

**1 A reproducible and empirical approach for spatially-referenced
2 estimates of seagrass depth of colonization**

3 Marcus W. Beck¹, James D. Hagy III²

¹*ORISE Research Participation Program*

USEPA National Health and Environmental Effects Research Laboratory

Gulf Ecology Division, 1 Sabine Island Drive, Gulf Breeze, FL 32561

Phone: 850-934-2480, Fax: 850-934-2401, Email: beck.marcus@epa.gov

²*USEPA National Health and Environmental Effects Research Laboratory*

Gulf Ecology Division, 1 Sabine Island Drive, Gulf Breeze, FL 32561

Phone: 850-934-2455, Fax: 850-934-2401, Email: hagy.jim@epa.gov

1 Introduction

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

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

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

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

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

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

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

73 **2 Methods**

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

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

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

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

78 including relationships with water clarity.

79 **2.1 Locations and data sources**

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

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

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

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

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

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

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

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

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

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

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

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

92 0820 (Big Bend region), 0902 (Tampa Bay), and 1502 (Indian River Lagoon), where the first two

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

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

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

116 the North American Vertical Datum of 1988 (NAVD) and the Indian River Lagoon data were {acro:NAV
117 referenced to mean sea level. Depth layers were combined with seagrass coverage layers using
118 standard union techniques for raster and vector layers in ArcMap 10.1 (Environmental Systems
119 Research Institute 2012). To reduce computation time, depth layers were first masked using a 1
120 km buffer of the seagrass coverage layer. The final layer used for analysis was a point layer with
121 attributes describing location (latitude, longitude, segment), depth (m), and seagrass (present,
122 absent). Additional details describing the data are available in Hagy, In review.

123 Depth values in each seagrass layer were further adjusted to local mean sea level (MSL) {acro:MSL}
124 for each location. Depth data that were referenced to a tidal datum were converted to local MSL
125 by adding the difference between MSL and the source datum. The Tampa Bay dataset referenced
126 to NAVD was adjusted using the NOAA VDatum tool.

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

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

138 the x-axis is considered the maximum depth of colonization. The median portion of this curve is
139 considered the median depth of the deepwater edge of seagrass.

140 Considerable spatial heterogeneity in the observed seagrass growth patterns suggests that
141 a segment-wide estimate of seagrass DoC may be inadequate for fully characterizing growth
142 patterns, particularly for the examples in the current analysis. Fig. 2 illustrates spatial variation in
143 seagrass distribution for a location in the Big Bend region of Florida. Using methods in [Hagy, In](#)
144 [review](#), the estimate for median seagrass DoC for the segment is over- and under-estimated for
145 different areas of the segment. In particular, DoC is greatly over-estimated at the outflow of the
146 Steinhatchee where high concentrations of dissolved organic matter naturally limit seagrass
147 growth. This example suggests that estimates of DoC may be needed at finer spatial scales to
148 provide a more robust determination of restoration targets and nutrient criteria.

149 **2.3 Estimating seagrass depth of colonization using spatial information**

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

159 The spatially-referenced approach for estimating DoC begins by creating a grid of

160 evenly-spaced points within the segment. The same process for estimating DoC is used for each
161 point. Alternatively, a single location of interest can be chosen rather than a grid-based design.
162 Seagrass depth data (i.e., merged bathymetric and seagrass coverage data) that occur within a set
163 radius from the chosen locations are selected for estimating seagrass DoC values. The estimate
164 for each location is quantified from a plot of the proportion of bathymetric soundings that contain
165 seagrass at each depth bin (Fig. 4a). Although the chosen radius for selecting depth points is
166 problem-specific, the minimum radius must sample a sufficient number of points for estimating
167 DoC. In general, an appropriate radius will produce a plot that indicates a decrease in the
168 proportion of points that are occupied by seagrass with increasing depth.

169 A curve is fit to the sampled depth points using non-linear regression to characterize the
170 reduction in seagrass as a function of depth. Specifically, a decreasing logistic growth curve is fit
171 to the plot to create a monotonic and asymptotic function of the sample data. The curve is fit by
172 minimizing the residual sums-of-squares with the Gauss-Newton algorithm (Bates and Chambers
173 1992) and user-supplied starting parameters that are an approximate estimate of the curve
174 characteristics. The model has the following form:

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

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

178 Finally, a simple linear curve is fit through the inflection point (β) of the logistic curve to
179 estimate depth of colonization (Fig. 4c). The inflection point is the depth at which seagrass are

decreasing at a maximum rate and is used as the slope of the linear curve. Three measures describing seagrass growth characteristics are obtained. The maximum depth of seagrass colonization, DOC_{max} , is the x-axis intercept of the linear curve. The minimum depth of seagrass growth, DOC_{min} is the location where the linear curve intercepts the asymptote of the logistic growth curve. This depth can be considered the start of the decline in seagrass coverage with increasing depth. The median depth of seagrass colonization, DOC_{med} , is the depth halfway between DOC_{min} and DOC_{max} . DOC_{med} was typically but not always the inflection point of the logistic growth curve. Functionally, each measure has specific ecological significance. The median and maximum depth estimates describe the growth limitations of seagrasses as a function of water clarity, whereas minimum depth of growth was often where the highest percentage of seagrass coverage was observed in the sample. Median and maximum depth estimates differ in that the former describes the median depth of the deep water edge, whereas the latter describes a nominal characterization of maximum depth independent of outliers.

Estimates for each of the three DoC measures are obtained only if specific criteria are met. These criteria were implemented as a safety measure that ensures a sufficient amount and appropriate quality of data are used. First, estimates are provided only if a sufficient number of seagrass depth points are present within the radius of the grid point to estimate a logistic growth curve. This criteria applies to the sample size as well as the number of points with seagrass in the sample. That is, the curve cannot be estimated for small samples or if an insufficient number of points contain seagrass regardless of sample size. Second, estimates are provided only if an inflection point is present on the logistic curve within the range of the sampled depth data. This criteria may apply under two scenarios where the curve is estimated but a trend is not adequately described by the sampled data. That is, a curve may be estimated that describes only the initial

203 decrease in points occupied as a function of depth but the observed points do not occur at depths
204 deeper than the predicted inflection point. The opposite scenario may occur when a curve is
205 estimated but only the deeper locations beyond the inflection point are present in the sample.
206 Finally, the estimate for DOC_{min} is set to zero depth if the linear curve through the inflection
207 point intercepts the asymptote at x-axis values less than zero. The estimate for DOC_{med} is also
208 shifted to the depth value halfway between DOC_{min} and DOC_{max} .

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

214 **2.4 Comparison with segment-based approach and sensitivity analysis**

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

225 within the segment while also minimizing redundancy of information described by each location.
226 In other words, radii were set such that the seagrass depth points sampled by each grid location
227 were only partially overlapped by those sampled by neighboring points.

228 The ability to characterize heterogeneity in seagrass growth patterns using the grid-based
229 approach can be informed by evaluating the level of confidence associated with DoC estimates.
230 Confidence intervals for non-linear regression can be estimated using a Monte Carlo simulation
231 approach that considers the variance and covariance between the model parameters and the depth
232 measurements ([Hilborn and Mangel 1997](#)). For simplicity, we assume that the observation
233 uncertainty associated with the depth measurements is zero such that the variability associated
234 with parameter estimates is considered the primary source of uncertainty. A 95% confidence
235 interval for each DoC estimates was constructed by repeated sampling of a multivariate normal
236 distribution followed by prediction of the proportion of points occupied by seagrass as in eq. (1).
237 The sampling distribution assumes:

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

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

245 The uncertainty associated with the DoC estimates were based on the upper and lower

246 limits of the estimated inflection point on the logistic growth curve. This approach was used
247 because uncertainty in the inflection point is directly related to uncertainty in each of the DoC
248 estimates that are based on the linear curve fit through the inflection point. Specifically, linear
249 curves were fit through the upper and lower estimates of the inflection point to identify upper and
250 lower limits for the estimates of DOC_{min} , DOC_{med} , and DOC_{max} . These values were compared
251 with the initial estimates from the linear curve that was fit through the predicted logistic curve
252 (i.e., Fig. 4e). This approach provided an indication of uncertainty for individual estimates for a
253 set radius. Uncertainty estimates were obtained for each DoC estimate for the grids in each
254 segment.

255 **2.5 Developing a spatially coherent relationship of water clarity with depth 256 of colonization**

257 Information describing seagrass light requirements can be obtained from the maximum
258 depth estimates by evaluating spatial relationships with water clarity. In particular, increased
259 resolution of seagrass depth estimates compared with measures of water clarity can potentially
260 improve the ability to empirically describe light requirements and areas where seagrass are
261 growing at depths deeper or shallower than expected. Secchi measurements provide a precise
262 estimate of water clarity and have been obtained at numerous locations documented in the Florida
263 Department of Environmental Protection's Impaired Waters Rule (IWR) database. {acro:IWR}
264 Secchi data for Florida coastal waters were obtained from update 40 of the IWR database for all
265 of Tampa Bay (2010 coverage) and the Indian River Lagoon (2009 coverage) given the spatial
266 coverage of secchi observations relative to the other segments used in the current analysis. All
267 seagrass for a given year and all secchi data for each bay were evaluated. This approach was
268 chosen rather than evaluating individual segments as above to examine a larger water clarity

gradient for each bay. All secchi data were screened to exclude observations that were flagged indicating that the value was lower than the maximum depth of the observation point. Secchi data were also compared with bathymetric data to verify unflagged values were not missed by initial screening. Secchi observations that were measured at the same geographic location were averaged across all dates. This approach was preferred given that seagrass depth patterns are more representative of long-term trends in water clarity as opposed to individual secchi measures that may be highly variable (Dennison 1987, Dennison et al. 1993).

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

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

such that the irradiance of incident light at depth Z (I_z) can be estimated from the irradiance at the surface (I_O) and a light extinction coefficient (K_d). Minimum seagrass light requirements have also been estimated numerous times. For example, Duarte (1991) indicate that minimum light requirements for seagrass are on average 11% of surface irradiance. Others have shown that light requirements are species dependent and variable by latitude with estimates ranging from less than 5% to greater than 30% (Dennison et al. 1993). Estimated light requirements (e.g., 20%) can be used with eq. (3) to describe DOC_{max} :

$$0.20 = \exp(-K_d \cdot DOC_{max}) \quad (4)$$

286 A conversion factor is often used to estimate the light extinction coefficient from secchi depth Z_d ,
287 such that such that $c = K_d \cdot Z_d$, where c has been estimated as 1.7 (Poole and Atkins 1929, Idso
288 and Gilbert 1974). Thus, K_d can be replaced with the conversion factor and the equation is
289 rearranged to describe DOC_{max} as a function of secchi depth Z_d :

$$DOC_{max} = \frac{-\log(0.20)}{1.7} \cdot Z_d \quad (5) \quad \{\text{eqn:sgreg}\}$$

290 A regression of seagrass depth estimates against secchi measurements is expected to have a slope
291 corresponding to the constant in eq. (5). The geographic coordinates for each secchi measurement
292 were used as locations for estimating DOC_{max} in each segment. These estimates were compared
293 with the secchi estimates using linear regression forced through the origin. However, the
294 relationship is expected to vary depending on the specific radius around each sample point for
295 estimating DOC_{max} . An appropriate radius was chosen that minimized the difference between
296 the empirically estimated slope and that in eq. (5). Scatter in the regression through these points
297 can be considered biologically meaningful, such that points below the curve are locations where
298 seagrasses are observed at maximum depth with less irradiance than expected given eq. (5),
299 whereas points above the curve are those where seagrasses are growing deeper than expected. The
300 estimated light requirements of each point were plotted using the cartesian coordinates of each
301 secchi observation to evaluate spatial variation in seagrass growth as a function of light-limitation.
302 Light requirements were also summarized by individual segments in each bay to identify spatial
303 trends by relevant management units.

304 **3 Results**

305 Describe spatial heterogeneity within segments reasons why
306 Describe why estimates were unavailable in particular areas of each segment
307 Acknowledge that comparisons with segment wide estimate are specific to grid spacing
308 and radii that were used, thus the comparison is only useful for illustrating the presence of
309 heterogeneity within segments, as well as variation between segments. Absolute values will vary
310 with different spacing and radii.

311 Fig. 5

312 Table 2

313 Fig. 6

314 Table 3

315 Fig. 7

316 **4 Discussion**

317 **References**

- 318 Bates DM, Chambers JM. 1992. Nonlinear models. In: Chambers JM, Hastie TJ, editors,
319 Statistical Models in S, pages 421–454. Wadsworth and Brooks/Cole, Pacific Grove, California.
- 320 Bivand R, Rundel C. 2014. rgeos: Interface to Geometry Engine - Open Source (GEOS). R
321 package version 0.3-8.
- 322 Bivand RS, Pebesma EJ, Gómez-Rubio V. 2008. Applied Spatial Data Analysis with R. Springer,
323 New York, New York.
- 324 Choice ZD, Frazer TK, Jacoby CA. 2014. Light requirements of seagrasses determined from
325 historical records of light attenuatoin along the Gulf coast of peninsular Florida. Marine
326 Pollution Bulletin, 81(1):94–102.
- 327 Cloern JE. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some
328 general lessons from sustained investigation of San Francisco Bay, California. Review of
329 Geophysics, 34(2):127–168.
- 330 Coastal Planning and Engineering. 1997. Indian River Lagoon bathymetric survey. A final report
331 to St. John's River Water Management District. Technical Report Contract 95W142, Coastal
332 Planning and Engineering, Palatka, Florida.
- 333 Dennison WC. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution.
334 Aquatic Botany, 27(1):15–26.
- 335 Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA.
336 1993. Assessing water quality with submersed aquatic vegetation. BioScience, 43(2):86–94.
- 337 Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems.
338 Science, 321:926–929.
- 339 Duarte CM. 1991. Seagrass depth limits. Aquatic Botany, 40(4):363–377.
- 340 Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes.
341 Ophelia, 41:87–112.
- 342 Duarte CM, Conley DJ, Carstensen J, Sánchez-Camacho M. 2009. Return to *Neverland*: Shifting
343 baseline affect eutrophication restoration targets. Estuaries and Coasts, 32(1):29–36.
- 344 Environmental Systems Research Institute. 2012. ArcGIS v10.1. ESRI, Redlands, California.
- 345 Greening H, Janicki A. 2006. Toward reversal of eutrophic conditions in a subtropical estuary:
346 Water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida,
347 USA. Environmental Management, 38(2):163–178.
- 348 Hagy JD. In review. Seagrass depth of colonization in Florida estuaries.
- 349 Hale JA, Frazer TK, Tomasko DA, Hall MO. 2004. Changes in the distribution of seagrass species
350 along Florida's central gulf coast: Iverson and Bittaker revisited. Estuaries, 27(1):36–43.

- 351 Hilborn R, Mangel M. 1997. The Ecological Detective: Confronting Models with Data.
352 Princeton University Press, Princeton, New Jersey.
- 353 Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M. 2009. Associations of concern:
354 declining seagrasses and threatened dependent species. *Frontiers in Ecology and the
355 Environment*, 7(5):242–246.
- 356 Idso SB, Gilbert RG. 1974. On the universality of the Poole and Atkins secchi disk-light
357 extinction equation. *Journal of Applied Ecology*, 11(1):399–401.
- 358 Iverson RL, Bittaker HF. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico
359 coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5):577–602.
- 360 Janicki A, Wade D. 1996. Estimating critical external nitrogen loads for the Tampa Bay estuary:
361 An empirically based approach to setting management targets. Technical Report 06-96, Tampa
362 Bay National Estuary Program, St. Petersburg, Florida.
- 363 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *OIKOS*,
364 69(3):373–386.
- 365 Justić D, Legović T, Rottini-Sandrini L. 1987. Trends in oxygen content 1911–1984 and
366 occurrence of benthic mortality in the northern Adriatic Sea. *Estuarine, Coastal and Shelf
367 Science*, 25(4):435–445.
- 368 Kenworthy WJ, Fonseca MS. 1996. Light requirements of seagrasses *Halodule wrightii* and
369 *Syringodium filiforme* derived from the relationship between diffuse light attenuation and
370 maximum depth distribution. *Estuaries*, 19(3):740–750.
- 371 Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible
372 submersed aquatic vegetation habitat requirements. *Estuaries*, 24(1):1–17.
- 373 Nixon SW. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns.
374 *Ophelia*, 41:199–219.
- 375 Poole HH, Atkins WRG. 1929. Photo-electric measurements of submarine illumination
376 throughout the year. *Journal of the Marine Biological Association of the United Kingdom*,
377 16:297–324.
- 378 R Development Core Team. 2014. R: A language and environment for statistical computing,
379 v3.1.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- 380 Spears BM, Gunn IDM, Carvalho L, Winfield IJ, Dudley B, Murphy K, May L. 2009. An
381 evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven,
382 Scotland. *Aquatic Botany*, 91(2):75–81.
- 383 Steward JS, Virnstein RW, Morris LJ, Lowe EF. 2005. Setting seagrass depth, coverage, and light
384 targets for the Indian River Lagoon system, Florida. *Estuaries*, 28(6):923–935.

- 385 Tewfik A, Rasmussen JB, McCann KS. 2007. Simplification of seagrass food webs across a
386 gradient of nutrient enrichment. Canadian Journal of Fisheries and Aquatic Sciences,
387 64(7):956–967.
- 388 Tyler D, Zawada DG, Nayegandhi A, Brock JC, Crane MP, Yates KK, Smith KEL. 2007.
389 Topobathymetric data for Tampa Bay, Florida. Technical Report Open-File Report 2007-1051
390 (revised), US Geological Survey, US Department of the Interior, St. Petersburg, Florida.
- 391 USEPA (US Environmental Protection Agency). 1998. National strategy for the development of
392 regional nutrient criteria. Technical Report EPA-822-R-98-002, Office of Water, Office of
393 Research and Development, US Environmental Protection Agency, Washington, DC.
- 394 WFD. 2000. Water framework directive, 2000/60/ec. european communities official journal l327
395 22.12.2000, p. 73. <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex:32000L0060>.
- 396 Williams SL, Heck KL. 2001. Seagrass community ecology. In: Bertness MD, Gaines SD, Hay
397 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 Rule, update number 40.^{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. Dev.	Min	Max
0303					
DOC_{min}	1.92	1.65	0.54	0.52	2.30
DOC_{med}	2.26	2.01	0.34	1.52	2.46
DOC_{max}	2.60	2.36	0.35	1.90	2.85
0820					
DOC_{min}	1.50	1.71	0.96	0.06	3.23
DOC_{med}	2.92	2.07	0.94	0.52	3.46
DOC_{max}	4.34	2.42	0.97	0.69	3.97
0902					
DOC_{min}	0.52	0.45	0.34	0.00	1.03
DOC_{med}	0.79	0.82	0.31	0.29	1.59
DOC_{max}	1.07	1.18	0.38	0.59	2.15
1502					
DOC_{min}	1.25	1.33	0.24	0.90	2.02
DOC_{med}	1.51	1.50	0.23	0.98	2.08
DOC_{max}	1.77	1.66	0.23	1.06	2.16

Table 3: Summary of uncertainty for seagrass depth estimates (m) for each segment using all grid locations in Fig. 6. The uncertainty values are equally applicable to each seagrass depth measure (DOC_{min} , DOC_{med} , DOC_{max}).^{tab:sens_sum}

Segment	Mean	St. Dev	Min	Max
0303	0.49	0.45	0.12	1.63
0820	0.14	0.16	0.01	0.73
0902	0.43	0.29	0.12	1.19
1502	0.08	0.06	0.01	0.31

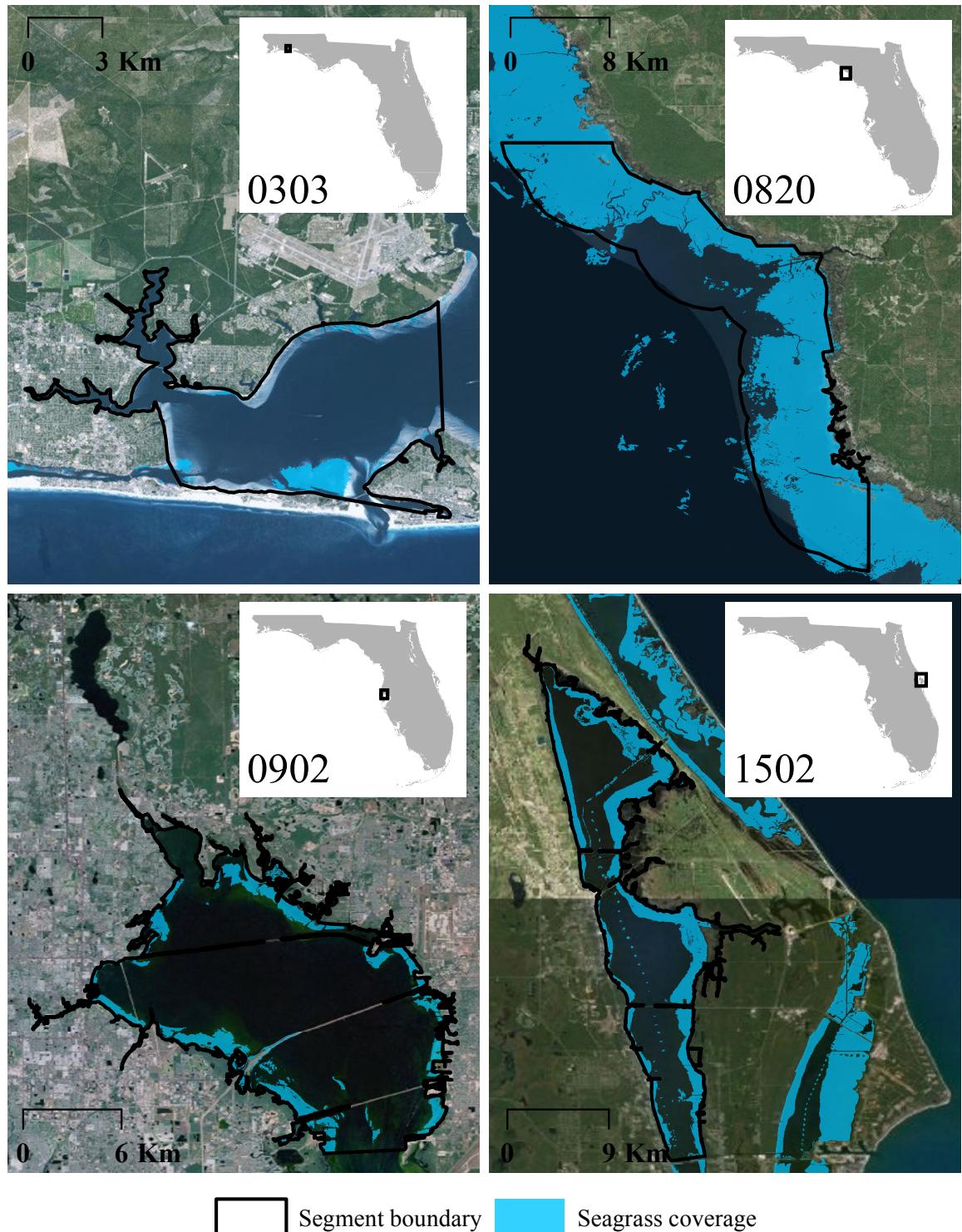


Fig. 1: Locations and seagrass coverage of estuary segments used to evaluate depth of colonization estimates. Seagrass coverage layers are from 2007 (Choctowatchee Bay, 0303), 2006 (Big Bend, 0820), 2010 (Old Tampa Bay, 0902), and 2009 (Indian River Lagoon, 1502).

{fig:seg_a}

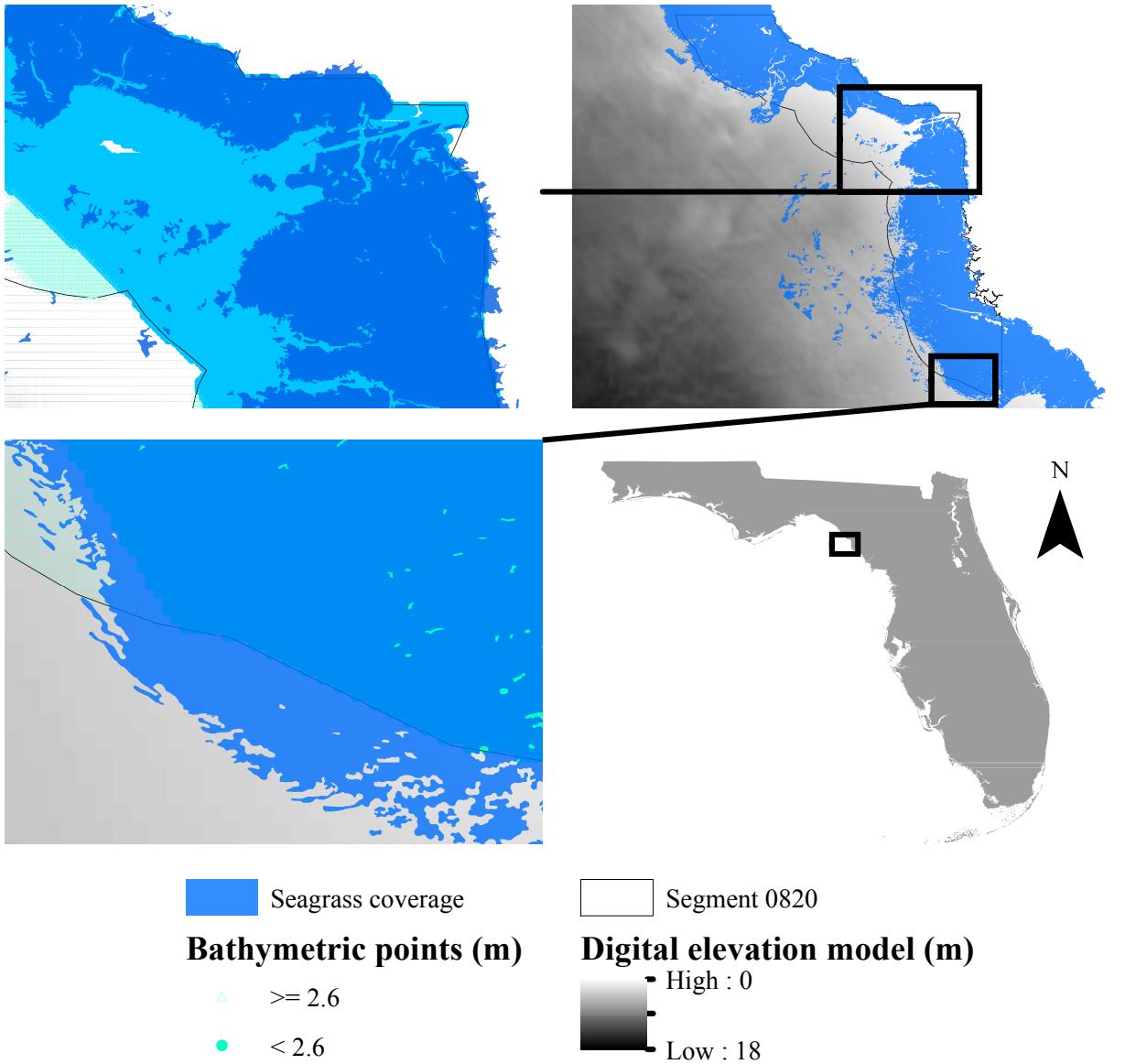


Fig. 2: Example of over- and under-estimates for seagrass depth of colonization for segment 820 in the Big Bend region, Florida. Layers include a seagrass coverage layer, bathymetric depth points, bathymetric digital elevation model, and spatial extents for the segment and Florida. The top-left figure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

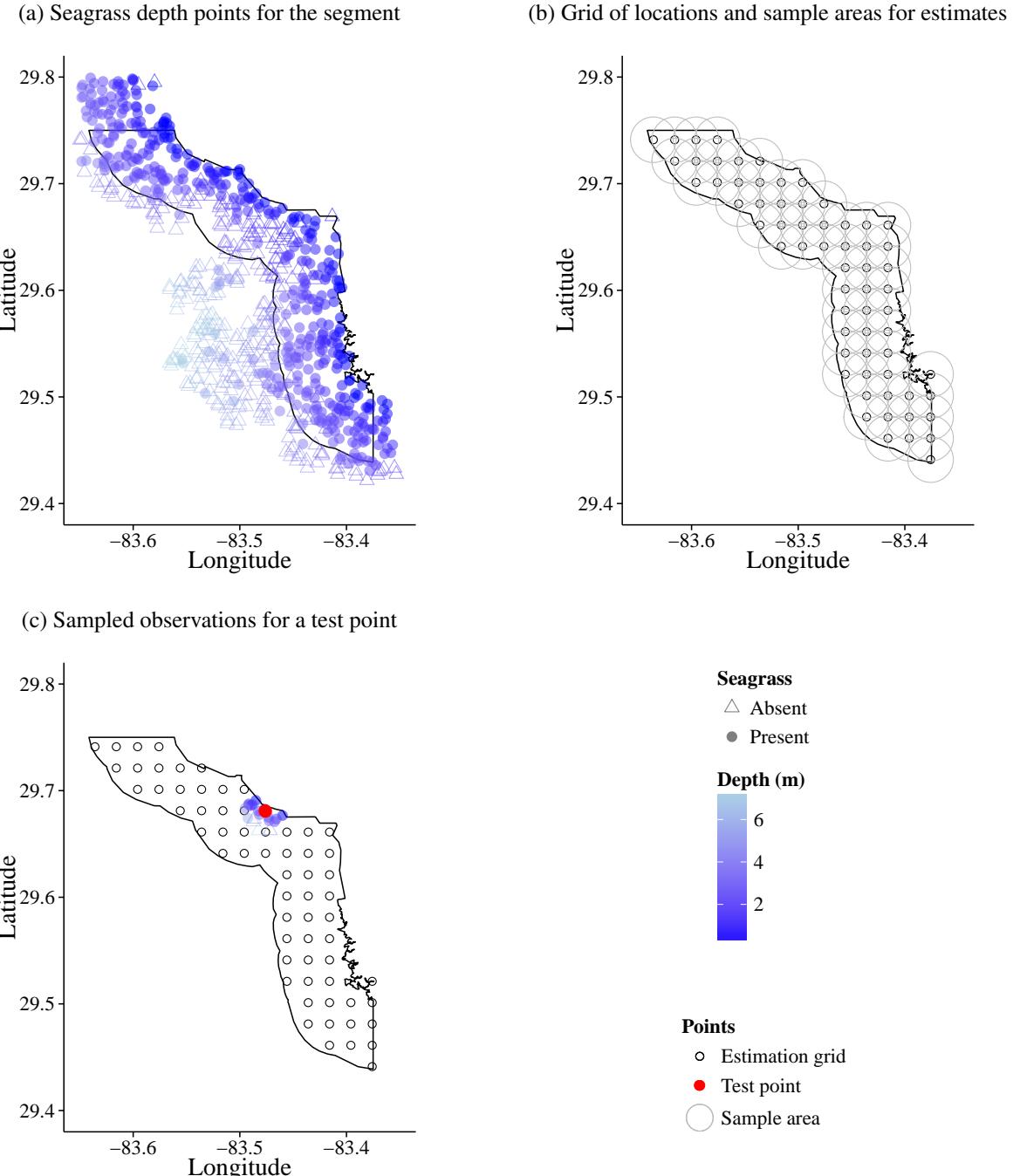


Fig. 3: Examples of data and grid locations for estimating seagrass depth of colonization for a region of the Big Bend, Florida. Fig. 3a shows the seagrass depth points that are used for sampling, Fig. 3b shows a grid of locations and sampling radii for estimating seagrass DoC, and Fig. 3c shows an example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

{fig:buff_}

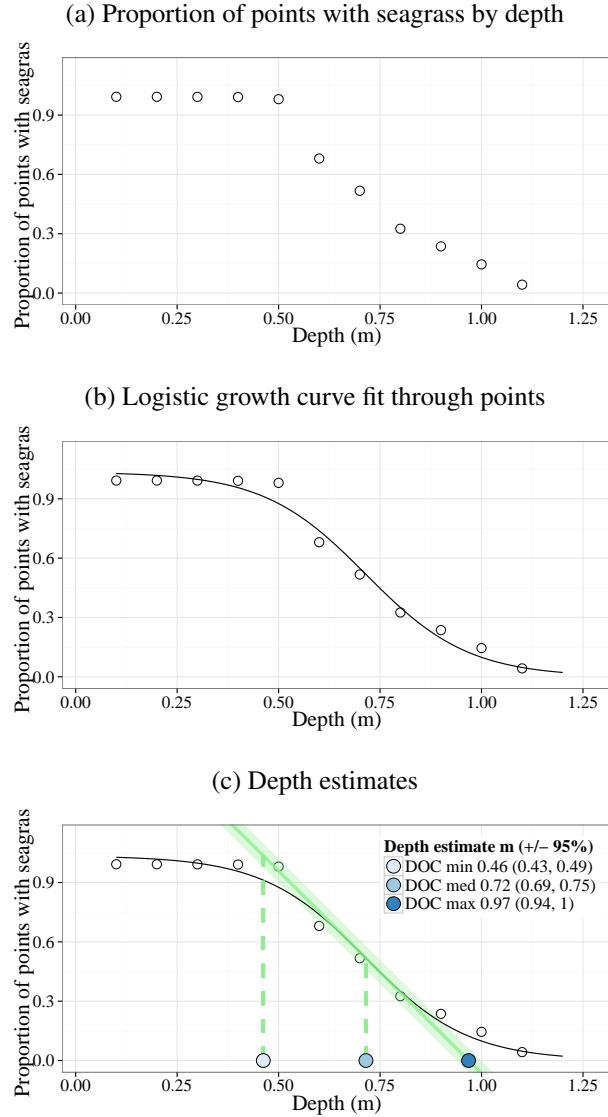


Fig. 4: Methods for estimating seagrass depth of colonization using sampled seagrass depth points around a single location. Fig. 4a is the proportion of points with seagrass by depth using depth points within the buffer of the test point in Fig. 3. Fig. 4b adds a decreasing logistic growth curve fit 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}

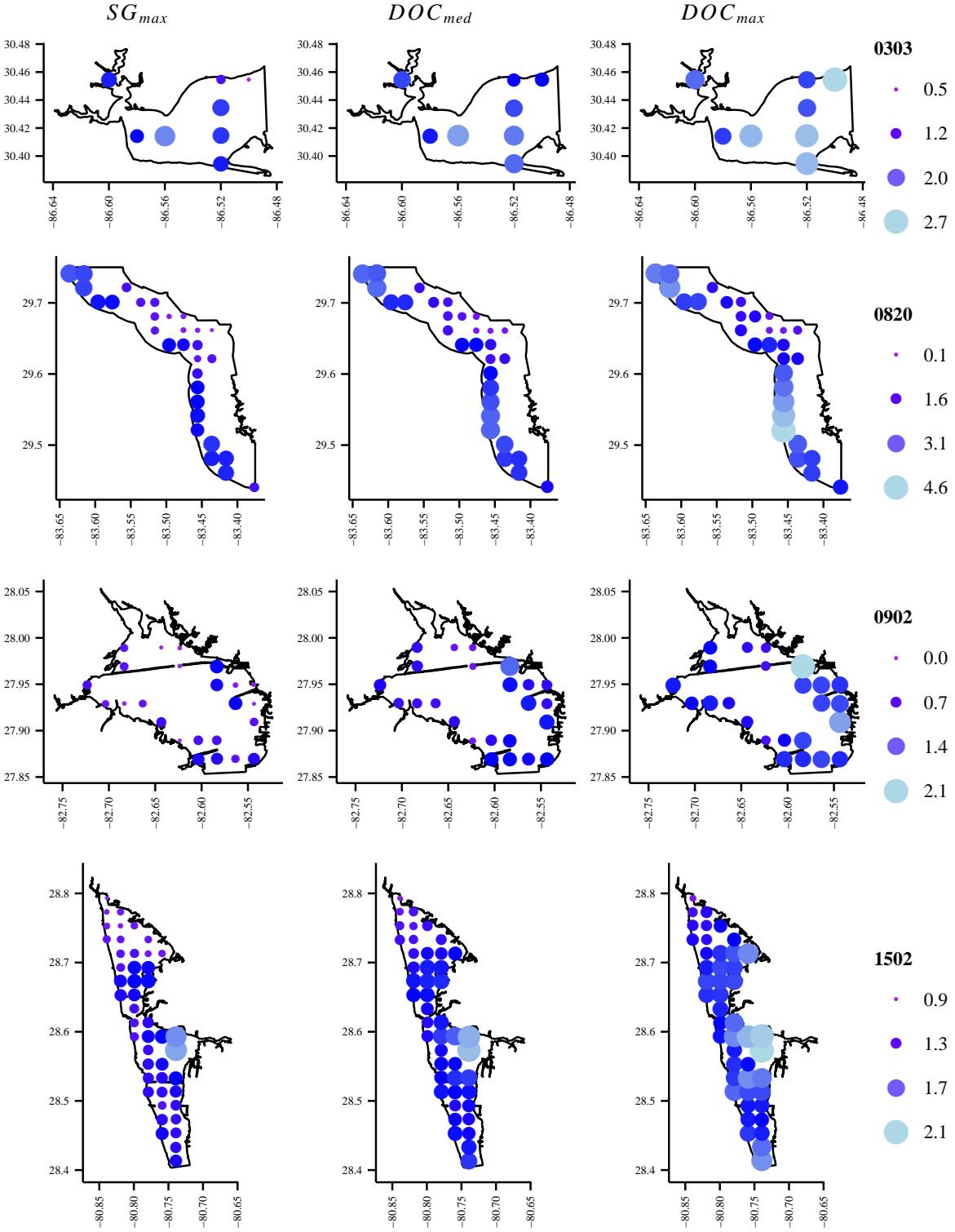


Fig. 5: Spatially-referenced estimates of seagrass depth limits (m) for four coastal segments of Florida. Estimates include minimum (DOC_{min}), median (DOC_{med}), and maximum depth of colonization (DOC_{max}). Estimates are assigned to grid locations for each segment, where grid spacing was fixed at 0.02 decimal degrees. Radii for sampling seagrass bathymetric data around each grid location were fixed at 0.06 decimal degrees.

{fig:all_e}

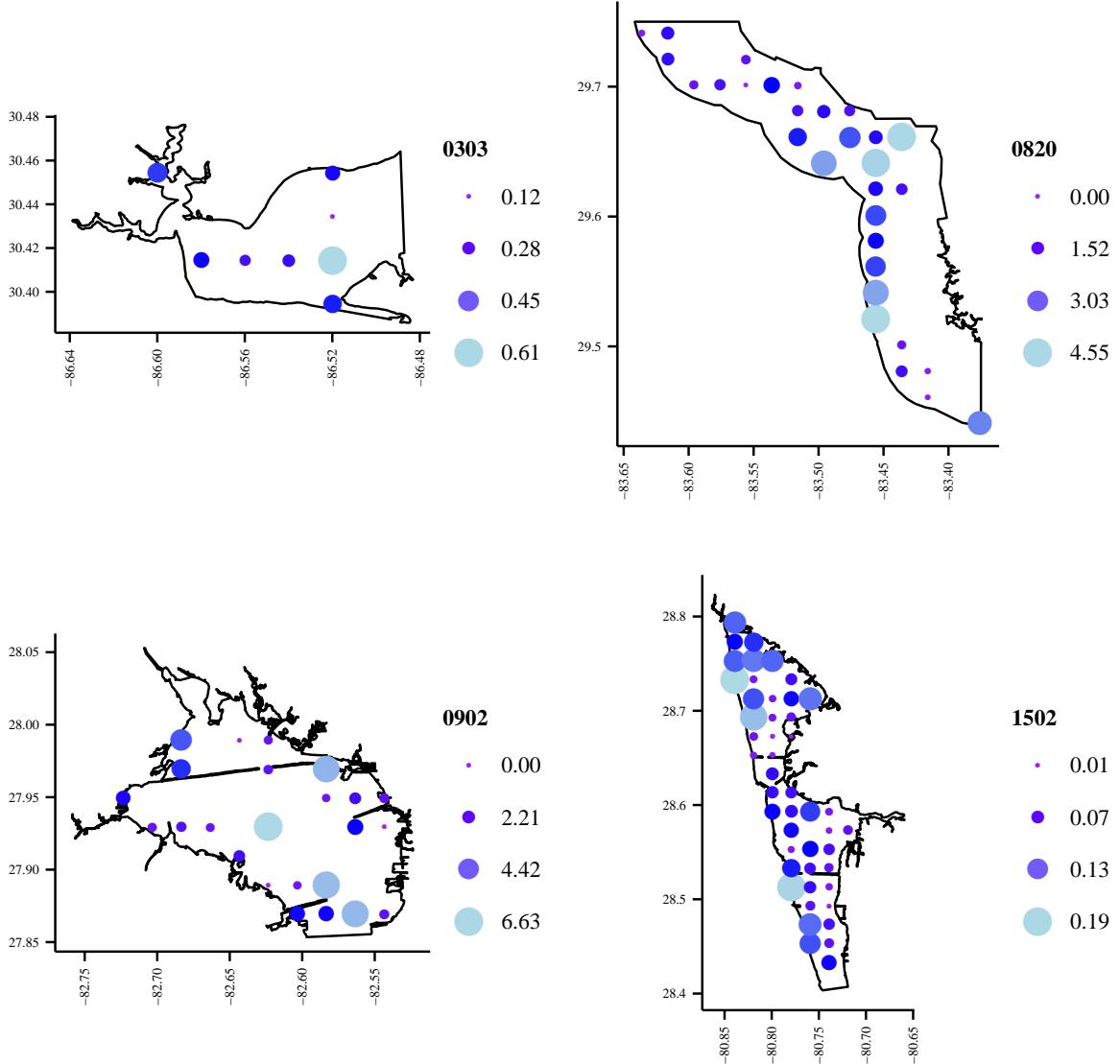


Fig. 6: Size of confidence intervals (m) for depth of colonization estimates in Fig. 5. Points are colored and sized based on the difference between the upper and lower bounds of a 95% confidence interval for all three DoC estimates (DOC_{min} , DOC_{med} , DOC_{max}). Bounds were obtained using Monte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

{fig:all_}

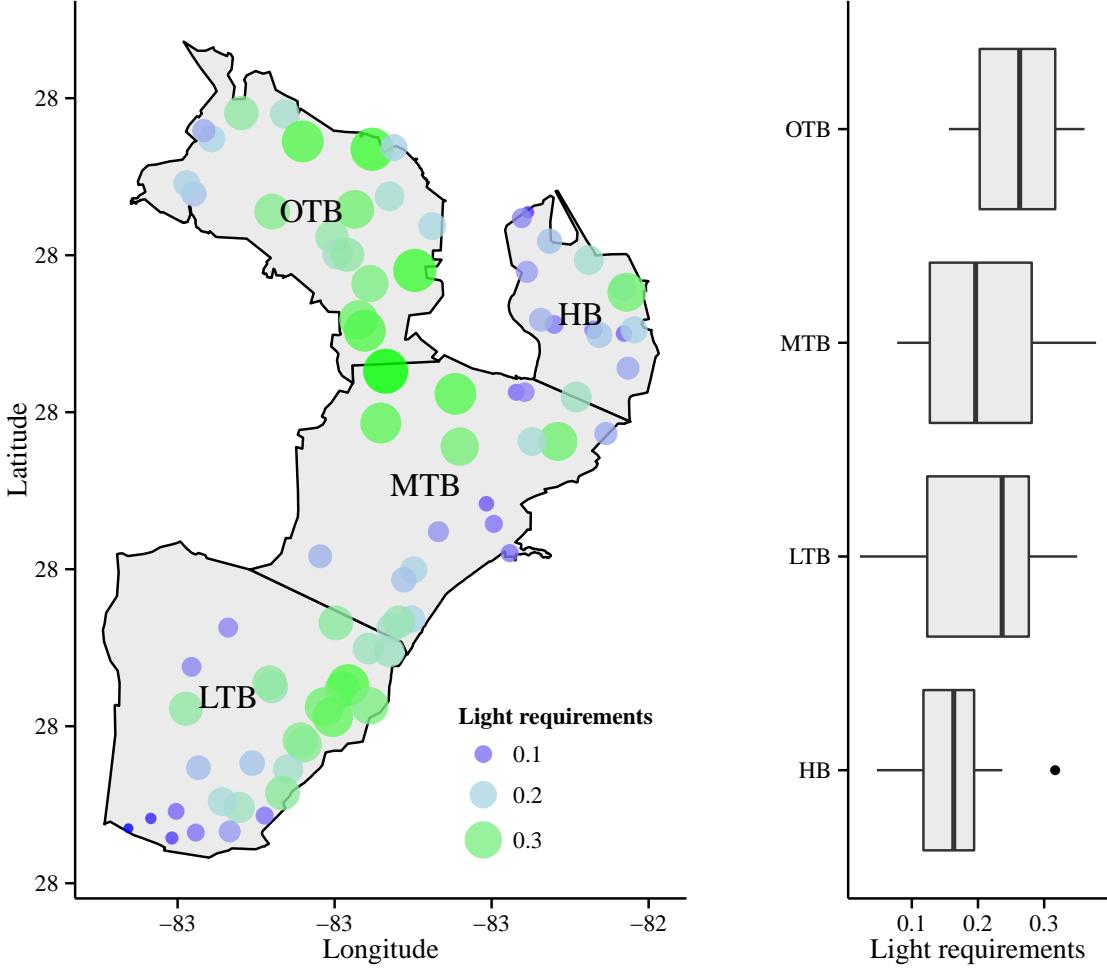


Fig. 7: Estimated light requirements of seagrass for multiple locations in Tampa Bay, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots where the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

{fig:light}

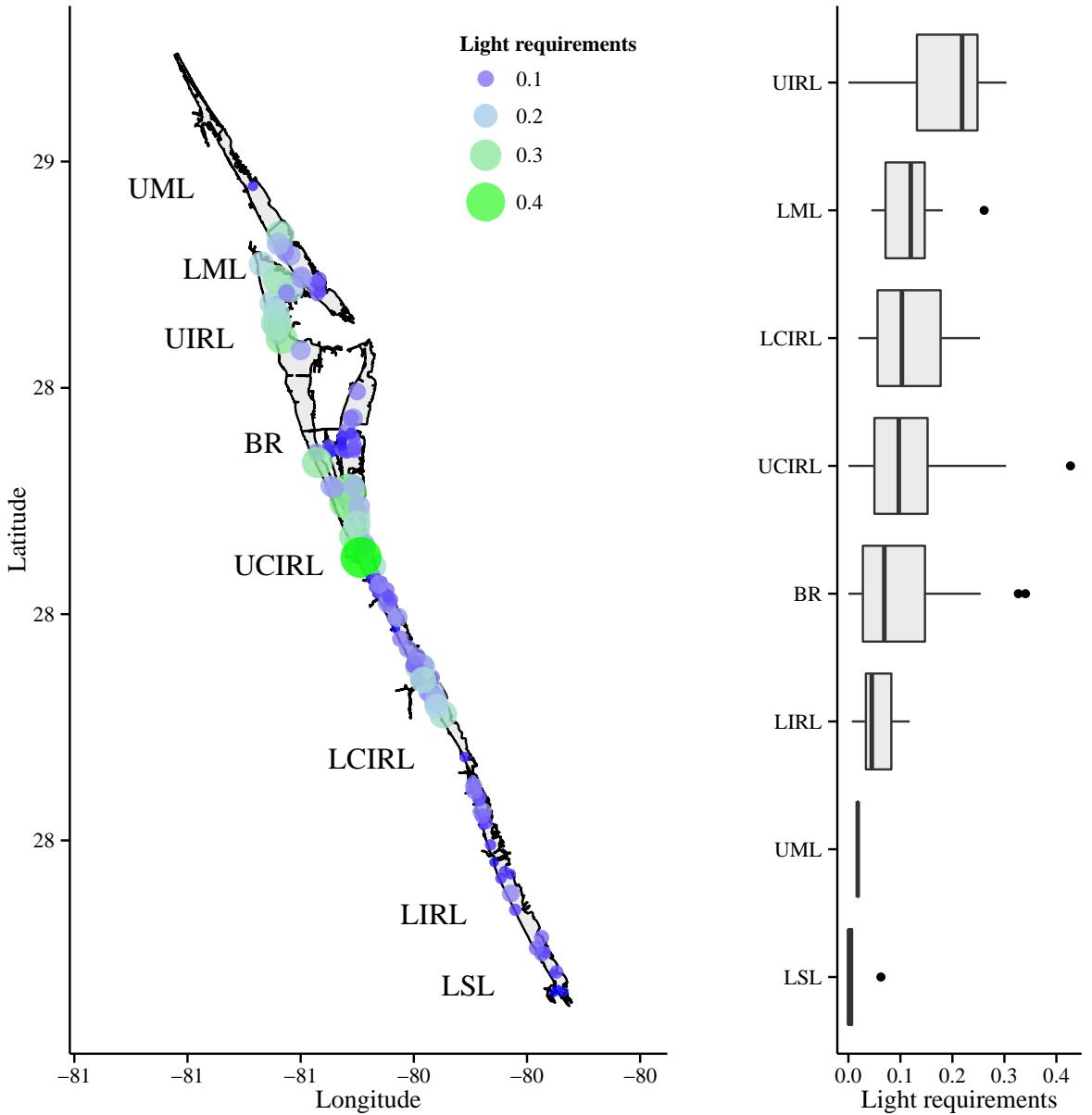


Fig. 8: Estimated light requirements of seagrass for multiple locations in Indian River Lagoon, Florida. Map locations are georeferenced observations of water clarity from secchi measurements in the Florida Impaired Waters Rule database, update 40. Data are also summarized by bay segment as boxplots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

{fig:light}