

¹ Spatially-referenced estimates of seagrass 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

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

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

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

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

71 from Florida although the technique is transferable to other regions with comparable data.

72 **2 Methods**

73 Development of a spatially-referenced approach to estimate seagrass depth of {acro:doc}

74 colonization (DoC) relied extensively on data and partially on methods described in [Hagy, In](#)

75 [review](#). The following is a summary of locations and data sources, methods and rationale for

76 incorporating spatial information in seagrass DoC estimates, and evaluation of the approach

77 including relationships with water clarity.

78 **2.1 Locations and data sources**

79 Four unique locations were chosen for the analysis: Choctowatchee Bay (Panhandle), Big

80 Bend region (northeast Gulf of Mexico), Tampa Bay (central Gulf Coast of Florida), and Indian

81 River Lagoon (east coast) ([Table 1](#) and [Fig. 1](#)). These locations represent different geographic

82 regions in the state, in addition to readily available data and observed gradients in water clarity

83 that likely contributed to heterogeneity in seagrass growth patterns. For example, the Big Bend

84 region was chosen based on location near an outflow of the Steinhatchee River where higher

85 concentrations of dissolved organic matter are observed. Seagrasses near the outflow were

86 observed to grow at shallower depths as compared to locations far from the river source. Coastal

87 regions and estuaries in Florida are divided into individual spatial units based on a segmentation

88 scheme developed by US Environmental Protection Agency (EPA) for the development of {acro:EPA}

89 numeric nutrient criteria. One segment from each geographic location was used for the analysis to

90 evaluate estimates of seagrass DoC. The segments included numbers 0303 (Choctowatchee Bay),

91 0820 (Big Bend region), 0902 (Tampa Bay), and 1502 (Indian River Lagoon), where the first two

92 digits indicate the estuary and the last two digits indicate the segment within the estuary.

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

107 Seagrass coverage maps were combined with bathymetric depth layers to characterize
108 location and depth of growth in each location. Bathymetric depth layers for each location were
109 obtained from the National Oceanic and Atmospheric Administration's (NOAA) National
110 Geophysical Data Center as either Digital Elevation Models (DEMs) or raw sounding data from {acro:DEM}
111 hydroacoustic surveys. Tampa Bay data provided by the Tampa Bay National Estuary Program
112 are described in [Tyler et al. \(2007\)](#). Bathymetic data for the Indian River Lagoon were obtained
113 from the St. John's Water Management District ([Coastal Planning and Engineering 1997](#)). NOAA
114 products were referenced to mean lower low water, whereas Tampa Bay data were referenced to
115 the North American Vertical Datum of 1988 and the Indian River Lagoon data were referenced to

116 mean sea level. Depth layers were combined with seagrass coverage layers using standard union
117 techniques of raster and vector layers in ArcMap 10.1 (Environmental Systems Research Institute
118 2012). To reduce computation time, depth layers were first masked using a 1 km buffer of the
119 seagrass coverage layer. The final layer used for analysis was a point layer with attributes
120 describing location (latitude, longitude, segment), depth (m), and seagrass (present, absent).
121 Additional details describing the data are available in Hagy, In review.

122 2.2 Segment-based estimates of seagrass depth of colonization

123 Methods in Hagy, In review describe an approach for estimating seagrass DoC at
124 individual coastal segments. Seagrass depth data described above are used to estimate maximum
125 (Z_{cMax}) and median ($Z_{c50\%}$) seagrass DoC, where the maximum depth is defined as the deepest
126 depth at which a “significant” coverage of seagrasses occurred in a segment and the median depth
127 is defined as the median depth occurring at the deep water edge. The seagrass depth points are
128 grouped into bins and the proportion of points within each depth bin that contain seagrass are
129 quantified. Both seagrass DoC estimates are obtained from a plot of proportion of points occupied
130 at each depth bin. In general, the plot is characterized by a decreasing trend such that the
131 proportion of occupied points by depth bin decreases and eventually flattens with increasing
132 depth. A regression is fit on this descending portion of the curve such that the intercept point on
133 the x-axis is considered the maximum depth of colonization. The median portion of this curve is
134 considered the median depth of the deepwater edge of seagrass.

135 Considerable spatial heterogeneity in the observed seagrass growth patterns suggests that
136 a segment-wide estimate of seagrass DoC may be inadequate for fully characterizing growth
137 patterns, particularly for the examples in the current analysis. Fig. 2 illustrates spatial variation in

138 seagrass distribution for a location in the Big Bend region of Florida. Using methods in Hagy, In
139 [review](#), the estimate for median seagrass DoC for the segment is over- and under-estimated for
140 different areas of the segment. In particular, DoC is greatly over-estimated at the outflow of the
141 Steinhatchee where high concentrations of dissolved organic matter naturally limit seagrass
142 growth. This example suggests that estimates of DoC may be needed at finer spatial scales to
143 provide a more robust determination of restoration targets and nutrient criteria.

144 **2.3 Estimating seagrass depth of colonization using spatial information**

145 The approach used to estimate seagrass DoC with spatial information has several key
146 differences with the original method. As before, seagrass DoC estimates are based on empirical
147 measures of the frequency occurrence of seagrass by increasing depth. The first difference is that
148 maximum DoC is estimated from a logistic growth curve fit through the data, in addition to a
149 simple linear regression in the previous example. Second, a third measure describing the depth at
150 which seagrass were most commonly located was defined, in addition to median and maximum
151 depth of growth. The third and most important difference is that the estimates are assigned to
152 discrete locations, using either a grid of points or as a single location of interest. Methods and
153 implications of these differences are described below.

154 The spatially-referenced approach for estimating DoC begins by creating a grid of
155 evenly-spaced points within the segment. The same process for estimating DoC is used for each
156 point. Alternatively, a single location of interest can be chosen rather than a grid-based design.
157 Seagrass depth data (i.e., merged bathymetric and seagrass coverage data) that occur within a set
158 radius from the chosen locations are selected for estimating seagrass DoC values. The estimate
159 for each location is quantified from a plot of the proportion of bathymetric soundings that contain

160 seagrass at each depth bin (Fig. 4a). Although the chosen radius for selecting depth points is
161 problem-specific, the minimum radius must sample a sufficient number of points for estimating
162 DoC. In general, an appropriate radius will produce a plot that indicates a decrease in the
163 proportion of points that are occupied by seagrass with increasing depth.

164 A curve is fit to the sampled depth points using non-linear regression to characterize the
165 reduction in seagrass as a function of depth. Specifically, a decreasing logistic growth curve is fit
166 to the plot to create a monotonic and asymptotic function of the sample data. The curve is fit by
167 minimizing the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers
168 1992) and user-supplied starting parameters that are an approximate estimate of the curve
169 characteristics. The model has the following form:

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

170 where the proportion of points occupied by seagrass at each depth is defined by a logistic curve
171 with an asymptote α , a midpoint inflection β , and a scale parameter γ . Starting values α , β , and γ
172 were estimated empirically from the observed data.

173 Finally, a simple linear curve is fit through the inflection point (β) of the logistic curve to
174 estimate depth of colonization (Fig. 4c). The inflection point is the depth at which seagrass are
175 decreasing at a maximum rate and is used as the slope of the linear curve. Three measures
176 describing seagrass growth characteristics are obtained. The maximum depth of seagrass
177 colonization, DOC_{max} , is the x-axis intercept of the linear curve. The depth of maximum
178 seagrass occupancy, SG_{max} is the location where the linear curve intercepts the asymptote of the
179 logistic growth curve. The median depth of seagrass colonization, DOC_{med} , is the depth halfway

180 between SG_{max} and DOC_{max} . DOC_{med} was typically but not always the inflection point of the
181 logistic growth curve. Functionally, each measure has specific ecological significance. The
182 median and maximum depth estimates describe the growth limitations of seagrasses as a function
183 of water clarity, whereas the maximum occupancy depth is considered the depth were most
184 seagrasses were encountered in the sample. Median and maximum depth estimates differ in that
185 the former describes the median depth of the deep water edge, whereas the latter describes a
186 nominal characterization of maximum depth independent of outliers.

187 Estimates for each of the three DoC measures are obtained only if specific criteria are met.
188 These criteria were implemented as a safety measure that ensures a sufficient amount and
189 appropriate quality of data are used. First, estimates are provided only if a sufficient number of
190 seagrass depth points are present within the radius of the grid point to estimate a logistic growth
191 curve. This criteria applies to the sample size as well as the number of points with seagrass in the
192 sample. That is, the curve cannot be estimated for small samples or if an insufficient number of
193 points contain seagrass regardless of sample size. Second, estimates are provided only if an
194 inflection point is present on the logistic curve within the range of the sampled depth data. This
195 criteria may apply under two scenarios where the curve is estimated but a trend is not adequately
196 described by the sampled data. That is, a curve may be estimated that describes only the initial
197 decrease in points occupied as a function of depth but the observed points do not occur at depths
198 deeper than the predicted inflection point. The opposite scenario may occur when a curve is
199 estimated but only the deeper locations beyond the inflection point are present in the sample.
200 Finally, the estimate for SG_{max} is set to zero if the linear curve through the inflection point
201 intercepts the asymptote at x-axis values less than zero. The estimate for DOC_{med} is also shifted
202 to the depth value halfway between SG_{max} and DOC_{max} .

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

208 **2.4 Comparison with segment-based approach and sensitivity analysis**

209 Spatially-referenced estimates for seagrass DoC were obtained for each of the four
210 segments described above. Segment-wide estimates obtained using methods in Hagy, In review
211 were used as a basis of comparison such that departures from these values were evidence of
212 spatial heterogeneity in seagrass growth patterns within each segment. A sampling grid of
213 locations for estimating each of the three depth values in Fig. 4 was created for each segment. The
214 grid is masked by the segment boundaries to remove locations that did not occur on the water,
215 whereas seagrass depth points used to estimate DoC extended beyond the segment boundaries.
216 Initial spacing between sample points was chosen arbitrarily as 0.02 decimal degrees, which is
217 approximately 2 km at 30 degrees N latitude. The sampling radius around each sampling location
218 in the grid was also chosen as 0.02 decimal degrees to allow for complete coverage of seagrass
219 within the segment while also minimizing redundancy of information described by each location.
220 In other words, radii were set such that the seagrass depth points sampled by each grid location
221 were only partially overlapped by those sampled by neighboring points.

222 The ability to characterize heterogeneity in seagrass growth patterns using the grid-based
223 approach can be informed by evaluating the level of confidence associated with DoC estimates.
224 Confidence intervals for non-linear regression can be estimated using a Monte Carlo simulation

225 approach that considers the variance and covariance between the model parameters and the depth
226 measurements (Hilborn and Mangel 1997). For simplicity, we assume that the observation
227 uncertainty associated with the depth measurements is zero such that the variability associated
228 with parameter estimates is considered the primary source of uncertainty. A 95% confidence
229 interval for each DoC estimates was constructed by repeated sampling of a multivariate normal
230 distribution followed by prediction of the proportion of points occupied by seagrass as in eq. (1).

231 The sampling distribution assumes:

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

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

239 The uncertainty associated with the DoC estimates were based on the upper and lower
240 limits of the estimated inflection point on the logistic growth curve. This approach was used
241 because uncertainty in the inflection point is directly related to uncertainty in each of the DoC
242 estimates that are based on the linear curve fit through the inflection point. Specifically, linear
243 curves were fit through the upper and lower estimates of the inflection point to identify upper and
244 lower limits for the estimates of SG_{max} , DOC_{med} , and DOC_{max} . These values were compared
245 with the initial estimates from the linear curve that was fit through the predicted logistic curve

246 (i.e., Fig. 4c). This approach provided an indication of uncertainty for individual estimates for a
247 set radius. Uncertainty estimates were obtained for each DoC estimate for the grids in each
248 segment.

249 **2.5 Developing a spatially coherent relationship of water clarity with depth 250 of colonization**

251 Potentially useful information can be obtained from the seagrass depth estimates for each
252 segment by evaluating the relationship with water clarity through space and time. In particular,
253 increased resolution of seagrass depth estimates compared with multiple measures of water clarity
254 can potentially improve the ability to empirically describe light requirements leading to the
255 development of numeric criteria. Secchi measurements provide a precise estimate of water clarity
256 and have been obtained at numerous locations described in the Florida Department of
257 Environmental Protection's Impaired Waters Rule (IWR) database. All available secchi {acro:IWR}
258 data for each of the four segments were obtained from the IWR database, update number 40.
259 Prior to analyses, all secchi data were screened to exclude observations that were coded with any
260 flags indicating that the value was lower than the maximum depth of the observation point. Secchi
261 data were also compared with bathymetric data to verify unflagged values were not missed by
262 initial screening.

263 The relationship between seagrass depth limits and secchi measurements were explored
264 using empirically estimated light requirements and attenuation equations. The traditional
265 Lambert-Beer equation describes the exponential decrease of light availability with depth:

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

266 such that the irradiance of incident light at depth Z (I_Z) can be estimated from the irradiance at
 267 the surface (I_O) and a light extinction coefficient (K_d). Minimum seagrass light requirements
 268 have also been estimated on average as approximately 11% surface irradiance (Duarte 1991),
 269 such that eq. (3) can be described by DOC_{max} :

$$0.11 = \exp(-K_d \cdot DOC_{max}) \quad (4)$$

270 A conversion factor is commonly used to estimate the light extinction coefficient from secchi
 271 depth Z_d , such that such that $1.44 = K_d \cdot Z_d$ (Holmes 1970). Thus, K_d is replaced with the the
 272 conversion factor and the equation is rearranged to describe DOC_{max} as a function of secchi
 273 depth Z_d :

$$DOC_{max} = \frac{-\log(0.11)}{1.44} \cdot Z_d \quad (5) \quad \{\text{eqn:sgreg}\}$$

274 A regression of seagrass depth estimates against secchi measurement is expected to have a slope
 275 corresponding to eq. (5), provided that the current approach for estimating maximum DoC is
 276 consistent with previous analyses that have empirically related seagrass depth limits with light
 277 requirements. The geographic coordinates for each secchi measurement were used as locations
 278 for estimating DOC_{max} in each segment. These estimates were compared with the secchi
 279 estimates using linear regression forced through the origin. The slope of the corresonding
 280 regression was compared with that in eq. (5) with the assumption that the two would not differ
 281 significantly. However, the relationship between the depth estimates and secchi measurements
 282 may vary depending on the specific radius around each sample point for estimating DOC_{max} .
 283 The effect of radius size on the relationship was also explored.

²⁸⁴ **3 Results**

²⁸⁵ Describe spatial heterogeneity within segments reasons why
²⁸⁶ Describe why estimates were unavailable in particular areas of each segment
²⁸⁷ Acknowledge that comparisons with segment wide estimate are specific to grid spacing
²⁸⁸ and radii tha twere used, thus the comparison is only useful for illustrating the presence of
²⁸⁹ heterogeneity within segments, as well as variation between segments. Absolute values will vary
²⁹⁰ with different spacing and radii.

²⁹¹ Fig. 5

²⁹² Table 2

²⁹³ Fig. 6

²⁹⁴ **4 Discussion**

295 **References**

- 296 Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors,
297 Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.
- 298 Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R
299 package version 0.3-8.
- 300 Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer,
301 New York, New York.
- 302 Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from
303 historical records of light attenuatoin along the Gulf coast of peninsular Florida. Marine
304 Pollution Bulletin, 81(1):94–102.
- 305 Cloern JE. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some
306 general lessons from sustained investigation of San Francisco Bay, California. Review of
307 Geophysics, 34(2):127–168.
- 308 Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report
309 to St. John's River Water Management District. Technical Report Contract 95W142, Coastal
310 Planning and Engineering, Palatka, Florida.
- 311 Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems.
312 Science, 321:926–929.
- 313 Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.
- 314 Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes.
315 Ophelia, 41:87–112.
- 316 Duarte CM, Conley DJ, Carstensen J, Sánchez-Camacho M. 2009. Return to *Neverland*: Shifting
317 baseline affect eutrophication restoration targets. Estuaries and Coasts, 32(1):29–36.
- 318 Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.
- 319 Greening H, Janicki A. 2006. Toward reversal of eutrophic conditions in a subtropical estuary:
320 Water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida,
321 USA. Environmental Management, 38(2):163–178.
- 322 Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.
- 323 Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species
324 along Florida's central gulf coast: Iverson and Bittaker revisited. Estuaries, 27(1):36–43.
- 325 Hilborn R, Mangel M. 1997. The Ecological Detective: Confronting Models with Data.
326 Princeton University Press, Princeton, New Jersey.
- 327 Holmes RW. 1970. The secchi disk in turbid coastal waters. Limnology and Oceanography,
328 15(5):688–694.

- 329 Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern:
330 declining seagrasses and threatened dependent species. *Frontiers in Ecology and the*
331 *Environment*, 7(5):242–246.
- 332 Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico
333 coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5):577–602.
- 334 Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary:
335 An empirically based approach to setting management targets. Technical Report 06-96, Tampa
336 Bay National Estuary Program, St. Petersburg, Florida.
- 337 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *OIKOS*,
338 69(3):373–386.
- 339 Justić D, Legović T, Rottini-Sandrini L. 1987. Trends in oxygen content 1911–1984 and
340 occurrence of benthic mortality in the northern Adriatic Sea. *Estuarine, Coastal and Shelf*
341 *Science*, 25(4):435–445.
- 342 Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and
343 *Syringodium filiforme* derived from the relationship between diffuse light attenuation and
344 maximum depth distribution. *Estuaries*, 19(3):740–750.
- 345 Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible
346 submersed aquatic vegetation habitat requirements. *Estuaries*, 24(1):1–17.
- 347 Nixon SW. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns.
348 *Ophelia*, 41:199–219.
- 349 R Development Core Team. 2014. R: A language and environment for statistical computing,
350 v3.1.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- 351 Spears BM, Gunn IDM, Carvalho L, Winfield IJ, Dudley B, Murphy K, May L. 2009. An
352 evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven,
353 Scotland. *Aquatic Botany*, 91(2):75–81.
- 354 Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light
355 targets for the Indian River Lagoon system, Florida. *Estuaries*, 28(6):923–935.
- 356 Tewfik A, Rasmussen JB, McCann KS. 2007. Simplification of seagrass food webs across a
357 gradient of nutrient enrichment. *Canadian Journal of Fisheries and Aquatic Sciences*,
358 64(7):956–967.
- 359 Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007.
360 Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051
361 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.
- 362 USEPA (US Environmental Protection Agency). 1998. National strategy for the development of
363 regional nutrient criteria. Technical Report EPA-822-R-98-002, Office of Water, Office of
364 Research and Development, US Environmental Protection Agency, Washington, DC.

³⁶⁵ WFD. 2000. Water framework directive, 2000/60/ec. european communities official journal l327
³⁶⁶ 22.12.2000, p. 73. <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex:32000L0060>.

³⁶⁷ Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay
³⁶⁸ ME, editors, *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts.

Table 1: Characteristics of coastal segments used to evaluate seagrass depth of colonization estimates. Segments are spatial units defined by US EPA for nutrient criteria development (see Fig. 1). 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 Record, update number 40 (IWR40).^{tab:seg_summ}

	Choctawhatchee Bay	Big Bend	Old Tampa Bay	Indian River Lagoon
Segment	0303	0820	0902	1502
Latitude	30.43	29.61	27.94	28.61
Longitude	-86.54	-83.48	-82.62	-80.77
Surface area	59.41	271.37	205.50	228.52
Seagrass area	3.51	203.02	24.48	74.89
Depth (mean)	5.31	1.41	2.56	1.40
Depth (max)	11.90	3.60	10.40	3.70
Secchi (mean)	2.13	1.34	1.34	1.34
Secchi (se)	0.07	0.19	0.01	0.01

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	Whole segment	Mean	St. Err.	Min	Max
0303					
SG_{max}	1.92	1.65	0.24	0.52	2.30
DOC_{med}	2.26	2.01	0.15	1.52	2.46
DOC_{max}	2.60	2.36	0.16	1.90	2.85
0820					
SG_{max}	1.50	1.71	0.43	0.06	3.23
DOC_{med}	2.92	2.07	0.42	0.52	3.46
DOC_{max}	4.34	2.42	0.43	0.69	3.97
0902					
SG_{max}	0.52	0.45	0.15	0.00	1.03
DOC_{med}	0.79	0.82	0.14	0.29	1.59
DOC_{max}	1.07	1.18	0.17	0.59	2.15
1502					
SG_{max}	1.25	1.33	0.11	0.90	2.02
DOC_{med}	1.51	1.50	0.10	0.98	2.08
DOC_{max}	1.77	1.66	0.10	1.06	2.16

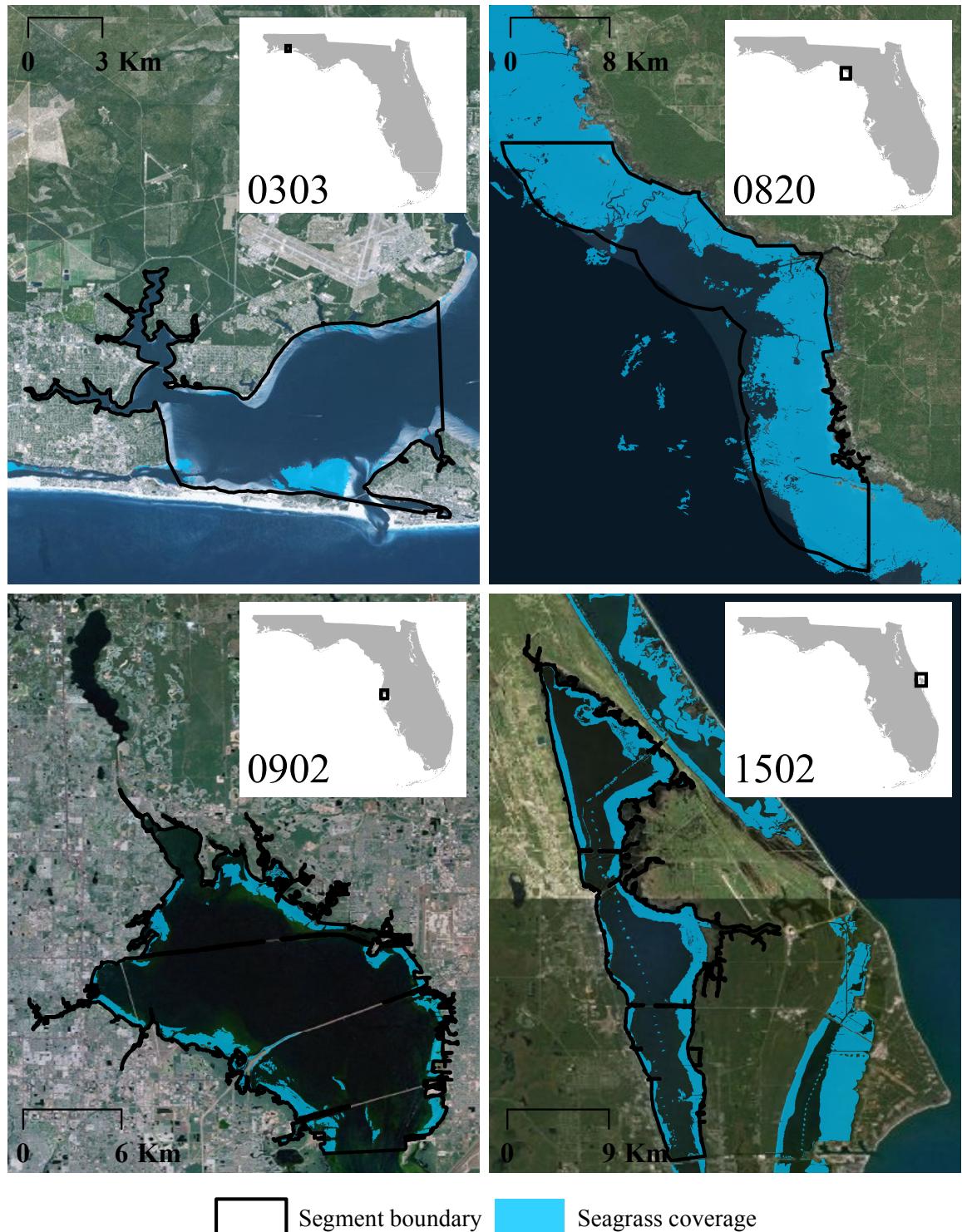


Fig. 1: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (Choctowatchee Bay, 0303), 2006 (Big Bend, 0820), 2010 (Old Tampa Bay, 0902), and 2009 (Indian River Lagoon, 1502).

{fig:seg_a}

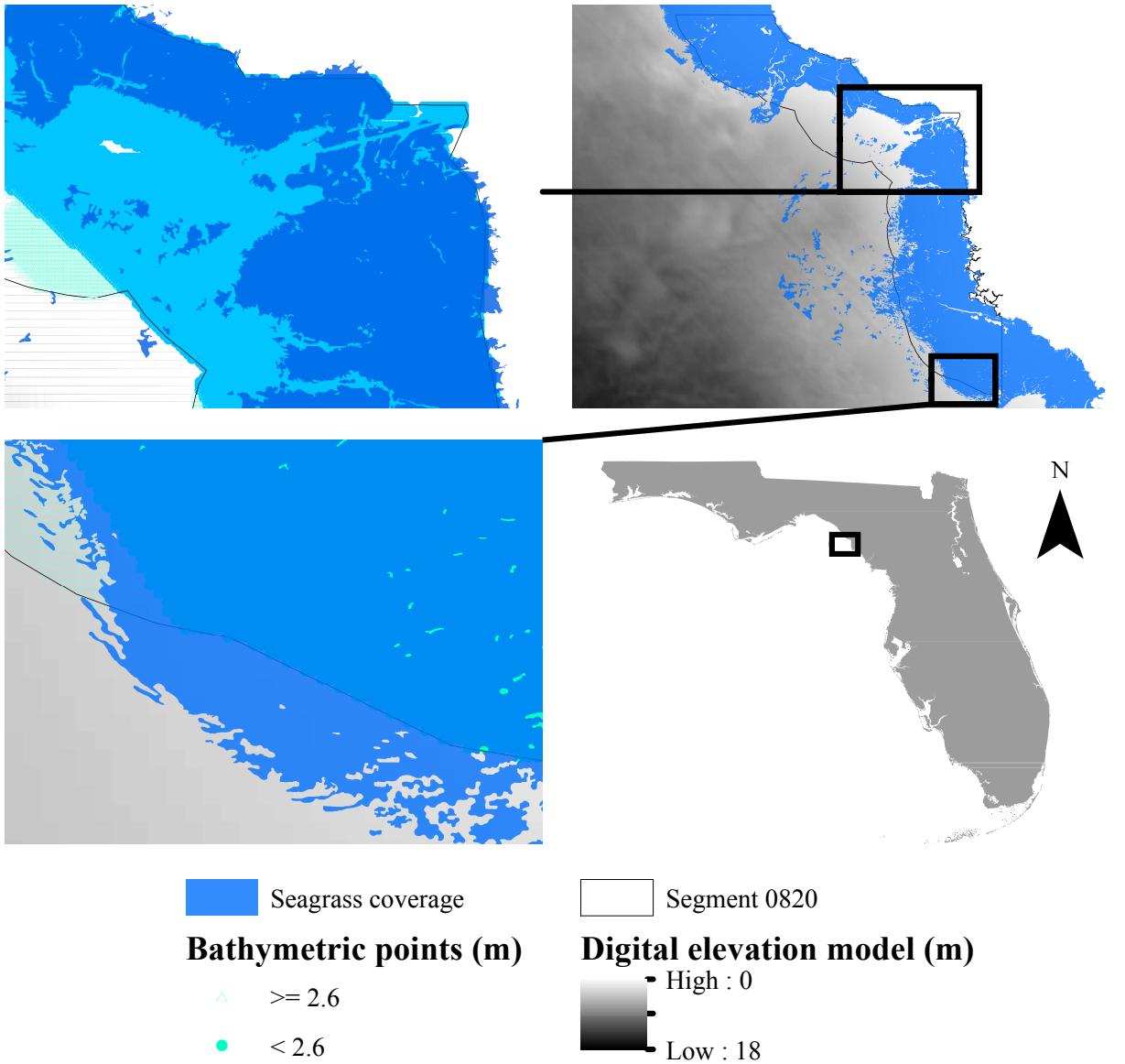
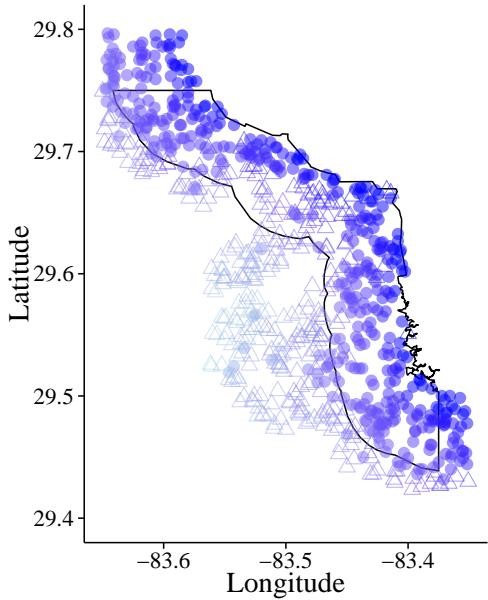


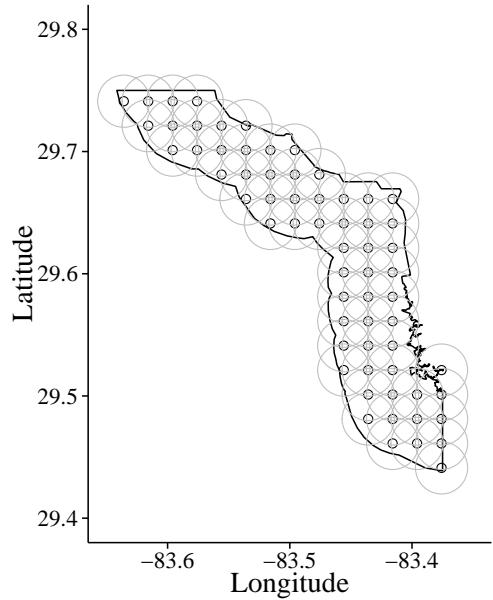
Fig. 2: Example of over- and under-estimates for seagrass depth of colonization for segment 820 in the Big Bend region, Florida. Layers include a seagrass coverage layer, bathymetric depth points, bathymetric digital elevation model, and spatial extents for the segment and Florida. The top-left figure 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).

{fig:wbid}

(a) Seagrass depth points for the segment



(b) Grid of locations and sample areas for estimates



(c) Sampled observations for a test point

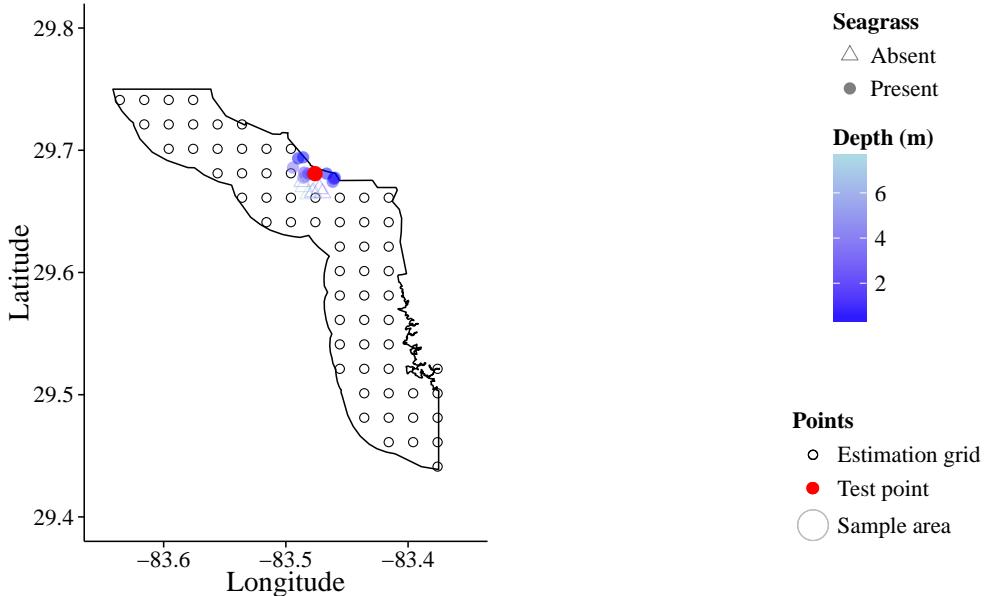


Fig. 3: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 3a shows the seagrass depth points that are used for sampling, Fig. 3b shows a grid of locations and sampling radii for estimating seagrass DoC, and Fig. 3c shows an example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

{fig:buff_}

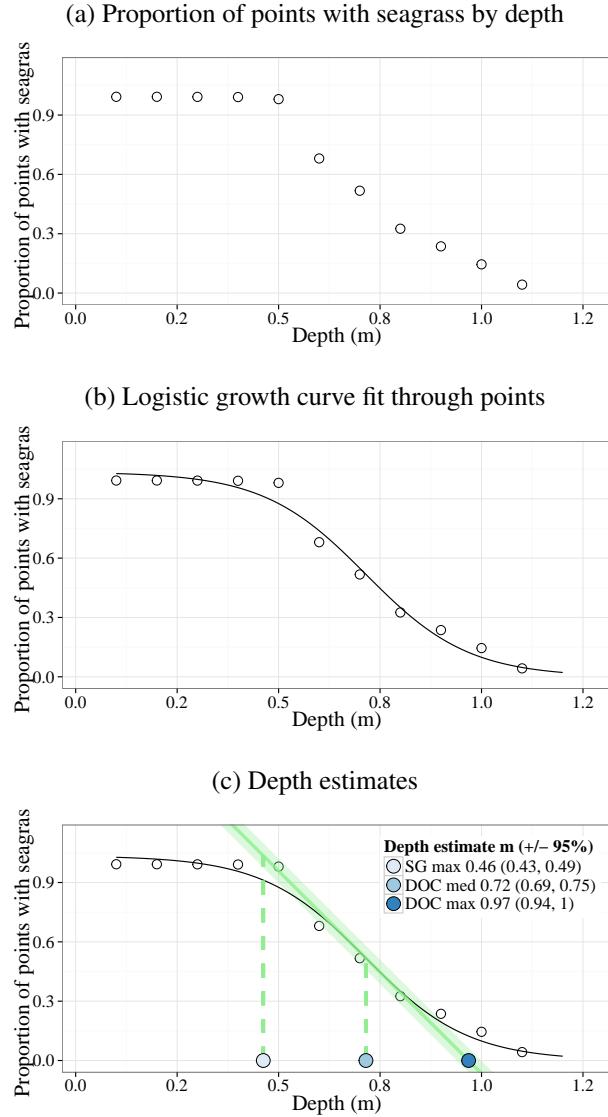


Fig. 4: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 4a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 3. Fig. 4b adds a decreasing logistic growth curve fit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

{fig:est_e}

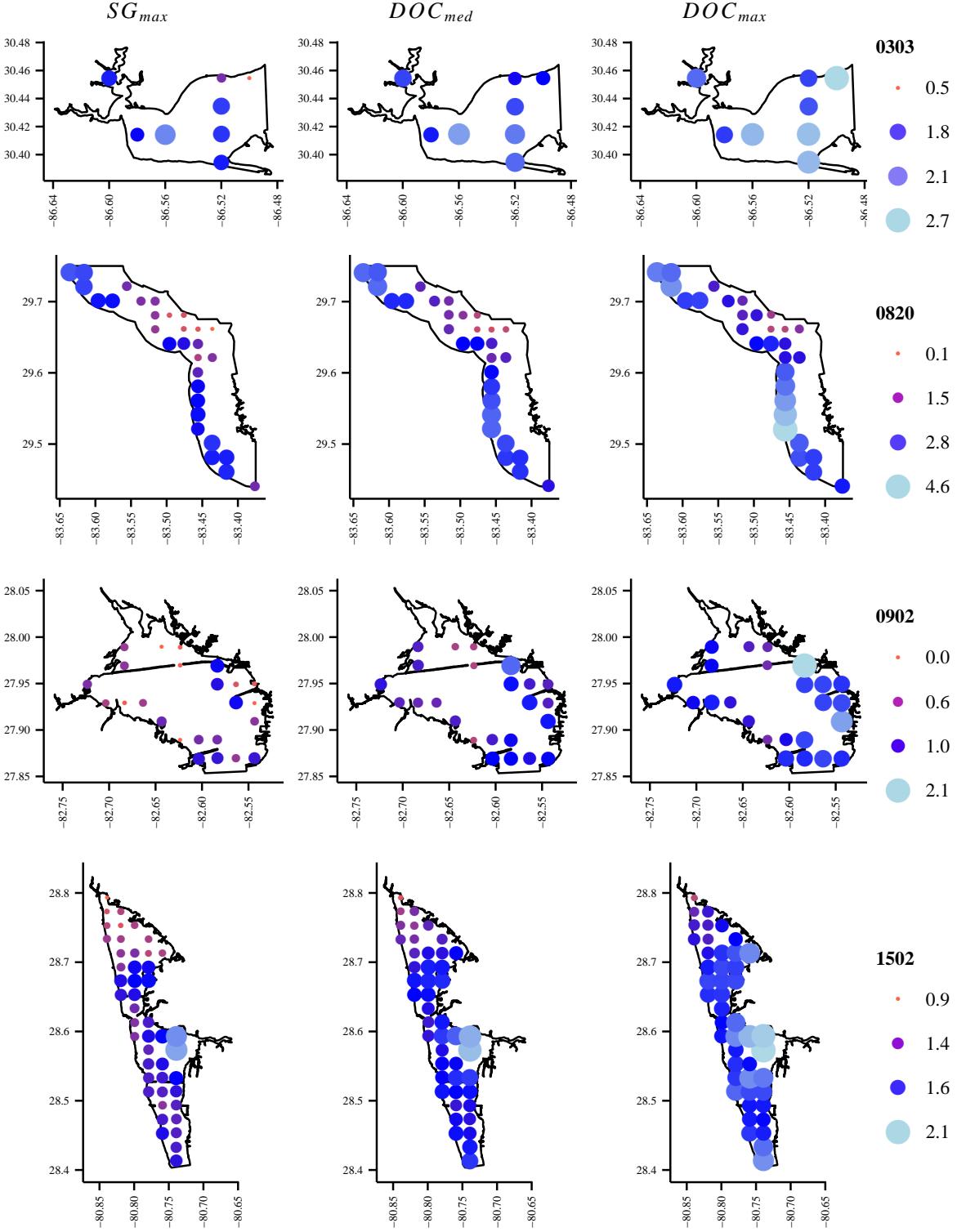


Fig. 5: Spatially-referenced estimates of seagrass depth limits (m) for four coastal segments of Florida. Estimates include depth of maximum seagrass growth (SG_{max}), median depth of colonization (DOC_{med}), and maximum depth of colonization (DOC_{max}). Estimates are assigned to grid locations for 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. {fig:all_e}

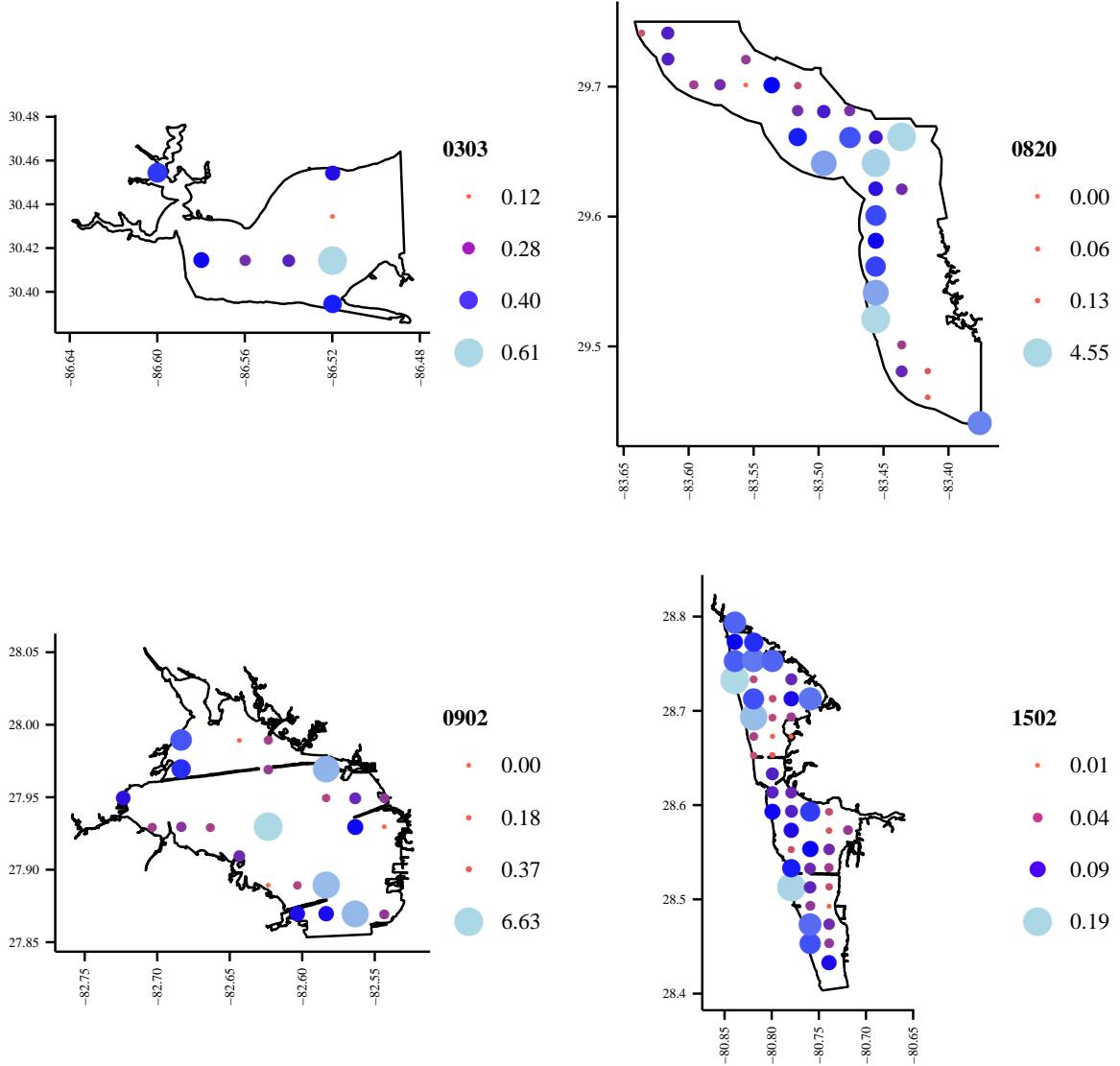


Fig. 6: Size of confidence intervals (m) for depth of colonization estimates in Fig. 5. Points are colored and sized based on the difference between the upper and lower bounds of a 95% confidence interval for all three DoC estimates (SG_{max} , DOC_{med} , DOC_{max}). Bounds were obtained using Monte Carlo simulations to estimate uncertainty associated with the inflection point of the estimated logistic curve (Fig. 4) for each sample.

{fig:all_}