highest depth of

86 colonization largely occurs around the outer perimeter of the mapped seagrass coverage (red line in

87 Fig. 1a). However, depth-dependent seagrass growth patterns are also evident at smaller spatial

88 scales within the segment, wherein the segment-scale depth of colonization overestimates the depth

89 distribution near the outflow of the Steinhatchee River, where high concentrations of colored

90 dissolved organic matter reduce water clarity locally (personal communication, N. Wellendorf,

91 Florida Department of Environmental Protection). An improved method for estimating depth of

92 colonization should have sufficient flexibility to characterize seagrass responses at a large scale,

93 such as the segment average, while still resolving important patterns at smaller scales, such as the

94 local impact of a river outflow. Developing and demonstrating this capability was one objective of

95 this study.

96   Another objective of this study was to combine spatially-resolved estimates of depth of

97 colonization with water clarity measures at the same spatial scales to characterize the pattern and

98 range of seagrass light requirements in estuaries. Although not always the case, the spatial

99 distribution of submersed aquatic plants is often associated with light availability (Barko *et al*.

100 1982; Hall *et al*. 1999; Dennison *et al*. 1993), wherein depth of colonization is controlled by light

101 requirements needed and average water clarity. Published estimates of seagrass light requirements

102 are quite variable. Duarte (1991) reported that seagrasses can extend to depths receiving an

103 average of 11% of surface irradiance, while estimates of light requirements for seagrass in

104 Chesapeake Bay were about 20% (Batiuk *et al*. 1992). Dennison *et al*. (1993) reported minimum

105 light requirements, defined as the percent light at the maximum depth limit, ranging from less than

106 5% to greater than 30% depending on site conditions. Estimates of ~20% are common in the

107 literature, approximating a value in the middle of published estimates (see also Kemp *et al*. 2004).

108 An estimate of ~ 20% for seagrass in Florida estuaries has been applied for management purposes

109 in Tampa Bay, Choctawhatchee Bay, and elsewhere in Florida (e.g., FDEP 2012; US EPA 2012)

110 and can be traced to the estimate of 22.5% for lower Tampa Bay from Dixon and Leverone (1995).

111   Sources of variation in estimates of seagrass light requirements are numerous and include

112 physiological differences among seagrass species, differences in attenuation of light on the surface

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113   of seagrass leaves, and variations in other physiological stressors such as salinity or water

114   temperature (Kenworthy *et al*.1991; Kemp *et al*. 2004; Choice *et al*. 2014).   Differences in

115   operational definitions and method of estimation are also likely to contribute to differences in

116   reported values. For example, Dennison *et al*. (1993) defined minimal light requirements as the

117   percent light at the maximal depth limit for seagrass – where depth limit was defined variously by

118   different included studies. Choice *et al*. (2014) applied a statistical method to data from individual

119   stations seeking to find the percentage of surface irradiance linked to seagrass percent cover or

120   shoot density of zero. In this study, we sought to generate more comparable estimates by broadly

121   applying the same method to characterize seagrass depth of colonization and relating it to estimates

122   of water clarity at similar scales. We defined light requirements following Dennison et al. (1993),

123   except that we operationally defined depth of colonization in terms of our approach.

124   To quantify water clarity at temporal and spatial scales relevant to understanding seagrass

125   distributions in coastal ecosystems, we used estimates derived from satellite remote sensing along

126   with more conventional water clarity observations (light profiles, Secchi depth). Ocean color data

127   from satellite remote sensing can provide consistent estimates of water clarity across a large spatial

128   extent, often with a high return frequency and sustained data collection, which is ideal for

129   characterizing average water clarity (Woodruff *et al*. 1999; Chen *et al*. 2007). Since seagrass

130   growth responds to relatively long-term seasonal and inter-annual patterns in water clarity, it is

131   ideal for matching with data from satellite remote sensing. Secchi depth or other measures of water

132   clarity can also be useful, either to validate remote sensing observations, or for direct use when

133   remote sensing cannot be used. However, uneven sampling in space and time can make it harder to

134   obtain sufficient long-term averages (Elsdon and Connell 2009). Moreover, Secchi depth

135   measurements can be problematic in shallow, relatively clear waters, where the Secchi disk is

136   likely to be visible on the bottom.

137   This study describes an algorithm for estimating seagrass depth of colonization and light

138   requirements at a variety of spatial scales using geospatial datasets describing seagrass coverage

139   and satellite remote sensing data of light attenuation in the water column. Study objectives were to

140   1) describe the method for estimating seagrass depth of colonization, 2) apply the technique to four

141   target estuaries in Florida to illustrate quantification of seagrass growth patterns, and 3) develop a

142   spatial description of relationships among depth limits and water clarity, characterizing patterns in

143   light requirements in each case study. We then apply the estimates to characterize spatial variation

144   in light requirements within and among regions.

145

146   **Methods**

147   *Study sites and data sources*

148   Study sites included four coastal areas in Florida: the Big Bend region (northeast Gulf

149   coast), Choctawhatchee Bay (panhandle), Tampa Bay (central Gulf coast), and Indian River

150   Lagoon (Atlantic coast; Table 1 and Fig. 2). Florida's estuaries and coastal waters are partitioned

151   into segments following a scheme developed by the US Environmental Protection Agency for

152   numeric nutrient criteria. The method for estimating depth of colonization was evaluated initially

153   using one segment in each of our 4 areas, chosen based on data availability and gradients in water

154   clarity. These segments included Big Bend (BB), Western Choctawhatchee Bay (WCB), Old

155   Tampa Bay (OTB), and Upper Indian River Lagoon (UIRL). The analysis was then expanded to

156   quantify spatially-resolved seagrass depth limits and associated light requirements for all the

157   segments in three of the estuaries, omitting the Big Bend from further analysis due to insufficient

158   water clarity data.

159   Geospatial data describing seagrass coverage and bathymetry were used to estimate depth

160   of colonization. These data are available for coastal regions of Florida from the US Geological

161   Survey, Florida Department of Environmental Protection, Florida Fish and Wildlife Conservation

162   Commission, and Florida's watershed management districts. Seagrass coverage maps were

163   obtained for a recent year in each of the study sites (Table 1). The original coverage maps were

164   produced by photo-interpreting aerial images to categorize seagrass as absent, discontinuous

165   (patchy), or continuous. We aggregated to two categories, present (continuous and patchy) and

166   absent.

167   Bathymetry data were obtained from the National Oceanic and Atmospheric

168   Administration's (NOAA) National Geophysical Data Center (http://www.ngdc.noaa.gov/) as

169   either Digital Elevation Models (DEMs) or as bathymetric sounding data from hydroacoustic or

170   other surveys. Tampa Bay bathymetry provided by the Tampa Bay National Estuary Program are

171   described in Tyler *et al*. (2007). Bathymetry for the Indian River Lagoon was obtained from the St.

172   John's Water Management District (CPE 1997). Because the vertical datum (i.e., MLLW,

173   NAVD88, etc.) varied, all bathymetric data were vertically adjusted to local mean sea level using

174 the NOAA VDatum tool (http://vdatum.noaa.gov/). Adjusted data were combined with seagrass

175 coverage layers using standard union techniques for raster and vector layers in ArcMap 10.1 (ESRI

176 2012). To reduce computation time, bathymetry layers were first masked using a 1 km buffer of the

177 seagrass coverage layer. Raster bathymetric layers were converted to point layers to combine with

178 seagrass coverage maps, described below.

179

180 *Quantifying water clarity*

181   Satellite remote sensing imagery was used to create a gridded 1 km^2 map of estimated water

182 clarity for Tampa Bay and Choctawhatchee Bay. Secchi depth measurements were used to

183 quantify water clarity for the Indian River Lagoon because light scattering from bottom reflectance

184 and reflectance from shoreline areas prevented use of satellite remote sensing measurements.

185   For Tampa Bay and Choctawhatchee Bay, daily MODIS (Aqua level-2) satellite data were

186 downloaded from the NASA website (http://oceancolor.gsfc.nasa.gov/) for the five years preceding

187 the year the seagrass imagery was acquired. Images were reprocessed using the SeaWiFS Data

188 Analysis System software (SeaDAS, Version 7.0). For Tampa Bay, water clarity was derived from

189 daily MODIS images using a previously-developed algorithm that estimates Secchi depth based on

190 satellite-derived estimates of the diffuse attenuation coefficient at 490 nm (K_d (490), Chen *et al*.

191 2007). Monthly and annual mean water clarity was calculated from the daily images and then

192 averaged to create a single layer. Similarly, K_d for Choctawhatchee Bay was derived from MODIS

193 using the QAA algorithm (Lee *et al*. 2005). Monthly field measurements of K_d obtained in 2010 at

194 ten locations in Choctawhatchee Bay were used to correct annual means of the un-validated

195 satellite values ($K_{d, MODIS}$) to match annual means of *in situ* measurements (model II regression:

196 $K_d=0.65K_{d,MODIS}$, $r^2=0.93$) Field K_d estimates were computed from regressions of underwater PAR

197 (4 pi Biospherical PAR sensor on SBE25 CTD profiler) vs. depth. The regression based on 2010

198 data was applied to all five years of annual mean satellite-derived K_d data prior to averaging to

199 create a single layer for further analysis.

200   For Indian River Lagoon, secchi depth data (meters, Z_{Secchi}) collected within ten years prior

201 to the seagrass coverage data (i.e., 1999–2009) were obtained from the state of Florida's impaired

202 waters rule (IWR) database, update 40. A 10-year averaging period was used for Indian River

203 Lagoon to compensate for uneven temporal coverage, whereas 5-year averages were used for the

204 other estuaries. Stations with less than five observations were removed as were observations

205   flagged as a lower limit (i.e., Secchi disk visible on bottom). As an additional data quality screen,

206   Secchi data were compared with bathymetry to ensure that the reported Secchi depth was less than

207   water depth.

208

209   *Estimating seagrass depth of colonization*

210   Seagrass depth of colonization (Z_c) was computed by overlaying seagrass coverage maps

211   and bathymetry data to generate a point shapefile with attributes of location, depth (m), and

212   seagrass presence or absence. The proportion of points with seagrass present was computed within

213   discrete depth bins, spanning the full range of depths. Depth bins were dynamically selected,

214   ensuring that bins were no larger than 0.5 m and contained no more than 50 bathymetric soundings.

215   For whole segments using a large radius, these limits were changed to 0.1 m and 1000 points. If a

216   very large number of soundings were present, this approach generated a larger number of narrower

217   bins, while producing the opposite given a smaller number of observations. Three depth of

218   colonization metrics were derived from the empirical pattern of seagrass presence vs. depth. These

219   included minimum ($Z_{c,min}$), median ($Z_{c,med}$), and maximum ($Z_{c,max}$) depth of colonization. These

220   terms each describe meaningful points on the depth distribution of the seagrass coverage map. $Z_{c,max}$

221   is the deepest depth at which a significant coverage of mappable seagrasses occurred, excluding

222   infrequent observations at deeper depths. $Z_{c,med}$ is the median depth of the deep water edge of

223   seagrass. Finally, $Z_{c,min}$ approximates the depth at which seagrass percent cover begins to decline

224   with increasing depth, which may occur at $Z=0$ m.

225   The algorithm for estimating Z_c was implemented recursively for locations on a grid

226   covering the study area, resulting in a map of depth of colonization. It was also implemented at a

227   single central location in estuary segments with a radius large enough to encompass all

228   observations in the segment. At each location, the seagrass-depth data (i.e., merged bathymetric

229   and seagrass coverage data) was extracted within a radius from the chosen location (Fig. 1).

230   Geospatial data were imported and processed using functions in the rgeos and sp packages in R

231   (Bivand *et al*. 2008; Bivand and Rundel 2014). A Z_c estimate for each location was then quantified

232   by computing the proportions of points containing seagrass as a function of depth (Fig. 3a). The

233   radius for selecting data was made large enough to encompass both a sufficient number of data

234   points and a gradient in seagrass coverage with respect to water depth, but small enough to resolve

235   spatial patterns. An overly large radius will decrease the spatial resolution of the resulting estimates

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236 and could encompass areas with differences in the depth distribution of seagrass. In general, a

237 sufficient radius will result in a plot illustrating a decreasing proportion of points with seagrass

238 with increasing depth (Fig. 3).

239   At each location, a logistic function was fitted to the extracted depth points using non-linear

240 regression, quantifying the decrease in seagrass cover with respect to depth (Equation 1; Fig. 3):

241
$$P = \frac{\alpha}{1 + \exp\big((\beta - Z)/\gamma\big)} \tag{1}$$

242 where the proportion of points with seagrass present, P, within each depth bin, centered at Z, was

243 defined by a logistic curve with an upper asymptote α, an inflection point β, and a scale parameter

244 γ. The curve was fitted by minimizing the residual sums-of-squares with the Gauss-Newton

245 algorithm (Bates and Chambers 1992). Initial parameter values for fitting were estimated as

246 $\alpha=\max(P)$, $\beta=\text{median}(Z)$ and $\gamma=75^{\text{th}}$ percentile(Z) - median(Z). The maximum rate of decrease in

247 seagrass coverage respect to Z is $-\alpha/4\gamma$ and occurs at $Z=\beta$. The tangent at $Z=\beta$ passes through the

248 line P=α at $Z=\beta-2\gamma$ and through P=0 at $Z=\beta+2\gamma$. The three seagrass depth of colonization metrics

249 were defined in terms of these reference values as follows:

250     $$Z_{c,min} = \max(\beta - 2\gamma, 0) \tag{2}$$

251     $$Z_{c,max} = \beta + 2\gamma \tag{3}$$

252     $$Z_{c,med} = \begin{cases} \beta & \text{when } \beta\text{-}2\gamma > 0 \\ (\beta + 2\gamma)/2 & \text{otherwise} \end{cases} \tag{4}$$

253   Several quality control measures were implemented to reduce spurious estimates. First, Z_c

254 parameters (i.e., depth of colonization) were estimated only if the number of seagrass depth points

255 was sufficient for the logistic curve to be estimable. Second, estimates were provided only if the

256 fitted value for β, the inflection point on the logistic curve, was within the range of depth, Z, in the

257 data. It was possible for β-2γ to be less than zero, and this was common when seagrass cover

258 declined immediately as depth increased from zero (Fig. 3B). In these cases, $Z_{c,min}= 0$ and $Z_{c,med}$ is

259 half the depth from zero to $Z_{c,max}$ (Fig. 3B).

260   Estimates of parameter uncertainty from the logistic model were also used to evaluate the

261 quality and variability associated with individual depth of colonization estimates. Elements of the

262 model-estimated variance-covariance matrix for the model parameters α, β and γ were used to

263 estimate the variance of the depth of colonization parameters using equations for sums and

264 differences of normal random variables (Ku 1966):

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265

$$\sigma^2_{Z_{c,min}} = \begin{cases} \sigma^2_\beta + 4\sigma^2_\gamma - 4\sigma_{\beta\gamma} & \text{when } \beta\text{-}2\gamma>0 \\ \text{not defined} & \text{otherwise} \end{cases} \tag{5}$$

266

$$\sigma^2_{Z_{c,med}} = \begin{cases} \sigma^2_\beta & \text{when } \beta\text{-}2\gamma>0 \\ (\sigma^2_\beta + 4\sigma^2_\gamma + 4\sigma_{\beta\gamma})/4 & \text{otherwise} \end{cases} \tag{6}$$

267

$$\sigma^2_{Z_{c,max}} = \sigma^2_\beta + 4\sigma^2_\gamma + 4\sigma_{\beta\gamma} \tag{7}$$

268

269

270 We then estimated 95% prediction intervals for each parameter as the estimate $1.96 \pm \sqrt{\sigma^2}$ where

271 σ^2 is the appropriate estimate from eq. 5, 6 or 7. The value of $\sigma^2_{Z_{c,min}}$ is not defined when $\beta - 2\gamma < 0$

272 because $Z_{c,min}$ is fixed at zero (Fig. 3b). Given the estimated prediction intervals, we also

273 considered depth of colonization to be inestimable if the 95% prediction interval for $Z_{c,\,max}$ included

274 zero.

275

276 *Estimate of spatial distribution and mean depth of colonization*

277   Depth of colonization within estuary segments was estimated using (1) a single central

278 point in the segment and a large sampling radius, and (2) a grid of sample points. For the first

279 approach, a segment mean was generated using all the depth vs. seagrass observations within the

280 segment. The variance of Z_c was computed using eqs. 5, 6 and 7. For the second approach, Z_c was

281 estimated at each node on a regular grid of sample points distributed throughout each estuary

282 segment (Fig. 4). Nodes were spaced at an interval of 0.01 degrees latitude and longitude ($\approx$ 0.6 x

283 0.5 km at 30° N) and the sampling radius for each location was set to 0.02 degrees. To account for

284 spatial correlation among the estimates, segment means and standard errors were computed from

285 the gridded estimates using an intercept-only spatial mixed model, implemented using the nlme

286 package in R. An isotropic Gaussian correlation structure with a nugget effect was selected from

287 among other options based on the Akaike Information Criterion.

288

289 *Seagrass Light Requirements*

290   Seagrass light requirements were computed as the average fraction of surface irradiance

291 (PAR) reaching the depth of colonization, which was quantified for this purpose as $Z_{c,med}$. The

292 same calculations using $Z_{c,max}$ are included as online supplemental information. Depth of

293 colonization and water clarity were each quantified on identical grids. Grid size was selected to

294 maximize the number of matches between depth of colonization and water clarity measurements,

295 resulting in grid radii of 0.04 degrees for Choctawhatchee Bay, 0.1 degrees for Tampa Bay and

296 0.15 degrees for Indian River Lagoon. Grid cells centered more than 1 km from seagrass were not

297 included, preventing spurious comparison of seagrass depth of colonization with water clarity far

298 from shorelines. The percentage of surface irradiance (% SI) at the median depth of colonization

299 was computed using

300
$$\% SI = 100 \cdot \frac{I_Z}{I_O} = \exp(-K_d \cdot Z_{c,med}) \qquad (8)$$

301 where the light extinction coefficient (K_d) was obtained as a remote sensing product

302 (Choctawhatchee Bay), was computed from a remote sensing-derived estimate of Secchi depth

303 (Tampa Bay), or from field-based Secchi depth measurements (Indian River Lagoon). Where K_d

304 was derived from Secchi depth (Z_{Secchi}), it was computed using $K_d \cdot Z_{secchi} = 1.7$ (Poole and Atkins

305 1929; Idso and Gilbert 1974). The % SI at the maximum depth of colonization ($Z_{c,max}$) was also

306 estimated and is reported as supplemental information.

307   Segment means and standard errors for light requirements were computed from the

308 spatially-correlated gridded estimates using an intercept-only spatial mixed model, as for depth of

309 colonization. Tests for differences in mean light requirements among estuaries and estuary

310 segments were also implemented using a spatial mixed model implemented in R using nlme, in this

311 case with a single categorical fixed effect (estuary or estuary segment) and a Gaussian spatial

312 correlation structure with a nugget effect.

313

314 **Results**

315 *Segment characteristics and seagrass depth estimates*

316   The study areas varied in size and depth (Table 1). Area ranged from 59 km^2 for Western

317 Choctawhatchee Bay (WCB) to 271 km^2 for the Big Bend (BB). Mean depth was less than 5

318 meters in each segment, except for WCB, which was slightly deeper (5.3 m). Maximum depth was

11

319   greater in WCB (11.9 m) and Old Tampa Bay (OTB, 10.4 m) compared to BB (3.6 m) and Upper

320   Indian River Lagoon (UIRL, 3.7 m) segments. Seagrass coverage was extensive in BB (74.8 % of

321   total segment area), less in UIRL (32.8 %) and OTB (11.9 %), and very sparse in WCB (5.9 %),

322   where most seagrass was in a large patch located just west of the inlet to the Gulf of Mexico (Fig.

323   2). Seagrasses were distributed throughout BB except for a noticeable area of decreased coverage

324   near the outflow of the Steinhatchee River (Fig. 2, upper left). Seagrasses in OTB and UIRL were

325   distributed narrowly along the shorelines, consistent with strong depth-dependence. Seagrass

326   coverage declined toward the northern ends of both OTB and UIRL. Secchi depth was 1.3 to 1.5 m

327   in BB, OTB and UIRM, and 2.1 m in WCB.

328   Whole segment estimates (± prediction interval) for $Z_{c,med}$ varied from 0.95±0.07 m in OTB

329   to 2.29±0.19 in BB, with 95% prediction intervals equal to ±1% to 10% of the estimate (Table 2).

330   Estimates of $Z_{c,max}$ varied from 1.1 m to 3.8 m and were somewhat less precise, with 95%

331   prediction intervals equal to 3 to 20% of the estimate (Table 2). Means of spatially-resolved

332   estimates of $Z_{c,med}$ varied from 2% more than to 15% less than the whole-segment estimates (Table

333   2), within the margin of uncertainty for each, suggesting that the two approaches gave comparable

334   results. The difference was largest for BB, where the gridded estimates of depth of colonization

335   had a bi-modal distribution (i.e., lower estimates near the Steinhatchee outflow vs. higher values

336   distant from the river outflow (Fig. 4, upper left). The whole segment estimate of $Z_{c,max}$ for BB was

337   3.8 m, 65% more than the 2.3 m average of the gridded estimates, reflecting a greater influence of

338   the deeper-distributed seagrass on the whole segment calculation (Table 2; Fig. 4). Estimates for

339   $Z_{c,min}$ were as low as zero in BB and OTB (Table 2), indicating that seagrass coverage decreased

340   immediately with any increase in depth. The highest values for $Z_{c,min}$ were associated with

341   relatively deep seagrass distributions, as in WCB. In these cases, coverage did not decrease

342   initially with depth. Seagrass percent cover often increased initially with increasing depth, likely

343   reflecting stressors such as wave energy or desiccation during extreme low tides affecting the

344   shallow margin of the seagrass bed.

345   Gridded estimates provided further information on the distribution of seagrasses in each

346   segment (Table 3; Fig. 4) and on the average depth of colonization in the entire estuary. Seagrass

347   Z_c estimates were computed for 255 locations in Choctawhatchee Bay, 218 locations in Tampa

348   Bay, and 45 locations in the Indian River Lagoon (Table 3 and Figs. 7, 8, 9). Mean $Z_{c,med}$ (±s.e.) for

349   the bays were 2.03±0.12, 1.16±0.10, and 1.10±0.11 m for Choctawhatchee Bay, Tampa Bay, and

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350   Indian River Lagoon, respectively. Mean $Z_{c,med}$ for Tampa Bay and Indian River Lagoon were not

351   significantly different, while $Z_{c,med}$ was significantly higher in Choctawhatchee Bay than either

352   other bay (p<0.01; Table 3).

353   Spatial heterogeneity in depth of colonization was particularly apparent for BB and UIRL

354   (Fig. 4). As previously mentioned, depth of colonization in the Big Bend segment was reduced in

355   the vicinity of the Steinhatchee River discharge. Seagrasses were also limited to shallower depths

356   at the north end of the Upper Indian River Lagoon segment, but grew at maximum depths up to 2.2

357   m on the eastern portion of the Upper Indian River Lagoon segment near the Merritt Island

358   National Wildlife Refuge (Fig. 2). Seagrasses in Old Tampa Bay grew slightly deeper in the eastern

359   and southern portion of the segment and declined to shallower depths near freshwater inflow

360   channels on the northern margin (Fig. 4, Fig. 8). The deepest growing seagrass in western

361   Choctawhatchee Bay was closest to Destin Pass, where regular tidal exchange with Gulf of Mexico

362   waters maintains increased water clarity (Fig. 4). Z_c could not be estimated where seagrasses were

363   sparse or absent as in the center of Old Tampa Bay and western Choctawhatchee Bay, or where

364   there was an insufficient gradient in water depth, as in several areas of the Big Bend segment (Fig.

365   4).

366   Despite apparent gradients in depth of colonization aligned with the major axis of each

367   estuary (Fig. 4, 7, 8, 9), segment means for $Z_{c,med}$ were mostly not statistically different (Table 3).

368   In Tampa Bay, $Z_{c,med}$ was ~0.5 m less (p<0.05) in Old Tampa Bay than in the Lower or Middle

369   Tampa Bay (p<0.05) segments. Differences among the other segments were not statistically

370   significant. For Choctawhatchee Bay, $Z_{c,med}$ in the eastern segment was 1.1 m and 1.5 m less than

371   in the central and western bay, respectively. Similarly, the apparent differences in $Z_{c,med}$ in lower

372   Indian River Lagoon vs. elsewhere in the lagoon (Fig. 9) were also not statistically significant.

373

374   *Seagrass light requirements*

375   Estimates of water clarity, seagrass depth of colonization, and corresponding light

376   requirements for all locations in Choctawhatchee Bay, Tampa Bay, and the Indian River Lagoon

377   indicated substantial variation, both between and within the different bays. Satellite-derived

378   estimates of light attenuation for Choctawhatchee Bay (as K_d) and Tampa Bay (as clarity) resolved

379   spatial variation in average water clarity (Figs. 5 and 6). For Choctawhatchee Bay, K_d increased

380   from the western and central segments toward the eastern segment, which is adjacent to the

381 Choctawhatchee River discharge (Fig. 5). Similarly, water clarity decreased from lower and

382 central Tampa Bay into Old Tampa Bay and Hillsborough Bay. Although it would most likely not

383 affect the seagrass distribution near shore, water clarity was also greater in the central area of the

384 lower bay segments (Fig. 6). Secchi depth was highest in the southern Indian River Lagoon and

385 decreased to the north. Relatively few Secchi depth measurements were available for the Upper

386 Indian River Lagoon and Banana River segments, likely because water clarity exceeded the

387 maximum depth in shallow areas, resulting in right-censored measurements.

388   Whole-estuary means for percent surface irradiance (% SI) at $Z_{c,med}$ (i.e., seagrass light

389 requirement) was (mean±s.e.) 50±3.0 % SI for Choctawhatchee Bay, 41±2.5 % SI for Tampa Bay,

390 and 18±2.9 % SI for Indian River Lagoon. Based on Tukey contrasts, light requirements for

391 seagrass in Indian River Lagoon were lower (p<0.01) than for either of the other estuaries, whereas

392 Choctawhatchee Bay and Tampa Bay light requirements were similar (Table 3). Despite some

393 apparent spatial patterns in seagrass light requirements (Fig. 7, 8, 9), no significant differences

394 were found among segments within a single estuary. In Tampa Bay, the segment mean (±s.e.) %

395 SI at $Z_{c,med}$ ranged from 34±11.2% to 49±8.7 % (Table 3, Fig. 8). For Choctawhatchee Bay,

396 segment means were 46±6.4 % SI to 64±8.9 % SI, with the apparently higher values in eastern

397 Choctawhatchee Bay (Table 3, Fig. 7). A larger range was observed for Indian River Lagoon:

398 9.2±2.8 % SI to 24±6.4 % SI (Table 3, Fig. 9). Either small sample sizes, as for Indian River

399 Lagoon, or a small number of effectively independent samples given the spatial correlation of

400 residuals, reduced the statistical significance of apparent spatial differences in light requirements.

401

402 **Discussion**

403   Seagrass depth of colonization is an important measure of the status and condition of

404 seagrass communities in estuaries because it relates to water clarity and related anthropogenic

405 water quality changes, especially eutrophication caused by excess nutrient loading (Dennison *et al*.

406 1993; Short and Wyllie-Echeverria 1996; Burkholder *et al*. 2007). Because seagrasses are

407 ecologically important and sensitive to water quality changes, both seagrass coverage and depth of

408 colonization have been used to define water quality management objectives (Steward *et al*. 2005,

409 Environmental Protection Agency 2012; Greening *et al*. 2014). The methods developed and

410 demonstrated in this study are a rigorous, yet efficient and practical approach for computing

411 seagrass depth of colonization at a large scale using widely-available geospatial data sets

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412   describing seagrass areal extent and bathymetry. The method is automated via R code, and thus not

413   especially labor-intensive. Because it is automated, it is reproducible and could be applied to new

414   data from the studied estuaries or other estuaries with appropriate data. The method provides maps

415   of depth of colonization, resolving both means and spatial gradients at a range of scales from an

416   individual measurement to the whole estuary. Uncertainty is estimated for individual estimates of

417   depth of colonization, while both variability (s.d.) and uncertainty (s.e.) are quantified for segments

418   of estuaries and whole estuaries. Given these characteristics, our approach is a useful tool for large

419   scale assessment of seagrass distribution with respect to water depth wherever the required data are

420   available. Moreover, resolving spatial differences in depth of colonization and light requirements

421   provides valuable information to support further investigation of the causes and mechanisms

422   affecting the extent and spatial distribution of seagrass habitats.

423   Maps illustrating spatial patterns in depth of colonization quantified expected patterns in

424   depth of colonization, wherein seagrasses grew to greater depth when closer to ocean passes, where

425   water was clearer (Figs. 7, 8, 9). Differences among segment means were mostly not statistically

426   different, reflecting both variability in estimates at the scale of estuary segments and spatial

427   correlation of residuals, which reduced the effective number of degrees of freedom. For example,

428   if the seagrass distribution within a segment includes two areas with homogeneous depth of

429   colonization within but differences among them, this will tend to inflate uncertainty regarding the

430   segment means, leading to poor resolution of differences among segments. Possible solutions could

431   include a different segmentation approach or analysis of pattern without segmentation. If the

432   objective was to resolve changes in average depth of colonization over time, which would be of

433   interest ecologically, a statistically powerful approach could be an evaluation of pairwise changes

434   at each grid node. While we have not yet evaluated a time series of coverages in this way it would

435   be a useful extension of our research.

436   For the first time, we also combined estimates of water clarity for estuaries based on

437   satellite remote sensing and Secchi depth measurements to resolve spatial patterns in seagrass light

438   requirements. Like depth of colonization, maps of these values quantify gradients in light

439   requirements, even if "segments" delineated for management purposes did not clearly identify

440   regions that differed by light requirements. We would expect light requirements, as we defined

441   them, to be higher at locations closer to freshwater and nutrient sources because epiphytic algal

442   growth, salinity variations, color, or other factors such as sediment geochemistry could impose

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443   constraints on seagrass growth beyond those imposed by light attenuation in the water column

444   (Hemminga 1998; Kemp *et al*. 2004). The results neither conflicted with nor definitively

445   supported this expectation. For example, the highest light requirements in each of the estuaries

446   were furthest from tidal exchange and closest to sources of freshwater and nutrients (Fig. 7, 8, 9).

447   But, the differences were subtle and, given variations within segments, did not emerge as

448   significant differences among segment means. On the other hand, light requirements for seagrass

449   in Indian River Lagoon (IRL) was significantly less than for seagrass in Choctawhatchee Bay and

450   Tampa Bay. Light requirements for Choctawhatchee Bay and Tampa Bay were both more than the

451   20% estimate that has been referenced broadly in water quality management (Batiuk *et al*. 1992;

452   Dennison *et al*. 1993; Kemp *et al*. 2004) and locally within Florida (Dixon and Leverone 1995; US

453   EPA 2012). Light requirements for Tampa Bay were similar to 20% in only a few areas of the

454   Bay. Given the broad range in published estimates of seagrass light requirements (Dennison *et al.*

455   1993), our estimates are not outside the norm. Nonetheless, it is useful to consider possible

456   explanations and implications associated with these results, especially with respect to the range

457   within our own estimates.

458   Some of the differences in light requirements that we observed may relate to species

459   composition, since the physiology of seagrass species is far from invariant. For example, *Halodule*

460   *wrightii* is the most abundant seagrass in western Choctawhatchee Bay (Yarbro and Carlson 2015)

461   and has higher light requirements than several other abundant species in Florida (Choice *et al*.

462   2014) including *Thalassia testudinum*, which dominates the more oceanic areas of Tampa Bay.

463   Choice *et al*. (2014) found that light requirements for *Syringodium filiforme* were much less, as low

464   as 8-15 % SI, although Kenworthy (1993) found that the depth distribution of *H. wrightii* and *S.*

465   *filiforme* were similar in the lower Indian River Lagoon, implying their light requirements may be

466   similar. Estimates of light requirements for several species of *Halophila* indicate a potential to

467   grow at 5% SI or less (Kenworthy and Haunert 1991), consistent with some of our lowest estimates

468   from Lower Indian River Lagoon (Fig. 9). Neither *S. filiforme* nor any of the *Halophila* spp.

469   appear to be dominant species in Tampa Bay or Choctawhatchee Bay, perhaps limiting seagrass

470   distributions in those estuaries to higher light environments compared with lower Indian River

471   Lagoon. Although we cannot be certain the extent to which species composition can explain the

472   differences that we observed in %SI at the depth of colonization, the key observation is that

473   differences were observed, that seagrass species vary in their physiology and responses to a range

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474   of factors, and therefore, that it may be useful to understand and manage seagrass habitats utilizing

475   local information where possible. Another consideration related to species composition is that our

476   estimates are likely to be driven by the deepest growing species. Water clarity changes could alter

477   competitive relationships among species within the mappable seagrass area, which would not be

478   apparent in our analysis.

479   Our estimates of % SI at the depth of colonization necessarily also depend on our approach

480   to estimating depth of colonization, as do others in the literature. Depth of colonization is a

481   reference point along a gradient of decreasing seagrass cover (presumably) associated with

482   increasing light limitation and related physiological stress (e.g., Fig. 3 in Hemminga 1998). In

483   some studies, percent cover was estimated by diver observation (Choice *et al*. 2014), enabling a

484   statistical approach (e.g., moving split window) that directly resolves a threshold for rapid decline

485   in percent cover with respect to % SI at the scale of a single quadrat. To scale up the analysis, we

486   needed to use seagrass coverage maps based on photointerpretation which necessarily imposes a

487   binary classification (present/absent). By inferring the probability of seagrass presence conditional

488   on depth, however, we obtained an estimate analogous to that of Choice *et al*. (2014), with the

489   parameter β (Fig. 3) estimating the threshold for most rapid decline in seagrass presence.

490   However, it is still unavoidable that seagrass will be both present at greater depths and stressed by

491   light limitation at lesser depths. In this regard, a strength of our approach is that we can estimate

492   the % SI associated with both the local extremes of the mappable seagrass distribution (i.e., $Z_{c,max}$;

493   Figs. S1, S2, S3) and the center of that depth distribution (i.e., $Z_{c,med}$). Moreover, by being linked

494   to aerial coverage data, the estimates are available for a range of spatial scales, are comparable

495   across all those scales, and can be quickly re-computed when new surveys are completed.

496   Our estimates also depend on an accurate characterization of average water clarity,

497   something that will always be challenging in the context of seagrass ecology. For example, since

498    $\%SI = e^{-k_d Z_c}$ and $k_d = k_{sd}/Z_{sd}$ and k_{sd} ~1.4 to 1.7, Secchi depth in seagrass habitats is often

499   similar to the depth of colonization, potentially leading to right censoring of Secchi measurements

500   when the disk would be visible on the bottom. Accurate light profiling is possible but also more

501   difficult in shallow water than in deeper water. Limitations on boat operations also favor sampling

502   during periods of calm winds, perhaps leading to under-sampling of periods when sediment

503   resuspension is above average. Quantifying water clarity via satellite remote sensing has

504   advantages but also presents both similar and new challenges. For example, concern regarding

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505   bottom reflectance led Chen *et al*. (2007) to exclude data if water depth was <2 m, excluding nearly

506   all seagrass areas. Water clarity estimates are therefore based on nearby, but deeper waters. If

507   attenuation is lower in open water, this will tend to increase the estimate of % SI at the depth of

508   colonization. On the other hand, the uniform and sustained spatial and temporal coverage provided

509   by satellite remote sensing is an advantage. Such uniform coverage may reduce spurious small-

510   scale variability.

511   Sustained trends in water quality are another factor that can affect estimates of light

512   requirements because seagrasses can be both slow to recover following disturbance and resistant to

513   stress in the first place. In particular, species such as *Thalassia testudinum* display a phalanx

514   growth strategy and buffer against periods of low light by tapping into below ground reserves,

515   making them slow to achieve a light-limited equilibrium distribution in the presence of water

516   quality trends. Improving trends in water clarity could lead to higher estimates of light

517   requirements, whereas the opposite may be true with declining trends in clarity. As a result,

518   considering both depth of colonization and changes in the apparent light requirements may be

519   useful for understanding the status and trends related to seagrass habitats.

520   This study has implications for both seagrass ecology and environmental management.

521   Scientifically, the ability to resolve patterns in several parameters related to depth of colonization

522   as well as % SI at the depth of colonization could be a useful tool for generating testable

523   hypotheses. For example, persistent differences in spatial patterns of depth distributions may

524   suggest hypotheses regarding the causes and could stimulate research to identify local drivers.

525   Similarly, we could seek to better understand temporal changes in depth of colonization, but

526   without a consistent approach to quantifying it, we may not be aware of such changes. For

527   example, despite extensive documentation of changes in the area of seagrass habitat in Tampa Bay

528   since 1950 (Greening *et al*. 2014), little attention has been given to trends in the depth distribution

529   during the same period. Simultaneous analysis of each could provide additional insights into

530   patterns and processes associated with seagrass recovery from eutrophication impacts.

531   There are several important management implications related to our method and results.

532   Localized patterns in depth of colonization, such as in the case of the Steinhatchee River outflow,

533   illustrate that management goals related to seagrass depth distribution and water clarity may not be

534   applicable throughout water quality segments drawn without considering local drivers. At a

535   slightly larger scale, differences among segments and among entire estuaries show that it can be

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536 both important and (fortunately) possible to consider local differences in the water quality

537 requirements for seagrasses when developing and evaluating water quality goals over time. Even

538 though seagrasses are affected by factors other than water clarity, resistance and resilience in the

539 face of multiple stressors can be influenced by the physiological and energetic changes affected by

540 light availability (Burkholder *et al*. 2007). In the case of Tampa Bay, light availability generally

541 exceeds seagrass light requirements estimated in the early 1990s. This may have sustained the

542 seagrass recovery, which accelerated following a brief ENSO-related period of increased river flow

543 and decreased water clarity in the late 1990s (Greening *et al*. 2014).

544

545 **Acknowledgments**

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550 **References**

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683   Figure Captions

684   **Fig.1** Examples of data and grid locations for estimating seagrass depth of colonization for a region
685   of the Big Bend, Florida. (a) seagrass coverage and depth contours at 2 meter intervals, including
686   the whole segment estimate for depth of colonization; (b) a grid of sampling locations with
687   sampling radii for estimating Z_c and seagrass depth points derived from bathymetry and seagrass
688   coverage layers; (c) an example of sampled seagrass depth points for a test location. Estimates in
689   Fig. 3 were obtained from the test location in (c)
690
691   **Fig. 2** Locations and seagrass coverage of estuary segments used to evaluate depth of colonization
692   estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay),
693   2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay). SR=
694   Steinhatchee River outflow; MI= Merritt Island National Wildlife Refuge
695
696   **Fig. 3** Methods for estimating seagrass depth of colonization using sampled seagrass depth points
697   around a single location. Three depth estimates ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$) are based on a linear curve
698   through the inflection point of a logistic growth curve. The logistic curve is defined by the
699   parameters α, β, and γ and describes the decrease in the proportion of sample points with seagrass
700   as a function of depth below mean tide level (MTL). (A) The estimation method when the linear
701   curve intercepts α at a depth greater than zero. (B) The alternative method when the linear curve
702   intercepts α at depth less than zero
703
704   **Fig. 4** Spatially-resolved estimates of maximum seagrass depth of colonization (m) for four coastal
705   segments of Florida. Estimates are assigned to grid locations for each segment, where grid spacing
706   was fixed at 0.01 decimal degrees. Radii for sampling seagrass bathymetric data around each grid
707   location were fixed at 0.02 decimal degrees. From left to right, top to bottom: Big Bend, Old
708   Tampa Bay, Upper Indian R. Lagoon, Western Choctawhatchee Bay
709
710   **Fig. 5** Satellite estimated light attenuation for Choctawhatchee Bay as an average of all years from
711   2003 to 2007. See Fig. 7 for segment identification
712
713   **Fig. 6** Satellite estimated water clarity for Tampa Bay as an average of all years from 2006 to
714   2010. See Fig. 8 for segment identification
715
716   **Fig. 7** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
717   irradiance at $Z_{c,med}$) for multiple locations in Choctawhatchee Bay, Florida. Each location has both
718   water clarity estimates from satellite observations and an estimate of seagrass depth of colonization
719   with a search radius of 0.04 degrees. At right: Estimates summarized by bay segment where the
720   dimensions are the 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and
721   95th percentiles with outliers beyond. CCB: Central Choctawhatchee Bay, ECB: East
722   Choctawhatchee Bay, WCB: West Choctawhatchee Bay

723
724 **Fig. 8** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
725 irradiance at $Z_{c,med}$) for multiple locations in Tampa Bay, Florida. Each location has both a water
726 clarity estimate from satellite observations and an estimate of seagrass depth of colonization with
727 a search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile.
728 Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay,
729 LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay
730
731 **Fig. 9** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
732 irradiance at $Z_{c,med}$) for multiple locations in Indian River Lagoon, Florida. Each location has
733 both an average Secchi depth observation and an estimate of seagrass depth of colonization with
734 a search radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth.
735 Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th
736 percentiles with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon,
737 LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL:
738 Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito
739 Lagoon
740
741 Supplementary figures
742
743 **Fig. S1** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface
744 irradiance at $Z_{c,max}$) for multiple locations in Choctawhatchee Bay, Florida. Each location has
745 both water clarity estimates from satellite observations and an estimate of seagrass depth of
746 colonization with a search radius of 0.04 degrees. At right: Estimates summarized by bay
747 segment where the dimensions are the 25th percentile, median, and 75th percentile. Whiskers
748 extend to the 5th and 95th percentiles with outliers beyond. CCB: Central Choctawhatchee Bay,
749 ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay
750
751 **Fig. S2** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface
752 irradiance at $Z_{c,max}$) for multiple locations in Tampa Bay, Florida. Each location has both a water
753 clarity estimate from satellite observations and an estimate of seagrass depth of colonization with
754 a search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile.
755 Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay,
756 LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay
757
758 **Fig. S3** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface
759 irradiance at $Z_{c,max}$) for multiple locations in Indian River Lagoon, Florida. Each location has
760 both an average Secchi depth observation and an estimate of seagrass depth of colonization with
761 a search radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth.
762 Box plots show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th
763 percentiles with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon,
764 LIRL: Lower Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL:
765 Upper Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito
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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 square kilometers and meters, respectively. Secchi measurements (m) were obtained from the Florida Department of Environmental Protection's Impaired Waters Rule (IWR) database, update number 40. Secchi mean and standard errors are based on all observations within the ten years preceding each seagrass survey

	BB[a]	OTB	UIRL	WCB
Year[b]	2006	2010	2009	2007
Latitude	29.61	27.94	28.61	30.43
Longitude	-83.48	-82.62	-80.77	-86.54
Surface area	271.37	205.5	228.52	59.41
Seagrass area	203.02	24.48	74.89	3.51
Depth (mean)	1.41	2.56	1.4	5.31
Depth (max)	3.6	10.4	3.7	11.9
Secchi (mean)	1.34	1.41	1.3	2.14
Secchi (se)	0.19	0.02	0.02	0.08

[a]BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper Indian River Lagoon, WCB: Western Choctawhatchee Bay

[b]Seagrass coverage data sources, see methods for bathymetry data sources

BB: http://atoll.floridamarine.org/Data/metadata/SDE Current/seagrass bigbend 2006 poly.htm

OTB: http://www.swfwmd.state.fl.us/data/gis/layer library/category/swim

UIRL: http://www.sjrwmd.com/gisdevelopment/docs/themes.html

WCB: http://atoll.floridamarine.org/data/metadata/SDE Current/seagrass chotawhatchee 2007 poly.htm

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Table 2 Summary of seagrass depth estimates (m) for each segment in Fig. 4. Whole segment estimates and prediction intervals were obtained from a single point estimate that included all seagrass depth data for the segment. Mean, standard error, standard deviation, minimum, and maximum values are for multiple grid points within each segment in Fig. 4. Mean and standard error estimates were from intercept-only models that included Gaussian correlation structures to account for spatial dependencies between points

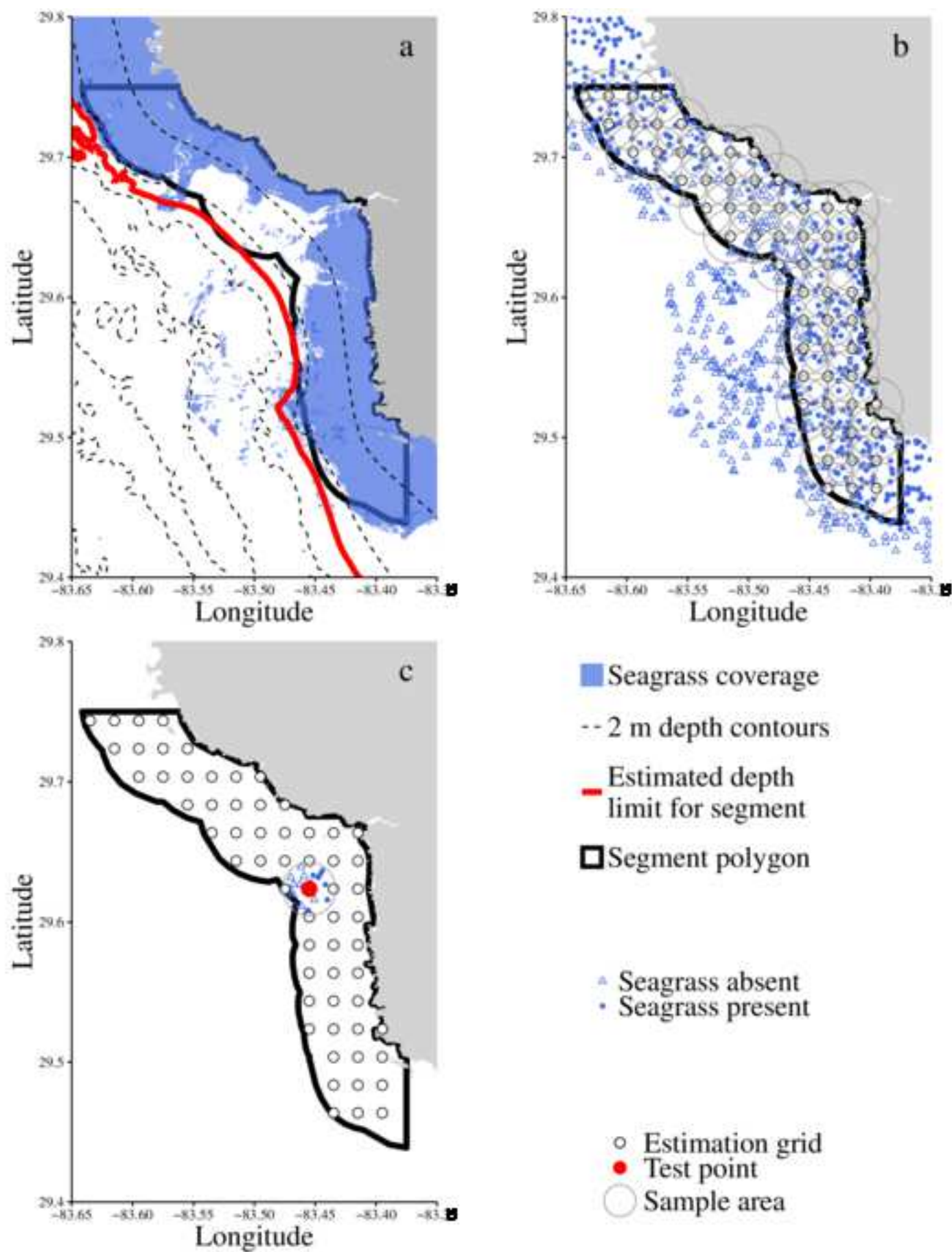| Segment[a]	Whole segment	Pred. Int. (+/-)	Mean	St. Err.	St. Dev.	Min	Max
BB							
$Z_{c,min}$	0.75	0.25	1.56	0.18	0.79	0	2.72
$Z_{c,med}$	2.29	0.19	1.94	0.17	0.76	0.55	2.97
$Z_{c,max}$	3.84	0.43	2.29	0.19	0.81	0.74	3.48
OTB							
$Z_{c,min}$	0.83	0.16	0.58	0.07	0.28	0.05	1.48
$Z_{c,med}$	0.95	0.07	0.86	0.08	0.3	0.33	1.74
$Z_{c,max}$	1.07	0.21	1.17	0.12	0.4	0.34	2.04
UIRL							
$Z_{c,min}$	1.19	0.04	1.36	0.06	0.27	0.75	2.01
$Z_{c,med}$	1.48	0.02	1.51	0.08	0.23	0.98	2.08
$Z_{c,max}$	1.77	0.05	1.63	0.08	0.23	1.11	2.16
WCB							
$Z_{c,min}$	1.84	0.42	1.58	0.11	0.34	0.78	2.29
$Z_{c,med}$	2.17	0.22	1.96	0.1	0.31	1.51	2.51
$Z_{c,max}$	2.5	0.47	2.36	0.14	0.39	1.75	3.1

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

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Table 3 Summary of median depth of colonization ($Z_{c,med}$, m) and light requirements (%) for all bay segments of Choctawhatchee Bay, Indian River Lagoon, and Tampa Bay. Superscripts for mean $Z_{c,med}$ denote significant differences among segments within estuaries (letters) or among estuaries (numbers). See Figs. 7 to 9 for spatial distribution of the results
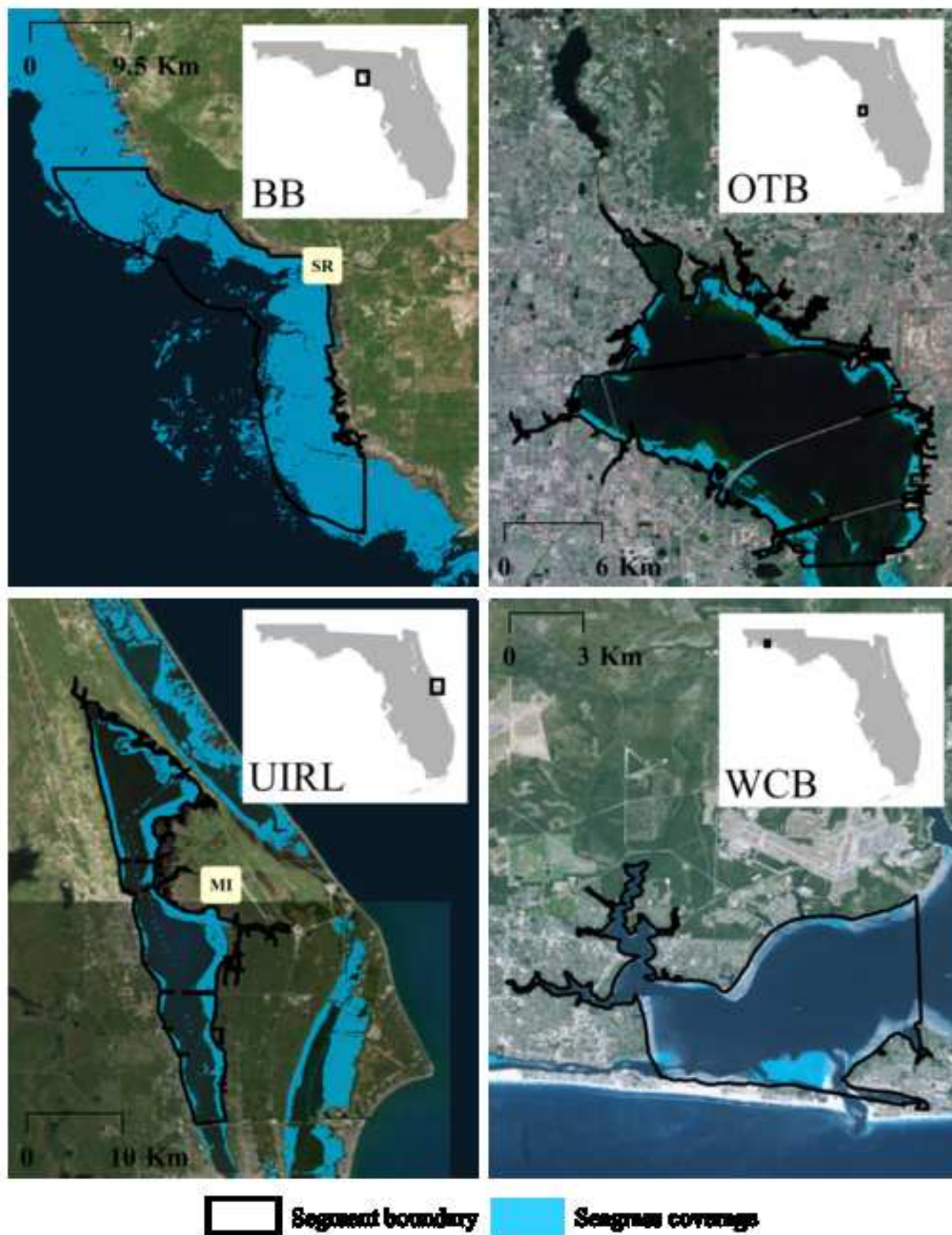
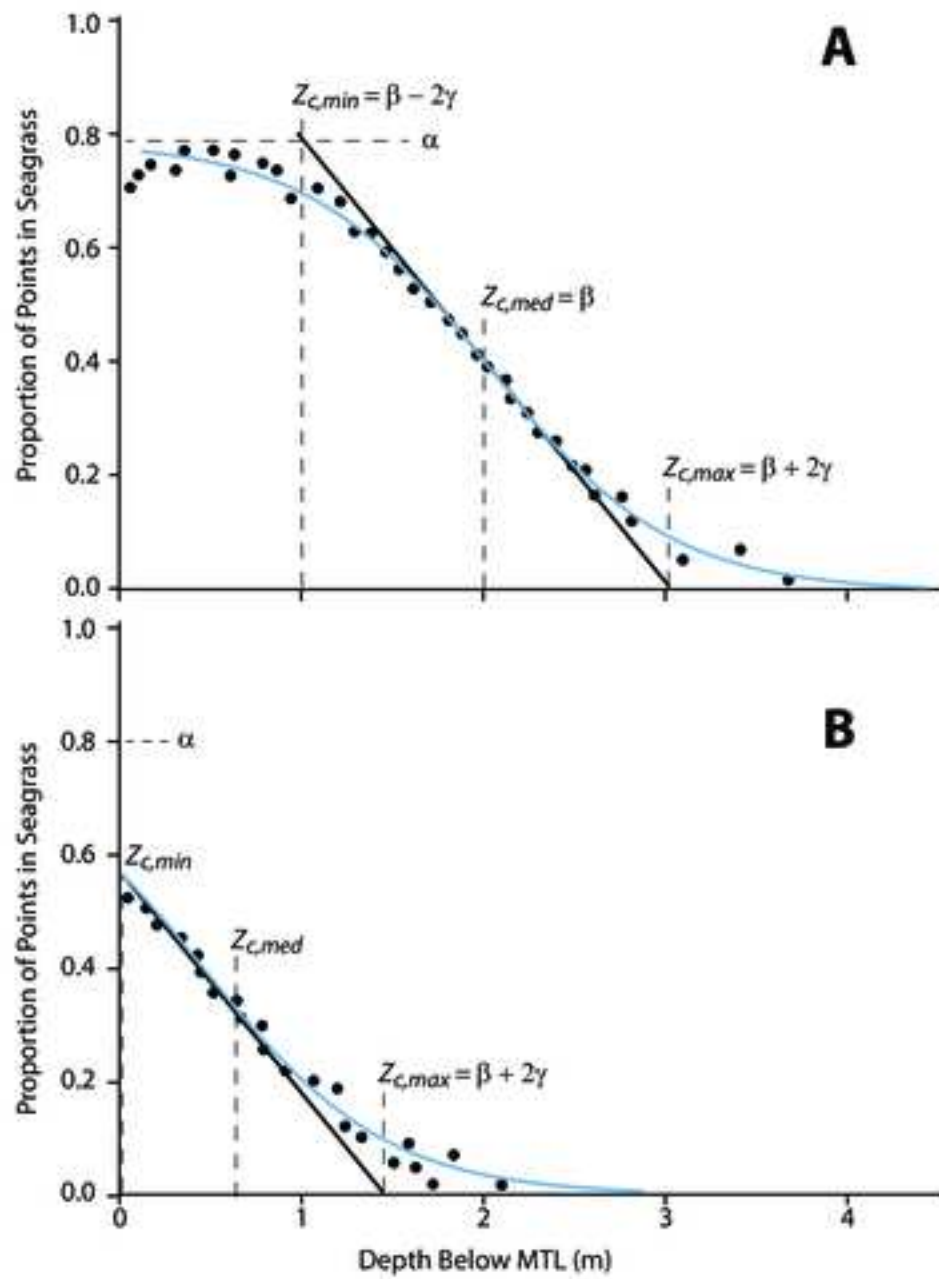| Segment[a]	n	$Z_{c,med}$				% light			
		Mean	St. Err.	Min	Max	Mean	St. Err.	Min	Max
Choctawhatchee Bay	255	2.0[1]	0.1	0.6	2.8	50[1]	3.0	20	87
CCB	111	2.0[b]	0.6	0.6	4.2	51	13.2	20	87
ECB	4	0.9[a]	0.1	0.7	0.9	64	8.9	55	75
WCB	140	2.3[b]	0.3	1.7	2.8	46	6.4	22	70
Indian River Lagoon	45	1.1[2]	0.1	0.8	1.6	18[2]	2.9	7.5	31
BR	2	1.0[a]	0.1	1	1.1	21	0.8	20	21
LCIRL	14	1.2[a]	0.3	0.9	1.6	14	6.3	5.8	25
LIRL	3	1.5[a]	0	1.5	1.6	9.2	2.8	6.0	11
LML	4	1.0[a]	0	1	1	22	2.2	19	24
UCIRL	17	0.9[a]	0.1	0.8	1.1	20	7	7.5	31
UIRL	1	1.0[a]	-	1	1	24	-	24	24
UML	4	0.8[a]	0.1	0.8	1	24	6.4	15	31
Tampa Bay	218	1.2[2]	0.1	0.6	1.6	41[1]	2.5	13	66
HB	20	1.1[ab]	0.2	0.8	1.3	34	11.2	13	56
LTB	60	1.3[b]	0.1	1.1	1.5	40	7.5	24	56
MTB	74	1.4[b]	0.1	1.1	1.6	36	7.6	17	58
OTB	64	0.8[a]	0.2	0.6	1.1	49	8.7	30	66

[a]CCB: 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.
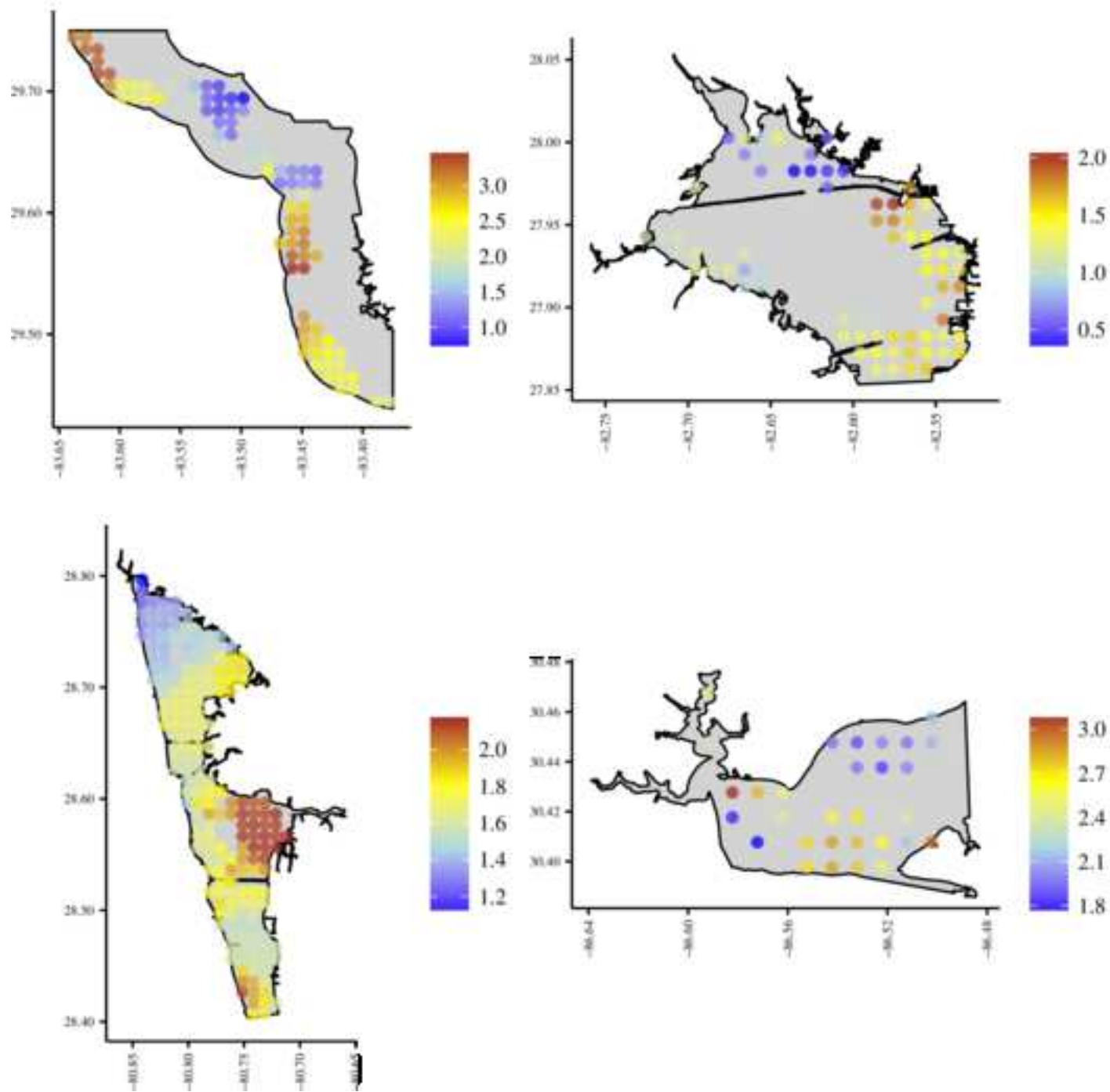
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Fig1
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Seagrass coverage

-- 2 m depth contours

Estimated depth limit for segment

☐ Segment polygon

△ Seagrass absent
· Seagrass present

○ Estimation grid
● Test point
○ Sample area

Fig2

Segment boundary   Seagrass coverage

Fig3

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Fig4

Fig5

Fig6

Fig7

Click here to download Figure Fig7.tif ⬇

Fig8

Fig9

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