Estuaries and Coasts

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

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Abstract:	Depth of colonization (Zc) is a useful seagrass growth metric that describes seagrass response to light availability. Similarly, percent surface irradiance at Zc (% SI) is an indicator of seagrass light requirements with applications in seagrass ecology and management. Methods for estimating Zc and % SI are highly variable making meaningful comparisons 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 MODIS satellite imagery, PAR profiles, and Secchi depth measurements were combined with seagrass growth estimates to produce maps of % SI at Zc,med and Zc,max. Among estuary segments, mean Zc,med varied from (±s.e.) 0.80±0.13 m for Old Tampa Bay to 2.33±0.26 m for Western Choctawhatchee Bay. Standard errors for Zc,med were 1-10% of the segment means. Percent SI at Zc,med averaged 18% for Indian River Lagoon (range = 9-24%), 42% for Tampa Bay (37-48%) and 58% for Choctawhatchee Bay (51-75%). Estimates of % SI 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 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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Wayne S. Gardner
Charles A. "Si" Simenstad
Co-Editors-In-Chief
Estuaries and Coasts

Enclosed please find our revised manuscript, "Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization," to be reconsidered for publication as an original research article in Estuaries and Coasts. This revision is our response to the second round of reviews.

We again thank the reviewers for their comments on our revised submission, particularly the detailed comments from the second reviewer. To summarize, we have clarified our methods for correcting remote sensing products, removed estimates from shallow water, and justified the use of open-water estimates with citations. Figure S1 has also been added to demonstrate our correction methods of satellite-derived K_d with *in situ* data.

We are confident that these revisions have improved the manuscript. Please feel free to contact me with any questions or concerns about our submission. We appreciate the opportunity to publish our work with Estuaries and Coasts.

On behalf of my co-authors,

Marcus W. Beck, PhD

Author responses reviewer comments, ESCO-S-16-00245R1, "Quantifying seagrass light requirements using an algorithm to spatially resolve depth of colonization". Line numbers in our responses refer to the revised manuscript. All author responses are in italics. Note that the second reviewer used CAPS *for new comments and () for old comments.*

Reviewer #1: Authors have positively responded to my previous comments and I find the manuscript ready for publication, I have just three comments.
1) All figures are a bit fuzzy, might just be the conversion to PDF, but hard to see axis.

The figures are automatically downgraded during PDF conversion. High quality originals are provided with the submission.

2) Can authors add location labels to maps in Fig 4 just to help reader remember which area is which.

Yes, these are added.

3) Changes in %SI over time could be due to water temperature, as increasing respiration would drive seagrasses to require a higher light environment.

Yes, we have previously mentioned the potential effect of water temperature on seagrass light requirements (line 121). We have added an additional sentence to clarify the precise relationship (line 122): 'For example, long-term or seasonal increases in water temperature could increase estimates of light requirements due to increased metabolic rates (Masini and Manning 1997).'

Reviewer #2: NEW COMMENTS ON CAPITAL LETTERS FOLLOWING PREVIOUS REVIEW AND RESPONSE BY AUTHORS IN PARENTHESES

(Also concerning is the lack of information about satellite imagery processing and results including number of pixels used, masks, errors, mean vs median values for outliers, etc. This combined with my previous point, gives the impression of a lack of familiarity or knowledge with remote sensing processing. A great addition to this work could be to include modeled Kd values from radiative transfer simulations, expanding future predictions of light availability (from in situ or remote sensing measurements) and seagrass distribution.

We agree that there is not extensive methodological detail regarding remote sensing. In our paper we were seeking to demonstrate an application of existing remote sensing methods. In this regard, our processing was standard, in keeping with previous work. Co-author C. Le is very familiar with remote sensing processing and has previously published papers specifically addressing many of the detailed topics. To keep the focus of the paper on seagrass, we have referred to published material describing our remote sensing methods as much as possible to avoid excessive information in our paper.)

AGREED THIS IS NOT A REMOTE SENSING PAPER PER SE, BUT IT IS THE FOCUS OF A SUBSTANTIAL PART OF THE RESEARCH, AND INCLUDES VALIDATIONS MADE BY THE AUTHORS AND NOT BY PREVIOUS STUDIES. AT THIS POINT I STILL WOULD LIKE TO SEE SOME MORE INFORMATION REGARDING THE IN SITU /

MODIS VALIDATION (AS THE AUTHORS STATED FOR THE PREVIOUS COMMENT, THIS WAS A "CRITICAL ISSUE"). E.G. ARE TEN IN SITU POINTS CORRELATED TO A SINGLE (1 KM?) PIXEL? OR A 3X3 AREA? WHAT ABOUT AREAS TOO CLOSE TO SHORE? DID YOU APPLIED A LAND MASK? IF SO, CAN THIS MASK FLAG CLOSE-TO-SHORE WATER PIXELS WHERE SEAGRASS (AND/OR IN SITU VALIDATION POINTS) ARE LOCATED? BOTTOM ALBEDO? REMOTE SENSING IS ACTUALLY ONE OF THE MANUSCRIPT'S 'KEY WORDS'.

The locations of in situ data for Choctawhatchee Bay were located along the primary axis from the eastern portion to the outflow with the Gulf of Mexico. Pixels in shallow waters were not used to correct the data, as seen in Figure S1 (new addition). Note that the pixel that appears relatively close to the shoreline is actually located at the pass that exchanges with the Gulf of Mexico. Using bathymetry maps, we calculated that the average depth of sampling locations was 7.2 m and the shallowest location was 3.5 m. Comparing these with our in situ estimates of Kd, optical depths at these locations were 1.9 to 3.7, indicating that these station are optically "deep."

We added content that describes the validation process in more detail, including Figure S1 and description of the regressions used to correct the estimates.

Lines 205 – 215: '…Monthly field measurements of K_d obtained in 2010 at ten optically deep locations in Choctawhatchee Bay were used to correct annual means of the un-validated satellite values ($K_{d,\ MODIS}$) to match annual means of in situ measurements (Figure S1a). The satellite estimates of K_d were corrected by comparing regression curves of in situ data and satellite estimates from corresponding pixels versus cumulative frequency of each type of measurement (Cumulative Freq = -0.34 + 1.75 · K_d, r^2 = 0.93 for in situ model; Cumulative Freq = -0.35 + 1.15 · $K_{d,\ MODIS}$, r^2 = 0.95 for satellite model). For any uncorrected satellite estimate (Figure S1b), the corresponding frequency estimate on the regression curve from the satellite data was identified, matched with the corresponding frequency for the in situ data, and then related to the associated in situ K_d value to yield the corrected satellite estimate…'

(We are not clear what the reviewer is suggesting about "predicting light availability." Predicting light availability is not our objective. Rather we want to know, how changes in water clarity might relate to the distribution of seagrasses.)

THIS WAS JUST A SUGGESTION. YET, FUTURE APPLICABILITY OF THIS WORK CAN BE UNDERMINED IF THERE ARE NO FULL SETS OF NEW DATA. MODELED LIGHT AVAILABILITY MAY BE USEFUL TO ESTIMATE Zc.

We understand the value of improving our quantitative description of optics in these waters, and agree that in the future, if there is even less data, it could be useful to have that to support use of remote sensing (i.e., if we didn't have any in situ observations at all). In other work (e.g., Le et al. 2015 L&O 60: 920), we describe some research we've done on optical properties in these estuaries. Fortunately, for this paper, we do have these measurements of K_d.

(Ln 181-184: Satellite images from the Tampa and Choctawhatchee Bays may and will also be affected by bottom reflectance. How did you deal with this for these two areas, since it is stated that only for Indian River Lagoon was an issue?

To estimate attenuation without excessive effect from bottom reflectance, it's necessary to have deeper areas within the study area. Indian River Lagoon does not have a deeper central basin where bottom reflectance is not a major issue. It is also very narrow, so that image resolution is a problem. Most pixels are contaminated by shorelines. Please see our response to the first reviewer regarding use of attenuation estimates in deeper water adjacent to seagrass beds.)

THEN I GO BACK TO A PREVIOUS COMMENT ABOUT SATELLITE IMAGERY PROCESSING. PIXELS CLOSE TO SHORELINES WILL BE CONTAMINATED WHETHER THE WHOLE BAY GETS DEEPER OR NOT. HOW DID YOU DEAL WITH THIS FOR YOUR CHOCTAWHATCHEE BAY PROCESSING? LAND MASK? BATHYMETRY CONTOURS?

We thank the reviewer for challenging us on this again. Looking at the issue again, we realized that there was a need to address this further, which we have done. Specifically, we recognized that while we validated our Kd estimates in optically deep water, there is the potential that we are using pixels in optically shallow water and that this could affect those estimates of Kd and therefore estimated % PAR on the bottom at these locations. The effect of bottom reflection in shallow water is evident in nearshore pixels in Figure S1 (new).

We can confirm that land pixels were screened out with a land mask, but we have added an additional step to ensure that we do not use affected pixels in our estimates of %PAR at the depth of colonization. All estimates of Kd that were used were for locations where we also estimated the seagrass depth of colonization in the vicinity of that location. We compared the water depth at each location with the estimated depth of colonization and screened out all the observations where the water depth was less. The effect is that we ended up comparing remotely sensed Kd for pixels located offshore and in slightly deeper water than the seagrass with which they were compared. Conversely, pixels located within a seagrass bed, at shallower depth than the deep-edge, or inshore of seagrass in shallower water were not used. Given that most estimates of the light requirements for seagrasses are in the range of 20-40%, the effect is that we screened out Kd estimates for waters with an optical depth less than approximately 1 to 1.6, without actually using the (potentially wrong) remotely sensed Kd values to determine the optical depth.

We recalculated all of our affected results using this additional screen, and found that only minor changes occurred and that these did not affect our conclusions. Ten percent of the locations in Choctawhatchee Bay and 13% in Tampa Bay were screened out. We changed all the affected values. These are reflected in Table 3 where there are now separate columns for the sample size (n) for the depth of colonization locations and associated estimates of light requirements, where the latter had locations removed if Zc > depth. The following was added in the text to make this clear:

Line 345: 'Surface irradiance at the seagrass edge was not estimated from remote sensing data if the associated depth of colonization estimate exceeded the actual bottom depth. These locations were removed to reduce potential bias from bottom reflectance in shallow waters (10% of locations in Choctawhatchee Bay, 13% in Tampa Bay).'

ALSO, YOU STATED THAT IT IS A "COMMON ASSUMPTION" THAT DEEPER AND ADJACENT SEAGRASS AREAS WILL HAVE SIMILAR LIGHT ATTENUATION (FROM YOUR RESPONSE TO FIRST REVIEWER AND THE DOCUMENT). IF SO, CAN YOU ADD SOME REFERENCES SUPPORTING THIS?

We added references from several locations in Florida, North Carolina and Chesapeake Bay where this assumption is evident in the work. We noticed that it was fairly easy to find papers where it is apparent that this assumption was made (i.e., all the monitoring locations are in open water, and they are looking at seagrass on the fringe of the estuary) but that authors didn't necessarily go out of their way to make it clear that they had made this assumption not did they necessarily present data to support the assumption. As examples, monitoring programs in Charlotte Harbor used largely open water monitoring in relation to seagrass (e.g., Corbett 2004, Corbett and Hale, 2006). A similar approach was used to evaluate light requirements of seagrass in Chesapeake Bay using water clarity data from monitoring sites that are overwhelmingly located in open water (http://www.chesapeakebay.net/documents/3676/map_of_mainstem_and_tributary_monitoring_stations.pdf). Biber et al. 2005 (Ch 13 in Estuarine Indicators, Fig. 13.2) evaluated water quality with respect to Seagrass in Pamlico Sound, North Carolina utilizing data from 9 stations in open water. These references were added to the manuscript (see below, Kemp et al. 2004 was previously cited). We have ourselves collected data (not for these estuaries) in some cases showing little difference, while also seeing anecdotally situations where there was quite obviously a difference, generally due to wind-driven sediment resuspension. However, we felt that a detailed examination of the assumption would not improve the manuscript, in part because like a lot of other people we don't have the data, because it's hard to measure.

(Table 3: Superscripts for mean Z_c and %light are confusing. A proper table showing statistical results (used analysis, significance levels, p-values, errors etc when appropriate) can be better.

We have modified the table and caption to simplify the information but we have not added additional tables because this method of presenting comparisons is not uncommon.)

STILL NOT CLEAR WHAT THE SUPERSCRIPTS FOR "Zc, med" MEAN. a STANDS FOR SEGMENT, THEN WHAT ARE a, ab, b AND SO ON?

To make the table easier to understand, we eliminated superscripts related to footnotes, as these were unnecessary. We retained superscripts as commonly used to illustrate the results of multiple comparison tests. To aid in interpretation, we added additional clarifying text in the caption:

"Superscripts for mean Zc,med denote significant differences in segment means. Segments with the same superscript are not significantly different. Multiple comparison tests are only within estuaries, not between estuaries."
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ADDITIONAL NEW COMMENTS:

Ln 47-48: Abstract: No need to mention "R", since you are not providing a new package, but just using existing ones. Same way you do not really mention SeaDAS for example.

This was removed from the abstract.

Ln 224-227: References

Added to line 239: 'Many studies have used open-water estimates to infer water clarity in adjacent seagrass beds (e.g., Kemp et al. 2004; Biber et al. 2005; Corbett and Hale 2006).'

Ln 248-249 and Fig 1: outflow of the Steinhatchee River not labeled.

This is now labelled.

Ln 454: Which Bay? Maybe better to state the whole Tampa Bay, or, the studied areas of Tampa Bay.

Changed.

Fig. S1: What do numbers represent?

The numbers are the sampling station designation. The caption was modified to clarify.

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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 (Z_c) is a useful seagrass growth metric that describes seagrass response to light availability. Similarly, percent surface irradiance at Z_c (% SI) is an indicator of seagrass light requirements with applications in seagrass ecology and management. Methods for estimating Z_c and % SI are highly variable making meaningful comparisons difficult. A new algorithm is presented to compute maps of median and maximum Z_c, $Z_{c, med}$ and $Z_{c,max}$, respectively, for four Florida coastal areas (Big Bend, Tampa Bay, Choctawhatchee Bay, Indian River Lagoon). Maps of light attenuation (K_d) based on MODIS satellite imagery, PAR profiles, and Secchi depth measurements were combined with seagrass growth estimates to produce maps of % SI at $Z_{c,med}$ and $Z_{c,max}$. Among estuary segments, mean $Z_{c,med}$ varied from (±s.e.) 0.80±0.13 m for Old Tampa Bay to 2.33±0.26 m for Western Choctawhatchee Bay. Standard errors for $Z_{c,med}$ were 1-10% of the segment means. Percent SI at $Z_{c,med}$ averaged 18% for Indian River Lagoon (range = 9-24%), 42% for Tampa Bay (37-48%) and 58% for Choctawhatchee Bay (51-75%). Estimates of % SI 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 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.

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

Introduction

Seagrasses are ecologically valuable components of aquatic ecosystems and 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 light attenuation. Seagrass coverage declines with water depth due to light attenuation, and declines more rapidly in productive aquatic ecosystems 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, light attenuation, 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" over time their exposure to stress. Thus, time scales of seagrass response better match time scales for monitoring and assessment of responses to 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 different spatial scales and would be valuable for a variety of scientific and policy applications. For large scale evaluation, 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 quality, such that any segmentation scheme is likely to include within-segment gradients in water quality and associated

82   seagrass depth of colonization. Local conditions may require adaptive assessment approaches that

83   can address interactive effects of environmental variables at different spatial scales.

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. The method should also have the potential to be applied widely

95   using available data sets to support seagrass conservation. Developing and demonstrating this

96   capability was one objective of this study.

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

98   colonization with light attenuation measures at the same spatial scales to characterize the pattern

99   and range of seagrass light requirements in estuaries. In this paper, we operationally define "light

100   requirements" as the average percentage of incident light present at the depth of colonization,

101   which is similar to PLW_{min} defined by Kemp et al. (2004) and also the definition suggested by

102   Dennison et al. (1993). This approach is practical and relates well to the data most often available

103   for policy and conservation applications, but comes with assumptions and caveats which we

104   appropriately address. Regardless of such complexity, the spatial distribution of submerged

105   aquatic plants is often associated with changes in water depth and light availability (Barko et al.

106   1982; Hall et al. 1999; Dennison et al. 1993), wherein depth of colonization is controlled by light

107   requirements and average light attenuation. Published estimates of seagrass light requirements are

108   species-specific and quite variable. Duarte (1991) reported that seagrasses can extend to depths

109   receiving an average of 11% of surface irradiance, while estimates of light requirements for

110   seagrass in Chesapeake Bay were about 20% (Batiuk et al. 1992). Dennison et al. (1993) reported

111   minimum light requirements, which they defined similarly as the percent light at the maximum

112   depth limit, ranging from less than 5% to greater than 30% depending on site conditions. Estimates

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113   of ~20% are common in the literature, approximating a value in the middle of published estimates

114   (see also Kemp et al. 2004). An estimate of ~20% for seagrass in Florida estuaries has been

115   applied for management purposes in Tampa Bay, Choctawhatchee Bay, and elsewhere in Florida

116   (e.g., FDEP 2012; US EPA 2012) and can be traced to the estimate of 22.5% for lower Tampa Bay

117   from Dixon and Leverone (1995).

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

119   physiological differences among seagrass species, differences in attenuation on the leaf surface by

120   attached algae and detritus (i.e., K_e in Kemp et al. 2004), and variations in other physiological

121   stressors such as salinity or water temperature (Kenworthy and Haunert 1991; Kemp et al. 2004;

122   Choice et al. 2014). For example, long-term or seasonal increases in water temperature could

123   increase estimates of light requirements due to increased metabolic rates (Masini and Manning

124   1997). Differences in operational definitions and method of estimation are also likely to contribute

125   to differences in reported values. For example, Dennison et al. (1993) defined minimal light

126   requirements as the percent light at the maximal depth limit for seagrass – where depth limit was

127   defined variously by different included studies. Choice et al. (2014) applied a statistical method to

128   data from individual stations seeking to find the percentage of surface irradiance linked to seagrass

129   percent cover or shoot density of zero. In this study, we sought to generate more comparable

130   estimates of depth of colonization and light requirements by broadly applying the same method to

131   characterize seagrass depth of colonization and relating it to estimates of light attenuation at similar

132   scales. To quantify light attenuation at temporal and spatial scales relevant to understanding

133   seagrass distributions in coastal ecosystems, we used estimates derived from satellite remote

134   sensing along with more conventional observations of water clarity, including profiles using

135   underwater radiometers and Secchi depth. Although *in situ* measures provide locally precise

136   estimates, ocean color data from satellite remote sensing can provide consistent estimates of light

137   attenuation across a large spatial extent, often with a high return frequency (e.g., ~8 days) and long-

138   term data collection, which is useful for characterizing average attenuation (Woodruff et al. 1999;

139   Chen et al. 2007).

140   The overall goal of this study is to present an algorithm for estimating seagrass depth of

141   colonization and light requirements using geospatial datasets describing seagrass coverage and

142   satellite remote sensing data of light attenuation in the water column. The approach allowed us to

143   generate consistent estimates of seagrass depth of colonization and light requirements, enabling

144 meaningful comparisons of each across space and time. This supports the management need to

145 evaluate status and trends, and to predict how water quality changes could affect seagrass extent

146 and distribution given existing relationships with light attenuation. Specific objectives were to 1)

147 describe the method for estimating seagrass depth of colonization, 2) apply the technique to target

148 locations in four Florida estuaries to illustrate quantification of seagrass growth patterns, and 3)

149 develop a spatial description of relationships among depth limits and light attenuation,

150 characterizing patterns in light requirements in each case study and between regions. The

151 analytical approach was also automated for use in the R statistical programming language (RDCT

152 2016), which allowed us to evaluate changes in seagrass light requirements in Tampa Bay over a

153 period of twenty-five years.

154

155 **Methods**

156 *Study sites and data sources*

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

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

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

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

161 numeric nutrient criteria (US EPA 2012). The method for estimating depth of colonization was

162 evaluated initially using one segment in each of the four areas, chosen based on geographic

163 coverage in Florida coastal areas and availability of seagrass data. These segments included Big

164 Bend (BB), Western Choctawhatchee Bay (WCB), Old Tampa Bay (OTB), and Upper Indian River

165 Lagoon (UIRL). The analysis was then expanded to quantify spatially-resolved seagrass depth

166 limits and associated light requirements for all the segments in three of the estuaries, omitting the

167 Big Bend from further analysis due to an insufficient number of light attenuation measurements.

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

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

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

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

172 obtained for a recent year in each of the study sites (Table 1), except for Tampa Bay, for which

173 coverages were obtained for every available year from 1988 to 2014. The original coverage maps

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

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

176 absent.

177   Bathymetry data were obtained from the National Oceanic and Atmospheric

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

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

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

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

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

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

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

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

186 2012). To reduce computation time, bathymetry layers were first masked to remove observations

187 more than 1 km from any seagrass polygon. Raster bathymetric layers were converted to point

188 layers to combine with seagrass coverage maps, as described below.

189

190 *Quantifying light attenuation*

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

192 attenuation for Tampa Bay and Choctawhatchee Bay. Secchi depth measurements were used to

193 quantify attenuation for the Indian River Lagoon because light scattering from bottom reflectance

194 and insufficient grid resolution prevented use of satellite remote sensing measurements in this very

195 narrow, back-bay estuary.

196   For Tampa Bay, daily MODIS (Aqua level-2) satellite data were downloaded from the

197 NASA website (http://oceancolor.gsfc.nasa.gov/) for the five years preceding the year the seagrass

198 imagery was acquired. Images were reprocessed using the SeaWiFS Data Analysis System

199 software (SeaDAS, Version 7.0). For Tampa Bay, light attenuation was derived from daily MODIS

200 images using a previously-developed algorithm that estimates Secchi depth using a regression

201 relating field observations and satellite-derived estimates of the diffuse attenuation coefficient at

202 490 nm (K_d (490), Chen et al. 2007). Monthly and annual mean Secchi depth was estimated from

203 the daily images and then averaged to create a single layer.

204   Similarly, K_d for Choctawhatchee Bay was derived from MODIS using the QAA algorithm

205 (Lee et al. 2005), which was also used by Chen et al. 2007 to estimate K_d (490). Monthly field

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206 measurements of K_d obtained in 2010 at ten optically deep locations in Choctawhatchee Bay were

207 used to correct annual means of the un-validated satellite values ($K_{d, MODIS}$) to match annual means

208 of *in situ* measurements (Figure S1a). The satellite estimates of K_d were corrected by comparing

209 regression curves of *in situ* data and satellite estimates from corresponding pixels versus

210 cumulative frequency of each type of measurement (*Cumulative Freq* = -0.34 + 1.75 · K_d, r^2 = 0.93

211 for *in situ* model; *Cumulative Freq* = -0.35 + 1.15 · $K_{d, MODIS}$, r^2 = 0.95 for satellite model). For any

212 uncorrected satellite estimate (Figure S1b), the corresponding cumulative estimate on the

213 regression curve from the satellite data was identified, matched with the corresponding percentile

214 for the *in situ* data, and then related to the associated in situ K_d value to yield the corrected satellite

215 estimate. Annual means were used to create the regressions and corrections for the remaining

216 years of satellite data from Choctawhatchee Bay. These were preferred rather than daily match-

217 ups, because many of the *in situ* observations would not generate match-ups due to cloud cover,

218 and because the annual mean was the time scale of interest. Field K_d estimates were estimated as

219 the slope relating log irradiance and log depth (i.e., $\log I_Z = \log I_O - K_d Z$) measured using a 4 pi

220 Biospherical PAR sensor on a SBE25 CTD. The empirical relationship for the 2010 data was

221 applied to all five years of annual mean satellite-derived K_d data prior to averaging to create a

222 single layer for further analysis.

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

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

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

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

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

228 flagged because the Secchi disk was visible on the bottom. As an additional data quality screen,

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

230 the water depth.

231 A land mask was applied to MODIS data for Tampa Bay and Choctawhatchee Bay and

232 pixels were further masked where water depth was less than the local estimate of seagrass depth of

233 colonization thereby eliminating data from optically shallow water. For all three estuaries, light

234 attenuation in deeper water adjacent to seagrass beds was assumed to be similar to attenuation at

235 the deep-edge of seagrass. In general, Secchi depth cannot be used to estimate water clarity

236 directly in a seagrass bed because the disk is visible on the bottom. Bottom reflectance similarly

237   limits application of remote sensing, with some exceptions (Barnes et al. 2013). Although PAR

238   profiles can in principle be made in shallow water, these often give less precise estimates of K_d

239   than deeper profiles. Many studies have similarly used open-water estimates to infer water clarity

240   in adjacent seagrass beds (e.g., Kemp et al. 2004; Biber et al. 2005; Corbett and Hale 2006).

241

242   *Estimating seagrass depth of colonization*

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

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

245   seagrass presence or absence. To relate depth and seagrass presence/absence, the proportion of

246   points with seagrass present was computed as a function of depth within discrete depth bins and

247   parameters describing the distribution were computed from the resulting function. The analysis

248   was repeated for observations within a particular search radius of grid nodes spanning the study

249   areas, generating a map of depth of colonization (Fig 1). The analysis was also repeated with a

250   large radius encompassing entire segments, resulting in whole-segment estimates. Further details

251   are provided below regarding search radius, depth bins, and computing depth of colonization

252   metrics.

253   Depth of colonization at particular locations was computed using observations found within

254   a search radius, which was 0.04 degrees for Choctawhatchee Bay, 0.1 degrees for Tampa Bay and

255   0.15 degrees for Indian River Lagoon. Analyses that focused on an individual segment at each

256   study location used a common search radius of 0.02 degrees for visual and scale comparisons in the

257   resulting figures. Geospatial data were imported and processed using functions in the rgeos and sp

258   packages in R (Bivand et al. 2008; Bivand and Rundel 2014). Although no particular radius is

259   "wrong," selection involves several trade-offs. A large search radius improves the precision of

260   estimates by finding more data, but may encompass areas that are ecologically dissimilar. As an

261   example, the radius to characterize depth of colonization at the outflow of the Steinhatchee River in

262   Fig. 1 was large enough to describe variation in growth affected by local water quality, but small

263   enough to not include observations well outside the influence of the river outflow. Moreover, a

264   radius much larger than the grid spacing inflates the computational requirements with little benefit.

265   A smaller search radius and closer grid spacing provides more spatial resolution, but also finds less

266   data, increasing uncertainty. A small radius may also encompass little or no depth gradient, in

267   which case the relationship between seagrass and depth cannot be quantified. An appropriate

268   search radius will in many cases result in a plot illustrating a decreasing proportion of points with

269   seagrass with increasing depth (Fig. 3). The appropriate scale may be related to the size of the

270   estuary. A larger radius was selected for Tampa Bay, which is the largest of the water bodies in

271   our study.

272   Depth bins, within which seagrass presence/absence proportions were computed, had

273   variable widths <0.5 m defined to include 1 to 50 bathymetric soundings (i.e., if a 0.5 m bin

274   includes more than 50 observations, the bin width is reduced). For whole segment estimates, these

275   parameters were changed to 0.1 m and 1 to 1000 points. This method created many narrow bins if

276   a large number of soundings was present and fewer, wider bins when fewer observations were

277   available. The result is that, other factors being equal, having more data resulted in lower estimates

278   of parameter uncertainty.

279   Three depth of colonization metrics were derived from the function relating seagrass

280   presence vs. depth (Fig 3). These included minimum ($Z_{c,min}$), median ($Z_{c,med}$), and maximum

281   ($Z_{c,max}$) depth of colonization. These terms each describe meaningful points on the depth

282   distribution of the seagrass coverage map. $Z_{c,\,max}$ is the deepest depth at which mappable seagrasses

283   occurred, excluding isolated patches (or outliers) at deeper depths. $Z_{c,med}$ is the median depth of the

284   deep water edge of seagrass. Finally, $Z_{c,min}$ approximates the depth at which seagrass percent cover

285   begins to decline with increasing depth, which may occur at $Z=0$ m.

286   At each sampled location, a logistic function was fitted to the extracted depth points using

287   non-linear regression, quantifying the decrease in seagrass cover with respect to depth (Equation 1;

288   Fig. 3):

289
$$P = \frac{\alpha}{1 + \exp((\beta - Z)/\gamma)} \qquad (1)$$

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

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

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

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

294   α=max(P), β=median(Z) and γ=75th percentile(Z) - median(Z). The maximum rate of decrease in

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

296   through the line $P=\alpha$ at $Z=\beta-2\gamma$ and through $P=0$ at $Z=\beta+2\gamma$. The three seagrass depth of

297   colonization metrics were defined in terms of these reference values as follows:

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

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

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

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

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

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

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

305   data. It was possible for $\beta\text{-}2\gamma$ to be less than zero, and this was common when seagrass cover

306   declined immediately as depth increased from zero. In these cases, $Z_{c,min}= 0$ and $Z_{c,med}$ is half the

307   depth from zero to $Z_{c,max}$ (Fig. 3b).

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

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

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

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

312   differences of normal random variables (Ku 1966):

313

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

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

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

317

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

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

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

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

322   zero.

323   Given estimates of depth of colonization for grid nodes, calculated as above, segment

324   means and standard errors were computed using an intercept-only spatial mixed model,

325   implemented using the nlme package in R (Pinheiro et al. 2016), thereby accounting for spatial

11

326   autocorrelation among the gridded estimates. An isotropic Gaussian correlation structure with a

327   nugget effect was selected from among other options based on the Akaike Information Criterion.

328   This approach made it possible to separate variability within the segment from uncertainty

329   regarding either individual node estimates or segment means. Whole segment estimates, calculated

330   using a single node with a large search radius also provided an estimate of uncertainty, but not an

331   estimate of variability within the segment.

332

333   *Seagrass Light Requirements*

334   Seagrass light requirements were estimated as the average fraction of surface irradiance

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

336   same calculations using $Z_{c,max}$ are included as supplemental information. Light attenuation was

337   quantified on the same grid as depth of colonization, which was selected to maximize the number

338   of matches between depth of colonization and light attenuation measurements. Grid cells centered

339   more than 1 km from seagrass were not included, preventing spurious comparison of seagrass

340   depth of colonization with light attenuation far from shorelines. The percentage of surface

341   irradiance (% SI) at the median depth of colonization was computed using

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

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

344   (Choctawhatchee Bay, Tampa Bay) or from field-based Secchi depth measurements (Indian River

345   Lagoon). Surface irradiance at the seagrass edge was not estimated from remote sensing data if the

346   associated depth of colonization estimate exceeded the actual bottom depth. These locations were

347   removed to reduce potential bias from bottom reflectance in shallow waters (10% of locations in

348   Choctawhatchee Bay, 13% in Tampa Bay). Where K_d was derived from Secchi depth (Z_{Secchi}), it

349   was computed using $K_d \cdot Z_{Secchi} = 1.7$. The product $K_d \cdot Z_{Secchi}$ varies in relation to the ratio of

350   scattering to absorption, with higher values for the product associated with greater scattering.   A

351   range of 1.1 to 2.0 (Liu et al. 2005) encompasses the values commonly applied in estuaries. An

352   analysis of 504 PAR profiles and corresponding Secchi depth measurements from Pensacola Bay,

353   FL (Murrell et al. 2009) had a mean (±s.e.) $K_d \cdot Z_{Secchi}$ of 1.63±0.03, which likely reflects a

354   relatively low ratio of scattering to absorption in the Florida estuaries (Davies-Colley and Vant

355   1988). The % SI at the maximum depth of colonization ($Z_{c,max}$) was also estimated and is reported

356   as supplemental information.

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

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

359   colonization. Tests for differences in mean light requirements between estuary segments were also

360   implemented using a spatial mixed model using the nlme package in R, in this case with a single

361   categorical fixed effect (estuary segment) and a Gaussian spatial correlation structure with a nugget

362   effect.

363

364   *Trends in seagrass light requirements in Tampa Bay*

365   To demonstrate a useful application of our analysis, we estimated changes in depth of

366   colonization and light requirements in Tampa Bay, where seagrass recovery has been a focus of

367   management efforts for decades (Greening et al. 2014) and nominally biennial seagrass surveys

368   were available for 1988 to 2014 (1988, 1990, 1992, 1994, 1996, 1999, 2001, 2004, 2006, 2008,

369   2010, 2012 and 2014). Light attenuation was estimated from monthly Secchi depth (TBEP 2011,

370   Fig. S2), rather than satellite estimates, which were not available for the full extent of the seagrass

371   time series. Secchi depth at each station was averaged by year then translated to light attenuation

372   using $K_d \cdot Z_{Secchi} = 1.7$, as above. Seagrass light requirements were estimated at each monitoring

373   station for each year with seagrass coverage, then evaluated to describe trends.

374

375   **Results**

376   *Segment characteristics and seagrass depth of colonization estimates*

377   The surface area of the study regions ranged from 59 km^2 for Western Choctawhatchee Bay

378   (WCB) to 271 km^2 for the Big Bend (BB) (Table 1). Mean depth was less than 5 m in each

379   segment, except for WCB, which was slightly deeper (5.3 m). Maximum depth was greater in

380   WCB (11.9 m) and Old Tampa Bay (OTB, 10.4 m) compared to BB (3.6 m) and Upper Indian

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

382   segment area), less in UIRL (32.8 %) and OTB (11.9 % in 2010), and very sparse in WCB (5.9 %),

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

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

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

13

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

387 coverage declined toward the northern ends of both OTB and UIRL.

388   Whole segment estimates (± prediction interval) based on single locations with large radii

389 for $Z_{c,med}$ varied from 0.95±0.07 m in OTB to 2.29±0.19 m in BB, with 95% prediction intervals

390 equal to ±1% to 10% of the estimate (Table 2). Estimates of $Z_{c,max}$ varied from 1.1 m to 3.8 m and

391 were somewhat less precise, with 95% prediction intervals equal to 3 to 20% of the estimate (Table

392 2). Means of spatially-resolved estimates of $Z_{c,med}$ for a grid of points in each segment varied from

393 2% more to 15% less than the whole-segment estimates (Table 2), within the margin of uncertainty

394 for each, suggesting that the two approaches gave comparable results. The difference was largest

395 for BB, where the gridded estimates of depth of colonization had a bi-modal distribution (i.e.,

396 lower estimates near the Steinhatchee outflow vs. higher values distant from the river outflow, Fig.

397 4 upper left). The whole segment estimate of $Z_{c,max}$ for BB was 3.8 m, 65% more than the 2.3 m

398 average of the gridded estimates, reflecting a greater influence of the deeper-distributed seagrass on

399 the whole segment calculation (Table 2; Fig. 4). Estimates for $Z_{c,min}$ were as low as zero in BB and

400 OTB (Table 2), indicating that seagrass coverage decreased immediately with any increase in

401 depth. The highest values for $Z_{c,min}$ were associated with relatively deep seagrass distributions, as

402 in WCB. In these cases, coverage increased initially with increasing depth, rather than decreasing.

403 Seagrass percent cover often increased initially with increasing depth, likely reflecting stressors

404 such as wave energy or desiccation during extreme low tides affecting the shallow margin of the

405 seagrass bed.

406   Spatial heterogeneity of the gridded estimates for depth of colonization was particularly

407 apparent for segments BB and UIRL (Fig. 4). As previously mentioned, depth of colonization in

408 the Big Bend segment was reduced in the vicinity of the Steinhatchee River discharge. Seagrasses

409 were also limited to shallower depths at the north end of the Upper Indian River Lagoon segment,

410 but grew at maximum depths up to 2.2 m on the eastern portion of the Upper Indian River Lagoon

411 segment near the Merritt Island National Wildlife Refuge (Fig. 2). Seagrasses in Old Tampa Bay

412 grew to slightly greater depth in the eastern and southern portion of the segment and were limited

413 to shallower depths near freshwater inflow channels on the northern margin (Fig. 4). The deepest

414 growing seagrass in Choctawhatchee Bay was closest to Destin Pass, where regular tidal exchange

415 with Gulf of Mexico waters keeps light attenuation low (Fig. 4). Z_c could not be estimated where

416 seagrasses were sparse or absent as in the center of Old Tampa Bay and western Choctawhatchee

417 Bay, or where there was an insufficient gradient in water depth, as in several areas of the Big Bend

418 segment (Fig. 4). However, depth of colonization can be estimated for locations that lack seagrass

419 if sufficient coverage is present within the search radius. As a result, gridded maps illustrate the

420 spatial patterns of depth of colonization, and do not repeat the spatial patterns of seagrass coverage

421 (i.e., Fig. 4 does not always resemble coverage in Fig. 2).

422   Gridded estimates for all segments in each bay (excluding Big Bend) provided further

423 information on seagrass depth of colonization within and among segments and the average depth of

424 colonization in each estuary (Table 3; Figs. 7, 8, 9). Seagrass Z_c estimates were computed for 338

425 locations in Choctawhatchee Bay, 252 locations in Tampa Bay, and 47 locations in the Indian

426 River Lagoon. Mean $Z_{c,med}$ (±s.e.) was 1.43±0.38 for Choctawhatchee Bay, 0.91±0.31 for Tampa

427 Bay, and 1.12±0.26 m for Indian River Lagoon. Mean $Z_{c,med}$ was not significantly different

428 between any of the bays. Means for segments within estuaries varied, although statistical

429 differences were difficult to determine in some locations due to low sample size (i.e., Indian River

430 Lagoon segments, Table 3). In Tampa Bay, $Z_{c,med}$ was ~0.5 m less in Old Tampa Bay than in the

431 Lower or Middle Tampa Bay segments, but was only significantly different ($p < 0.05$) compared

432 with the latter. Similarly, $Z_{c,med}$ in the eastern segment of Choctawhatchee Bay was 1.1 m and 1.5

433 m less than $Z_{c,med}$ in the central and western bay, respectively, although only the eastern and

434 western estimates were significantly different ($p < 0.05$). No statistical differences were observed

435 between segments of the Indian River Lagoon despite higher $Z_{c,med}$ in more southern segments (Fig.

436 9).

437

438 *Seagrass light requirements*

439   Estimates of light attenuation, seagrass depth of colonization, and corresponding light

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

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

442 estimates for Choctawhatchee Bay and Tampa Bay resolved spatial variation in average light

443 attenuation (Figs. 5 and 6). For Choctawhatchee Bay, K_d increased from the western and central

444 segments toward the eastern segment, which is adjacent to the Choctawhatchee River discharge

445 (Fig. 5). Similarly, attenuation increased from lower and central Tampa Bay into Old Tampa Bay

446 and Hillsborough Bay. Attenuation was also less in the central area of the lower bay segments

447 (Fig. 6). Secchi depth was highest in the southern Indian River Lagoon and decreased to the north.

448 Relatively few Secchi depth measurements were available for the Upper Indian River Lagoon and

449 Banana River segments, likely because maximum water clarity exceeded the maximum depth in

450 shallow areas, resulting in right-censored measurements.

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

452 requirement) was (mean±s.e.) 58±3.2 % SI for Choctawhatchee Bay, 42±2.6 % SI for Tampa Bay,

453 and 18±3.0 % SI for Indian River Lagoon. Based on Tukey contrasts, average light requirements

454 for seagrass were significantly different between all estuaries, particularly for Indian River Lagoon.

455 Despite some apparent spatial patterns in seagrass light requirements (Fig. 7, 8, 9), significant

456 differences were not found between segments of a single estuary, except for a marginally

457 significant difference between eastern and western Choctawhatchee Bay ($p = 0.04$). In Tampa Bay,

458 the segment mean (±s.e.) % SI at $Z_{c,med}$ ranged from 36±5.5 % SI to 48±5.6 % SI (Table 3, Fig. 8).

459 For Choctawhatchee Bay, segment means were 50±5.7 % SI to 75±8.7 % SI, with the apparently

460 higher values in eastern Choctawhatchee Bay (Table 3, Fig. 7). For Indian River Lagoon, segment

461 means ranged from 9±7.1 % SI to 24±8.6 % SI (Table 3, Fig. 9). Either small sample sizes, as for

462 Indian River Lagoon, or a small number of effectively independent samples given the spatial

463 correlation of residuals, reduced the statistical significance of apparent spatial differences in light

464 requirements between segments.

465   The final analysis illustrated the temporal evolution from 1988 to 2014 of seagrass depth of

466 colonization and light attenuation (Fig. 10, upper panel), and resulting expression as light

467 requirements (Fig. 10, lower panel) in Tampa Bay. Depth of colonization decreased in

468 Hillsborough Bay and Middle Tampa Bay during the early 1990s before rebounding strongly

469 toward the end of the time series (Fig 10, upper panel). Median light attenuation varied from year

470 to year, but decreased overall. We applied spatial mixed models to evaluate pairwise comparisons

471 at 18 grid nodes covering the whole Bay (Fig. S2) using the terminal ends of the time series to

472 evaluate overall changes from 1988 to 2014. Depth of colonization increased by 3 to 30 cm

473 between 1988 to 2014 (mean=16 cm, p<0.01). Light attenuation decreased by 0.04 to 0.5 m^{-1}.

474 Changes in light requirements (reflecting the interaction of both trends) were positive at 17 of 18

475 nodes and varied from -3.5% to 14% of surface irradiance between years. The largest increases in

476 depth of colonization were near the boundary between lower and middle Tampa Bay and in Old

477 Tampa Bay. The largest increases in light requirements were in Hillsborough Bay, where light

478 requirements were lowest early in the time series (Fig 10, lower panel).

479   As a final note, the estimates of light requirements for 2010 shown in Fig. 10 (lower panel)

480   differ from those in Fig. 8. These relate to the small number of locations for which Secchi depth

481   data were consistently available from 1988 through 2014 (Fig. S2), compared to the virtually

482   complete spatial coverage obtained from the satellite remote sensing data. Although the time series

483   values are not as representative of all values in the segment (i.e., as in Fig 8), they are consistent in

484   each year, and thus are a valid representation of change over time at those locations.

485

486   **Discussion**

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

488   seagrass communities in estuaries because it relates to light attenuation and related anthropogenic

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

490   1993; Short and Wyllie-Echeverria 1996; Burkholder et al. 2007). Because seagrasses are

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

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

493   US EPA 2012; Greening *et al*. 2014). For applications to water quality management, deriving

494   estimates and associated estimates of uncertainty at appropriate scales using a consistent

495   methodology is particularly important (US EPA 2012). The methods developed and demonstrated

496   in this study are a rigorous, yet efficient and practical approach for computing seagrass depth of

497   colonization at a large scale using widely-available geospatial data sets describing seagrass areal

498   extent and bathymetry. The method is automated via R code, and thus not especially labor-

499   intensive. Because it is automated, it is reproducible and can be applied to new data from the

500   studied estuaries or other estuaries with appropriate data. To demonstrate this, we applied the

501   analysis to 13 seagrass coverage maps for Tampa Bay, quantifying changes in depth of

502   colonization and light requirements from 1988 to 2014, which can be interpreted in the context of

503   long-term water quality changes (e.g., Beck and Hagy 2015). The method provides maps of depth

504   of colonization, resolving both means and spatial gradients at a range of scales from an individual

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

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

507   estuaries, whole estuaries, and temporal changes. Given these characteristics, our approach is a

508   novel tool for assessment of seagrass distribution with respect to water depth at different spatial

509   scales. Resolving spatial differences in depth of colonization and light requirements provides

17

510   valuable information to support further investigation of the causes and mechanisms affecting the

511   extent and spatial distribution of seagrass habitats and also informs policy development and

512   evaluation of ecosystem responses to water quality management.

513   Maps illustrating spatial patterns in depth of colonization quantified expected, but

514   previously unquantified spatial patterns, wherein seagrasses grew to greater depth when closer to

515   ocean passes, where water was clearer (Figs. 7, 8, 9). Differences among segment means were

516   mostly not statistically different, reflecting variability within segments in addition to variability

517   among segments. Evaluations of temporal changes, which may be even more important for policy

518   applications, could be evaluated without segmentation as pairwise differences of estimates by grid-

519   node. These revealed statistically significant changes in depth of colonization and light

520   requirements, as well as spatial patterns in such changes. Application to other estuaries with

521   substantial time series of water quality and seagrass distributions, such as Chesapeake Bay (Orth et

522   al. 2010), could glean valuable new insights from these data.

523   For the first time, we also combined estimates of light attenuation for estuaries based on

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

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

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

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

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

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

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

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

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

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

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

535   significant differences among segment means. Alternatively, light requirements for seagrass in

536   Indian River Lagoon were significantly less than for seagrass in Choctawhatchee Bay and Tampa

537   Bay. Light requirements for Choctawhatchee Bay and Tampa Bay were both more than the 20%

538   estimate that has been referenced broadly in water quality management (Batiuk et al. 1992;

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

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

18

541 Bay. We further note the differences in light requirements for Tampa Bay using grid-based

542 estimates at a uniform and fine spatial scale in Fig. 8, compared to those based on relatively few

543 locations at routine monitoring stations (Figs. 10 and S2). This highlights the need to consider

544 sampling regime and relevant scales for estimates of light requirements that apply to an entire

545 estuary. Regardless, our estimates are not outside the norm given the broad range in published

546 estimates of seagrass light requirements (Dennison et al. 1993).

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

548 species composition, since the physiology of seagrass is known to vary among seagrass species.

549 For example, *Halodule wrightii* is the most abundant seagrass in western Choctawhatchee Bay

550 (Yarbro and Carlson 2015) and has higher light requirements than several other abundant species in

551 Florida (Choice et al. 2014) including *Thalassia testudinum*, which dominates the more oceanic

552 areas of Tampa Bay. Choice et al. (2014) found that light requirements for *Syringodium filiforme*

553 were much less, as low as 8-15 % SI, although Kenworthy and Fonseca (1996) found that the depth

554 distribution of *H. wrightii* and *S. filiforme* were similar in the lower Indian River Lagoon, implying

555 their light requirements may be similar. Estimates of light requirements for several species of

556 *Halophila* indicate a potential to grow at 5% SI or less (Kenworthy and Haunert 1991), consistent

557 with some of our lowest estimates from Lower Indian River Lagoon (Fig. 9). Neither *S. filiforme*

558 nor any of the *Halophila* spp. appear to be dominant species in Tampa Bay or Choctawhatchee

559 Bay, perhaps limiting seagrass distributions in those estuaries to higher light environments

560 compared with lower Indian River Lagoon. Although we cannot be certain the extent to which

561 species composition can explain the differences we observed in % SI at the depth of colonization,

562 the key observation is that differences were observed, that seagrass species vary in their physiology

563 and responses to a range of factors, and therefore, that it may be useful to understand and manage

564 seagrass habitats utilizing local information where possible. Another consideration related to

565 species composition is that our estimates are likely driven by the deepest growing species. Light

566 attenuation changes could alter competitive relationships among species within the mappable

567 seagrass area, which would not be apparent in our analysis.

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

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

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

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

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

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

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

575   needed to use seagrass coverage maps based on photointerpretation, which imposes a binary

576   classification (present/absent). By inferring the probability of seagrass presence conditional on

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

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

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

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

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

582   Figs. S3, S4, S5) and the center of that depth distribution (i.e., $Z_{c,med}$). Moreover, by being linked

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

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

585   Our estimates also depend on an accurate characterization of average light attenuation,

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

587    $\% \, SI = \exp(-k_d \cdot Z_c)$, $k_d = k_{Secchi} \, / \, Z_{Secchi}$, and k_{Secchi} is generally between 1 and 2, Secchi depth in

588   seagrass habitats is often similar to the depth of colonization, potentially leading to right censoring

589   of Secchi measurements when the disk would be visible on the bottom. Accurate light profiling is

590   possible but is also difficult in shallow water. Limitations on boat operations also favor sampling

591   during calm winds, perhaps leading to under-sampling when sediment resuspension is above

592   average. Quantifying light attenuation via satellite remote sensing has advantages but also presents

593   similar and new challenges. For example, concern regarding bottom reflectance led Chen et al.

594   (2007) to exclude data if water depth was <2 m, excluding nearly all seagrass areas. Light

595   attenuation estimates for seagrass areas may therefore be based on nearby, but deeper waters,

596   whether measured via satellite remote sensing or boat-based estimates. If light attenuation is lower

597   in open water, this will tend to increase the estimate of % SI at the depth of colonization.

598   Conversely, it may not be preferable to measure attenuation on the interior of a seagrass beds, since

599   seagrass feedback effects may decrease light attenuation there (Gurbisz and Kemp 2014) and light

600   attenuation at the deeper perimeter has more relevance to seagrass depth of colonization. Thus,

601   using established satellite remote sensing methods, despite challenges and limitations, offers the

602   advantage of uniform and sustained spatial and temporal coverage.

20

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

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

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

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

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

608   quality trends. Improving trends in light attenuation, accompanied by a lagging response in depth

609   of colonization, as we observed for Tampa Bay, could explain our increasing estimates of light

610   requirements, whereas the opposite may be true with declining trends in clarity. Epiphytes on

611   seagrasses can also account for a significant fraction of total attenuation of light reaching seagrass

612   leaves, and epiphyte growth may also respond directly to the availability of light in the water (e.g.,

613   Stankelis et al. 2003, Kemp et al. 2004). As a result, simultaneously considering changes in depth

614   of colonization, light attenuation, and apparent light requirements may be useful for understanding

615   the status and trends related to seagrass habitats.

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

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

618   as well as % SI at the depth of colonization could be useful for generating testable hypotheses. For

619   example, persistent differences in spatial patterns of depth distributions may suggest hypotheses

620   regarding the causes and could stimulate research to identify local drivers. Similarly, we could

621   seek to better understand temporal changes in depth of colonization, but without a consistent

622   approach for quantifying, we may not be aware of such changes. For example, despite extensive

623   documentation of changes in the area of seagrass habitat in Tampa Bay (Greening et al. 2014) and

624   Chesapeake Bay (Orth et al. 2010), little attention has been given to associated trends in the depth

625   distribution. Our results in Fig. 10 demonstrate the novelty of our approach and its potential to

626   describe these previously undocumented changes in seagrass recovery from eutrophication impacts.

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

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

629   illustrate that management goals related to seagrass depth distribution and light attenuation may not

630   be applicable in water quality segments that are drawn without considering local drivers. At a

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

632   both important and possible to consider local differences in the water quality requirements for

633   seagrasses when developing and evaluating water quality goals over time. Even though seagrasses

21

634   are affected by factors other than light attenuation, resistance and resilience in the face of multiple

635   stressors can be influenced by the physiological and energetic changes affected by light availability

636   (Burkholder et al. 2007). In the case of Tampa Bay, light availability generally exceeds seagrass

637   light requirements estimated in the early 1990s. This may have sustained the seagrass recovery,

638   which accelerated following a brief ENSO-related period of increased river flow and increased

639   light attenuation in the late 1990s (Greening et al. 2014).

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795 Figure Captions

796 **Fig.1** Examples of data and grid locations for estimating seagrass depth of colonization for a region
797 of the Big Bend, Florida. (a) seagrass coverage and depth contours at 2 meter intervals, including
798 the whole segment estimate for depth of colonization and location of the outflow of the
799 Steinhatchee River (x); (b) a grid of sampling locations with sampling radii for estimating Z_c and
800 seagrass depth points derived from bathymetry and seagrass coverage layers; (c) an example of
801 sampled seagrass depth points for a test location
802
803 **Fig. 2** Locations and seagrass coverage of estuary segments used to evaluate depth of colonization
804 estimates. Seagrass coverage layers are from 2006 (BB: Big Bend), 2010 (OTB: Old Tampa Bay),
805 2009 (UIRL: Upper Indian R. Lagoon), and 2007 (WCB: Western Choctawhatchee Bay). SR=
806 Steinhatchee River outflow; MI= Merritt Island National Wildlife Refuge
807
808 **Fig. 3** Methods for estimating seagrass depth of colonization using sampled seagrass depth points
809 around a single location. Three depth estimates ($Z_{c,min}$, $Z_{c,med}$, $Z_{c,max}$) are based on a linear curve
810 through the inflection point of a logistic curve. The curve is defined by the parameters α, β, and γ
811 and describes the decrease in the proportion of sample points with seagrass as a function of depth
812 below mean tide level (MTL). (a) The estimation method when the linear curve intercepts α at a
813 depth greater than zero. (b) The alternative method when the linear curve intercepts α at depth less
814 than zero
815
816 **Fig. 4** Spatially-resolved estimates of maximum seagrass depth of colonization (m) for four coastal
817 segments of Florida. Estimates are assigned to grid locations for each segment, where grid spacing
818 was fixed at 0.01 decimal degrees. Radii for sampling seagrass bathymetric data around each grid
819 location were fixed at 0.02 decimal degrees. BB: Big Bend, OTB: Old Tampa Bay, UIRL: Upper
820 Indian R. Lagoon, WCB: Western Choctawhatchee Bay
821
822 **Fig. 5** Satellite estimated light attenuation for Choctawhatchee Bay as an average of years from
823 2003 to 2007. See Fig. 7 for segment identification
824
825 **Fig. 6** Satellite estimated light attenuation for Tampa Bay as an average of years from 2006 to
826 2010. See Fig. 8 for segment identification
827
828 **Fig. 7** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
829 irradiance at $Z_{c,med}$) for multiple locations in Choctawhatchee Bay, Florida. Each location has light
830 attenuation from satellite observations and an estimate of seagrass depth of colonization with a
831 search radius of 0.04 degrees. Box plots show the 25th percentile, median, and 75th percentile.
832 Whiskers extend to the 5th and 95th percentiles with outliers beyond. CCB: Central Choctawhatchee
833 Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay

834

835 **Fig. 8** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
836 irradiance at $Z_{c,med}$) for multiple locations in Tampa Bay, Florida. Each location has light
837 attenuation from satellite observations and an estimate of seagrass depth of colonization with a
838 search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile.
839 Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay,
840 LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

841

842 **Fig. 9** Median depth of seagrass colonization ($Z_{c,med}$, m) and light requirements (% surface
843 irradiance at $Z_{c,med}$) for multiple locations in Indian River Lagoon, Florida. Each location has an
844 average Secchi depth observation and an estimate of seagrass depth of colonization with a search
845 radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth. Box plots
846 show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles
847 with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower
848 Indian R. Lagoon, LML: Lower Mosquito Lagoon, UCIRL: Upper Central Indian R. Lagoon,
849 UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon

850

851 **Fig. 10** Annual changes in median light attenuation (K_d, m^{-1}) and depth of colonization ($Z_{c,med}$,
852 m) in segments of Tampa Bay from 1988 to 2014 (upper panels) and resulting changes in percent
853 of surface irradiance at the depth of colonization (lower panel). Contours in upper panels
854 illustrate isopleths of percent surface irradiance at depth of colonization (Equation 8). Box plots
855 show the distribution of light requirements at locations in each segment shown in Fig S2. HB:
856 Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

857

858 Supplementary figures

859

860 **Fig. S1** Uncorrected satellite estimates of light attenuation in Choctawhatchee Bay (a) and
861 example of correction with *in situ* data (b). *In situ* data of light attenuation were estimated as an
862 annual average (2010) for monthly data at the sampling sites labelled as points in (a) (mean
863 depth 7.2 m, minimum 3.5 m). The corresponding satellite data in the same grid cells were
864 compared to the *in situ* data based on regressions of each dataset with frequency estimates for
865 both. An example correction is shown in (b) where for any uncorrected satellite estimate (point
866 1), the corresponding frequency estimate on the regression curve from the satellite data was
867 identified (point 2), matched with the corresponding frequency for the *in situ* data (point 3), and
868 then related to the associated *in situ* light attenuation value (point 4) to yield the corrected
869 satellite estimate

870

871 **Fig. S2** Locations of selected water quality stations monitored by the Hillsborough County
872 Environmental Protection Commission (TBEP 2011). Secchi observations at each station were
873 used to evaluate changes in light requirements of seagrass at approximate biennial intervals from
874 1988 to 2014. Stations are labelled by their designation and were chosen based on continuity of
875 data for the period of interest. HB: Hillsborough Bay, LTB: Lower Tampa Bay, MTB: Middle
876 Tampa Bay, OTB: Old Tampa Bay

877

878 **Fig. S3** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface
879 irradiance at $Z_{c,max}$) for multiple locations in Choctawhatchee Bay, Florida. Each location has

880   light attenuation from satellite observations and an estimate of seagrass depth of colonization

881   with a search radius of 0.04 degrees. Box plots show the 25th percentile, median, and 75th

882   percentile. Whiskers extend to the 5th and 95th percentiles with outliers beyond. CCB: Central

883   Choctawhatchee Bay, ECB: East Choctawhatchee Bay, WCB: West Choctawhatchee Bay

884

885   **Fig. S4** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface

886   irradiance at $Z_{c,max}$) for multiple locations in Tampa Bay, Florida. Each location has light

887   attenuation from satellite observations and an estimate of seagrass depth of colonization with a

888   search radius of 0.1 degrees. Box plots show 25th percentile, median, and 75th percentile.

889   Whiskers extend to the 5th and 95th percentiles with outliers beyond. HB: Hillsborough Bay,

890   LTB: Lower Tampa Bay, MTB: Middle Tampa Bay, OTB: Old Tampa Bay

891

892   **Fig. S5** Maximum depth of seagrass colonization ($Z_{c,max}$, m) and light requirements (% surface

893   irradiance at $Z_{c,max}$) for multiple locations in Indian River Lagoon, Florida. Each location has an

894   average Secchi depth observation and an estimate of seagrass depth of colonization with a search

895   radius of 0.15 degrees. Map locations are georeferenced observations of Secchi depth. Box plots

896   show 25th percentile, median, and 75th percentile. Whiskers extend to the 5th and 95th percentiles

897   with outliers beyond. BR: Banana R., LCIRL: Lower Central Indian R. Lagoon, LIRL: Lower

898   Indian R. Lagoon, LML: Lower Mosquito Lagoon, LSL: Lower St. Lucie, UCIRL: Upper

899   Central Indian R. Lagoon, UIRL: Upper Indian R. Lagoon, UML: Upper Mosquito Lagoon

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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	OTB	UIRL	WCB
Year	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

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

Seagrass coverage data sources, see methods for bathymetry data sources

BB, WCB: http://geodata.myfwc.com/

OTB: http://data.swfwmd.opendata.arcgis.com/

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

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Table 2 Summary of seagrass depth estimates (m) for each segment in Fig. 4 and the year indicated in Table 1. 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	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

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 in segment means. Segments with the same superscript are not significantly different. Multiple comparison tests are only within estuaries, not between estuaries. See Figs. 7 to 9 for spatial distribution of the results

Segment	$Z_{c,med}$					% light				
	n	Mean	St. Err.	Min	Max	n	Mean	St. Err.	Min	Max
Choctawhatchee Bay										
CCB	171	1.9[ab]	0.2	0.5	4.2	156	59.4	4.6	23.4	91.7
ECB	16	0.8[a]	0.4	0.4	0.9	16	74.7	8.6	58.0	88.6
WCB	151	2.3[b]	0.3	1.6	2.8	131	50.5	5.7	35.5	77.9
Indian River Lagoon										
BR	2	1.0[c]	0.4	1.0	1.1	17	20.7	7.5	20.2	21.3
LCIRL	14	1.2[c]	0.3	0.9	1.6	2	13.6	6.4	5.8	24.7
LIRL	3	1.6[c]	0.4	1.5	1.6	3	9.2	7.1	6.0	11.2
LML	4	1.0[c]	0.4	1.0	1.0	14	22.1	6.9	19.3	24.3
UCIRL	17	1.0[c]	0.3	0.8	1.1	1	20.0	6.4	7.5	30.7
UIRL	1	1.0[c]	0.4	1.0	1.0	4	24.1	8.6	24.1	24.1
UML	6	1.0[c]	0.3	0.8	1.0	6	24.0	6.7	15.2	30.9
Tampa Bay										
HB	22	1.0[de]	0.2	0.6	1.3	19	43.2	6.9	17.7	50.8
LTB	70	1.3[de]	0.1	0.8	1.5	56	38.3	5.6	22.5	58.7
MTB	73	1.4[e]	0.1	1.1	1.6	62	36.5	5.5	15.2	50.2
OTB	87	0.8[d]	0.1	0.5	1.1	83	47.7	5.6	31.5	77.4

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.
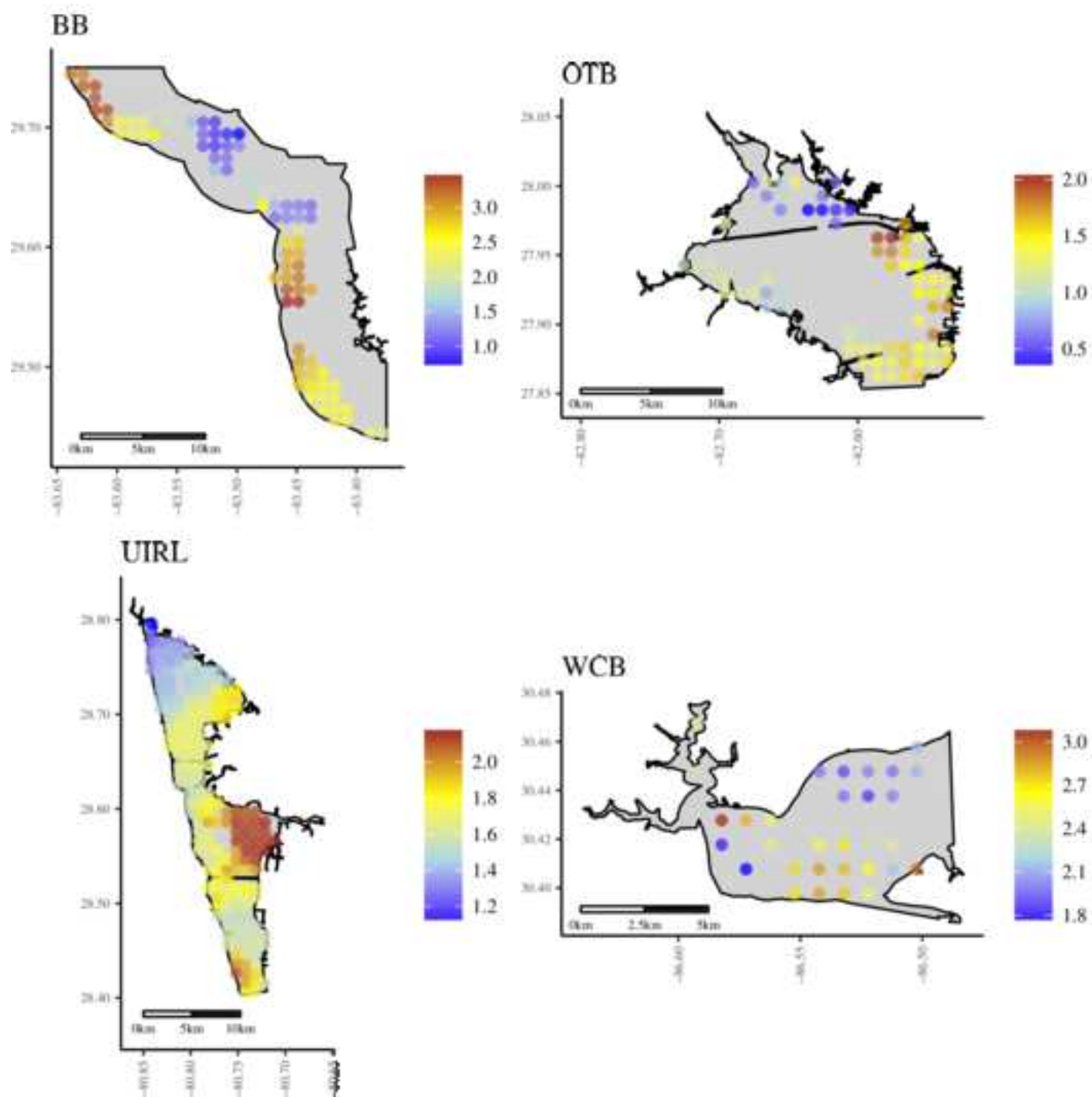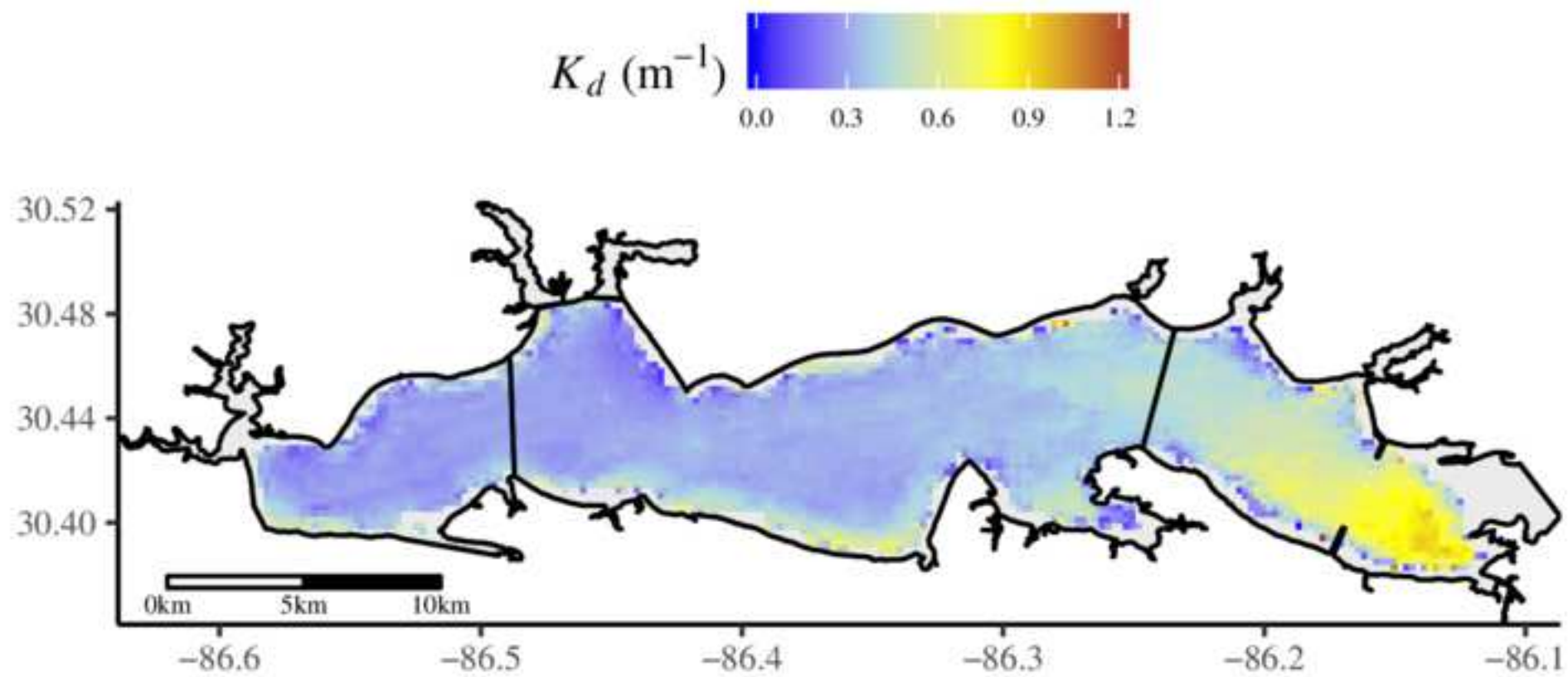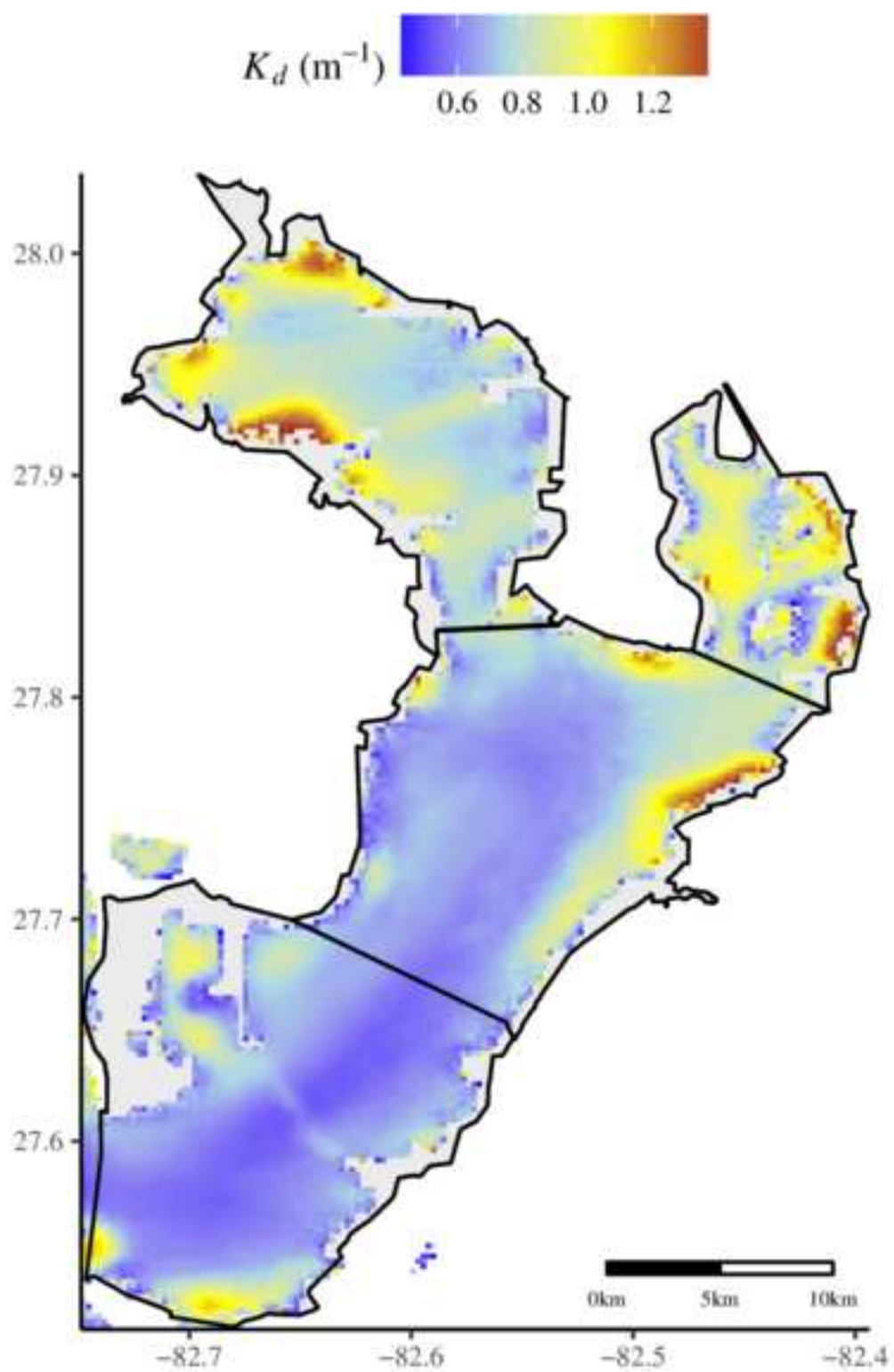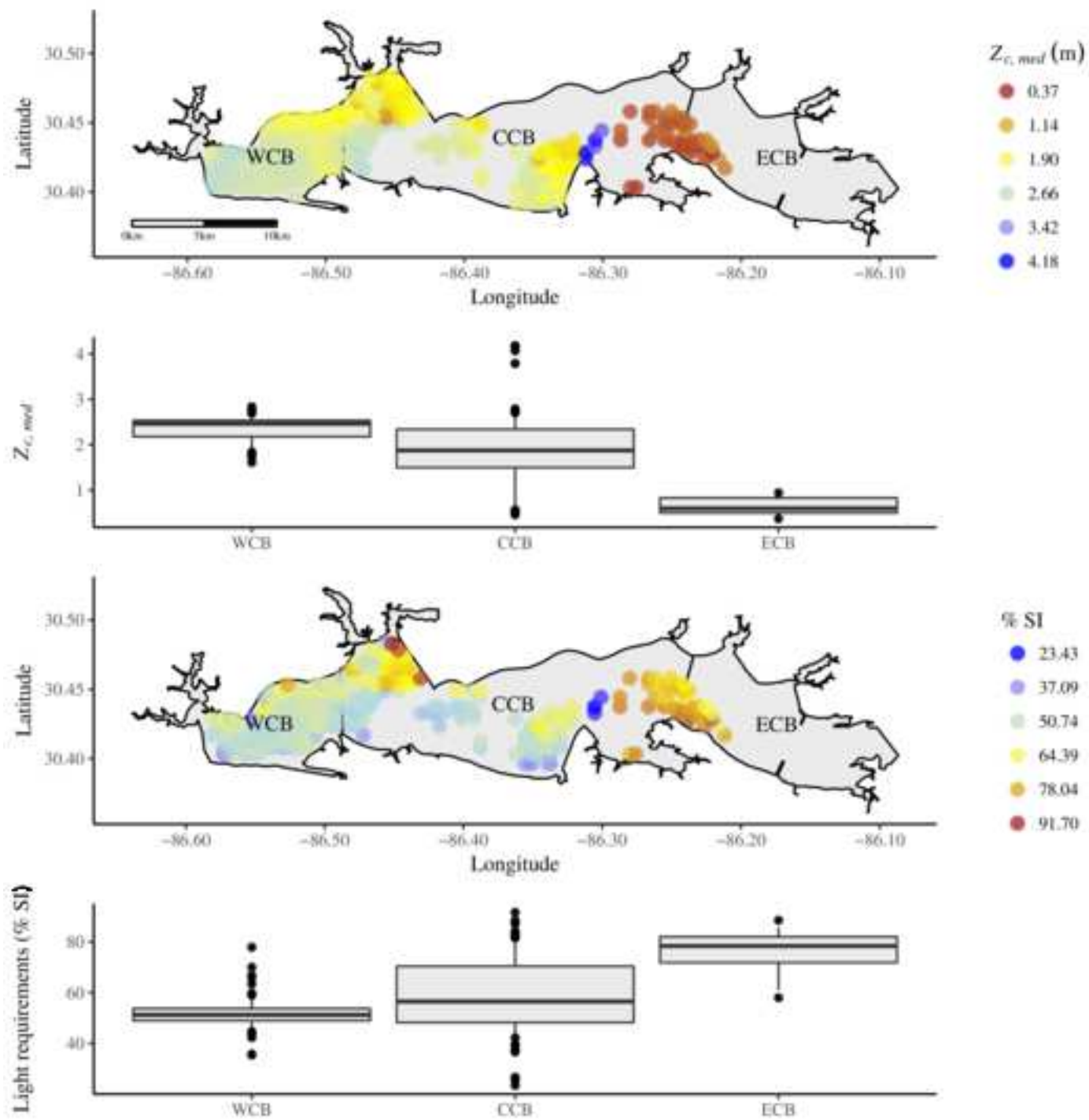
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Fig2

Click here to download Figure Fig2.tif

Segment boundary   Seagrass coverage
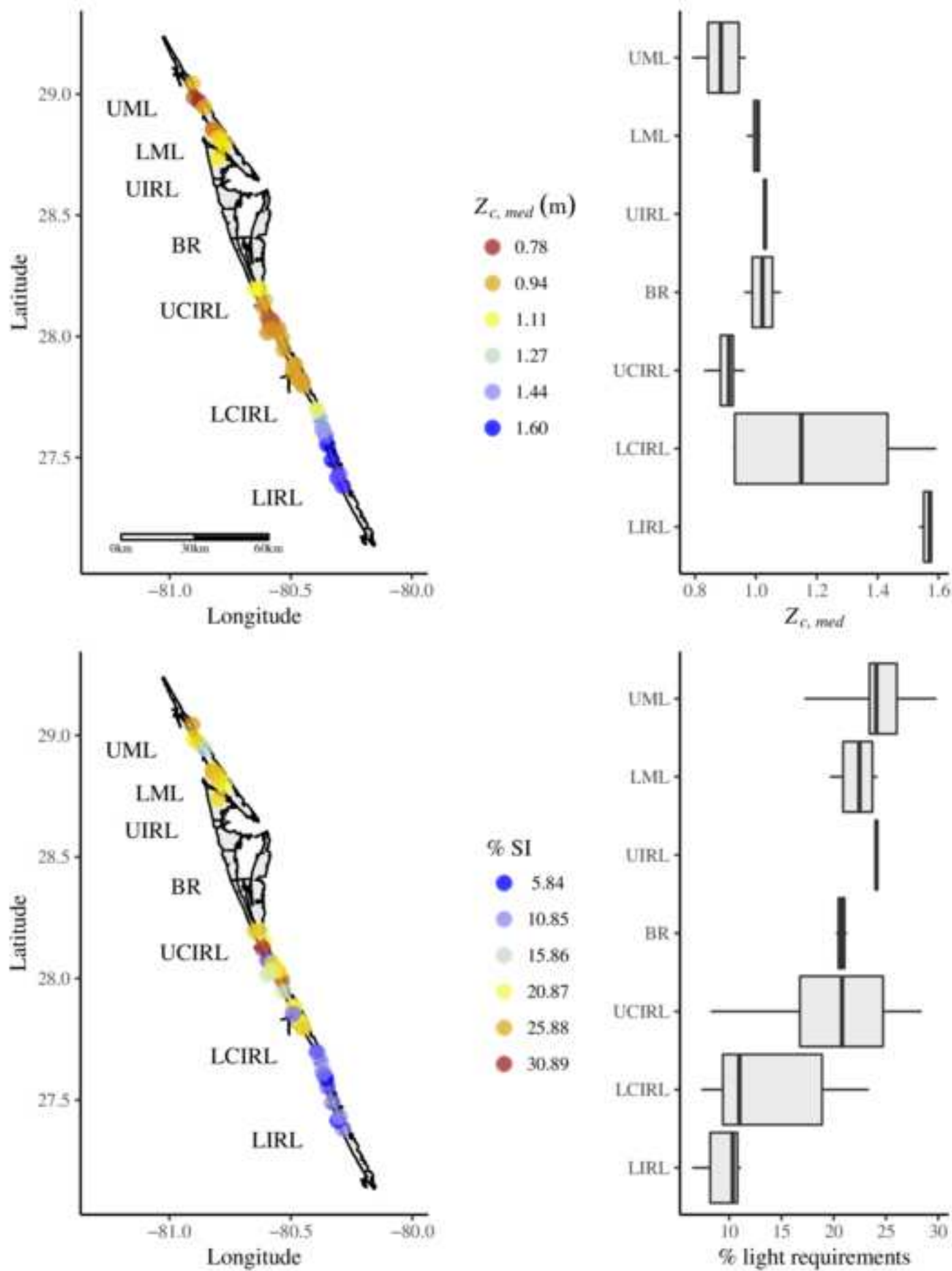
Fig3

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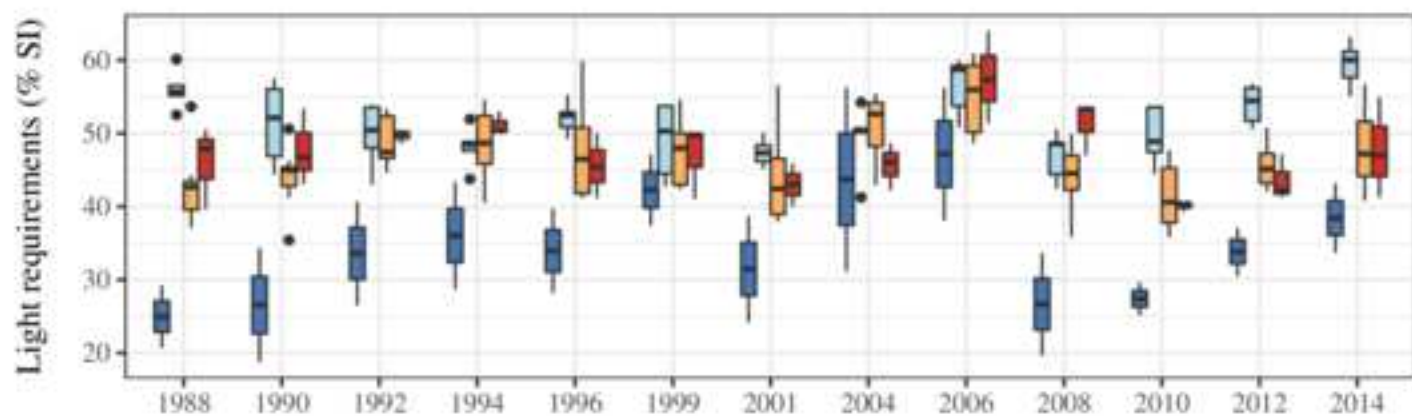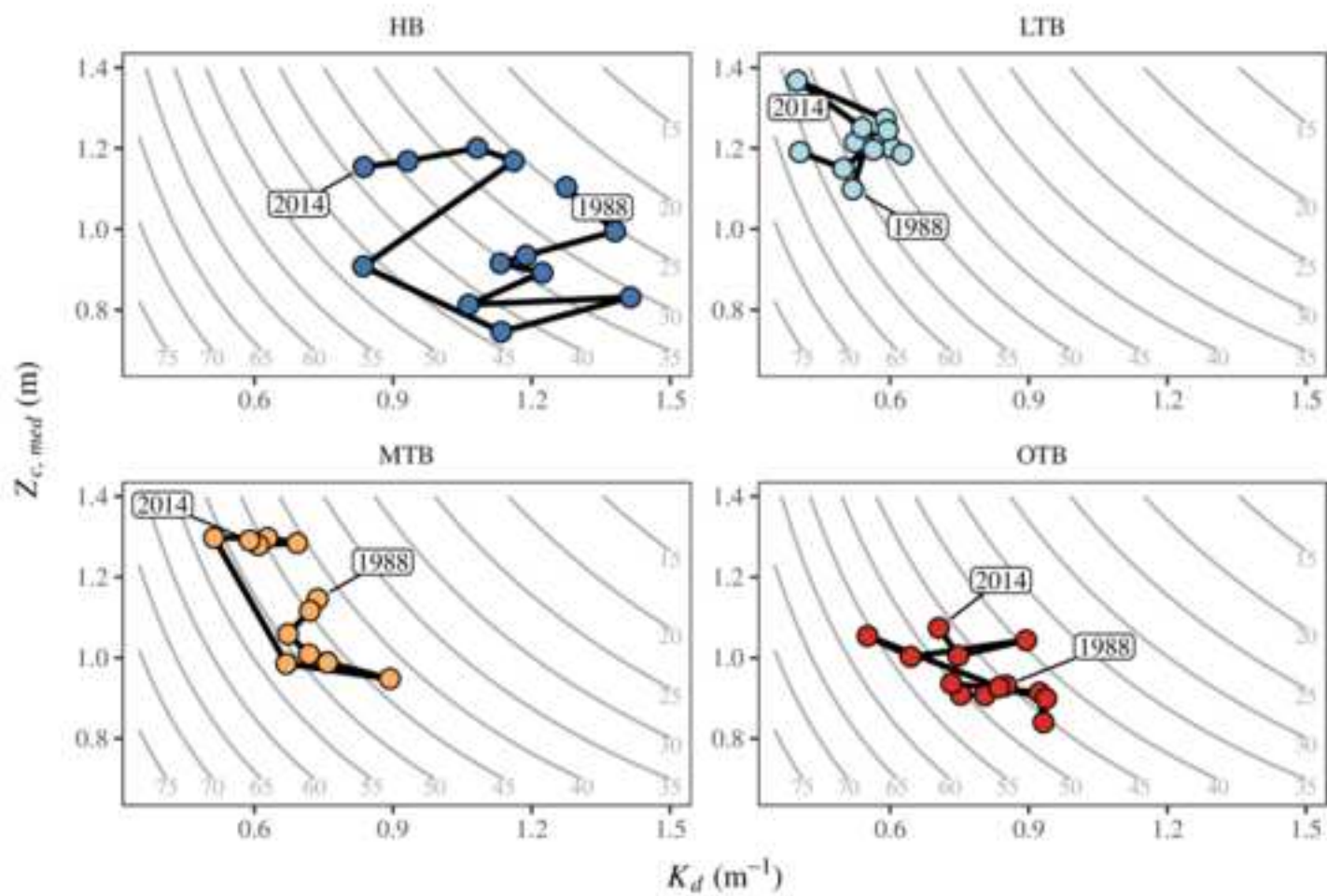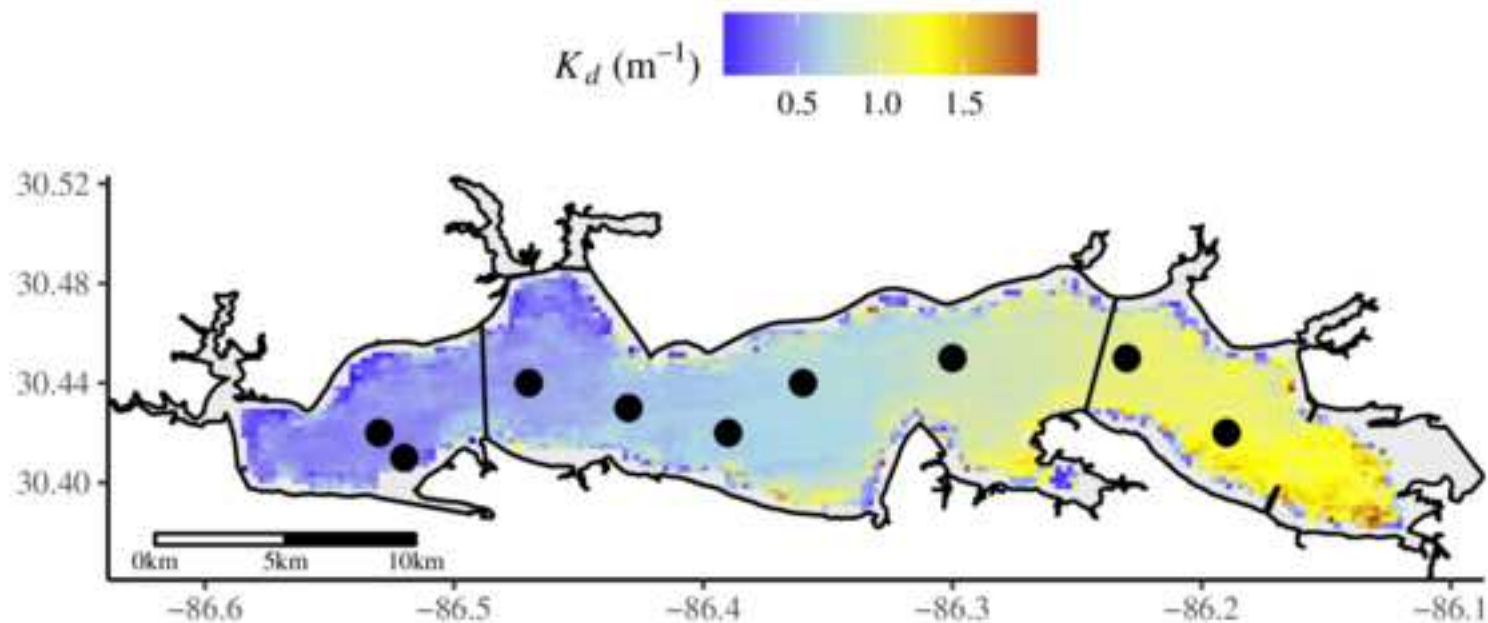
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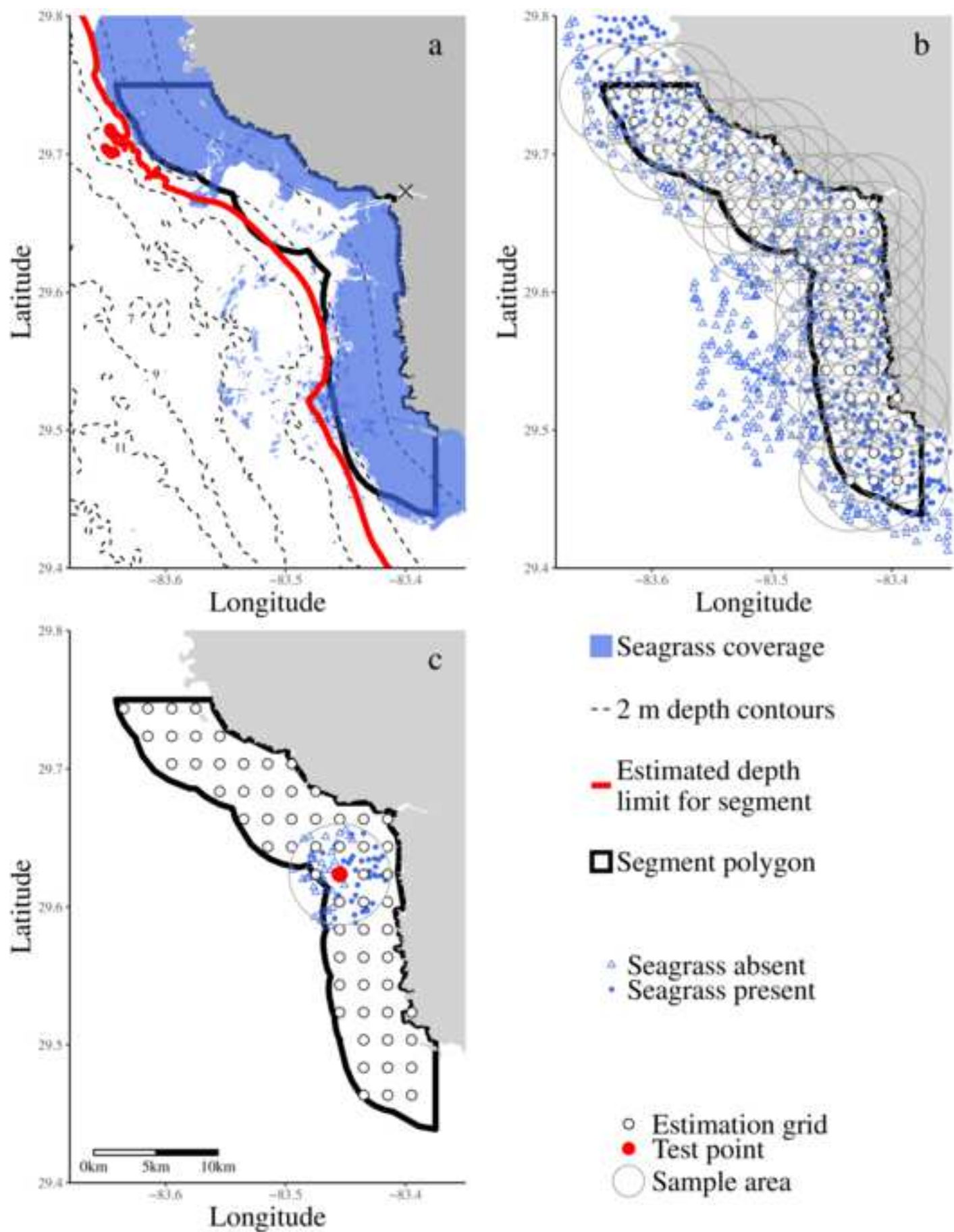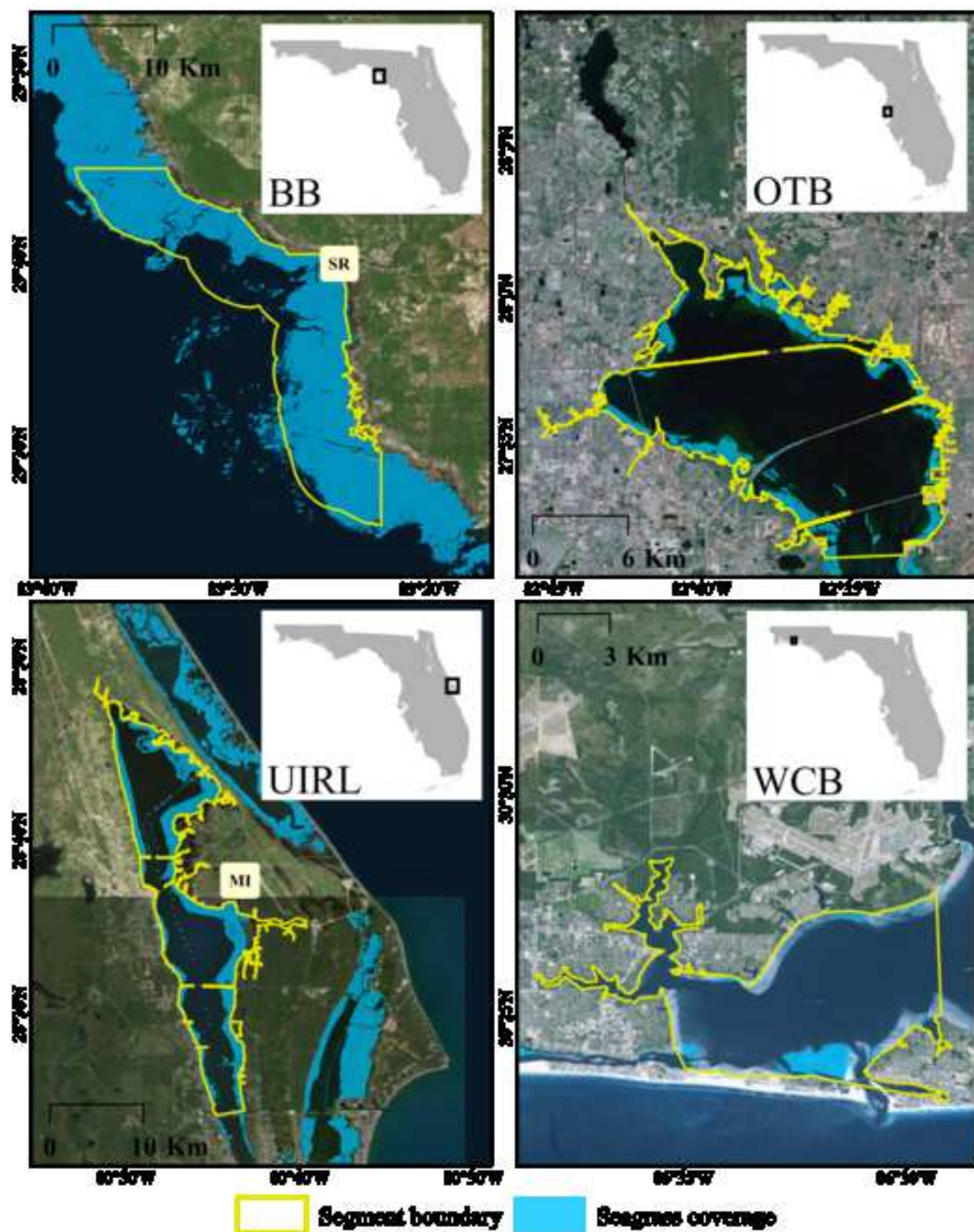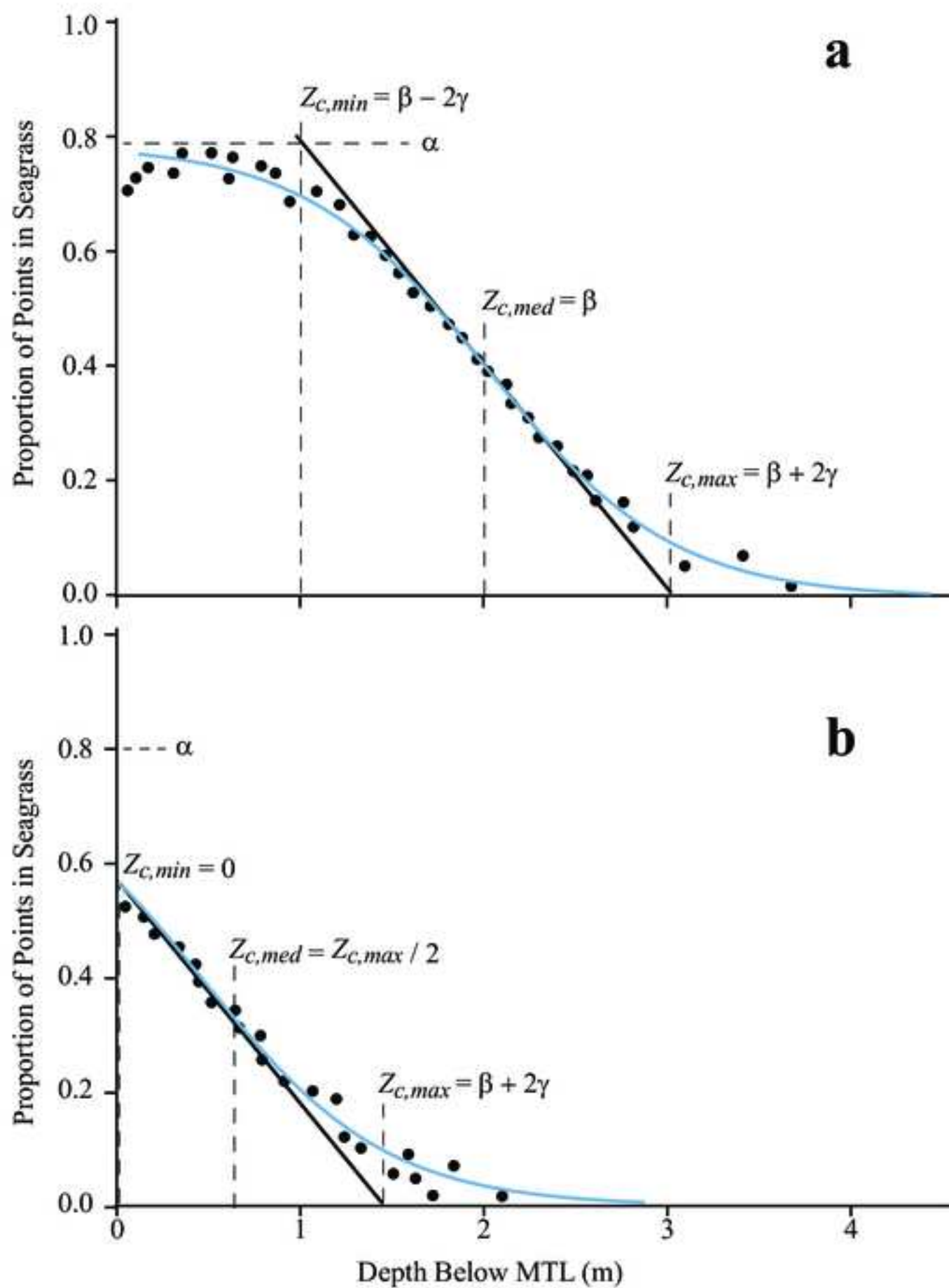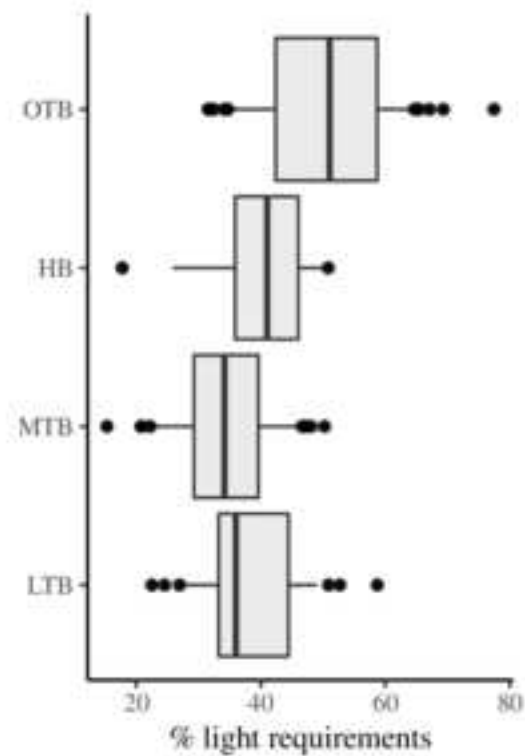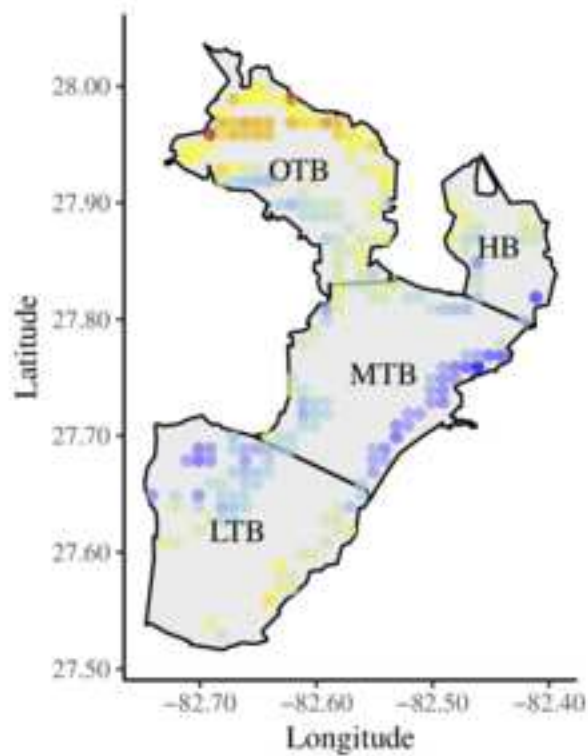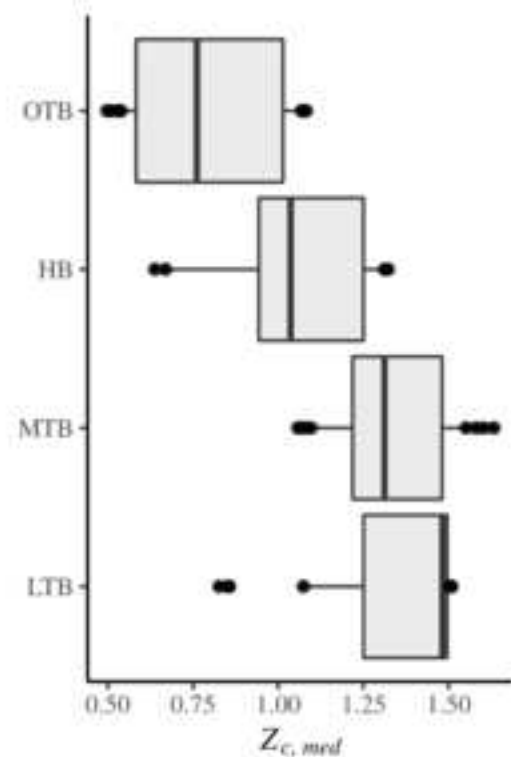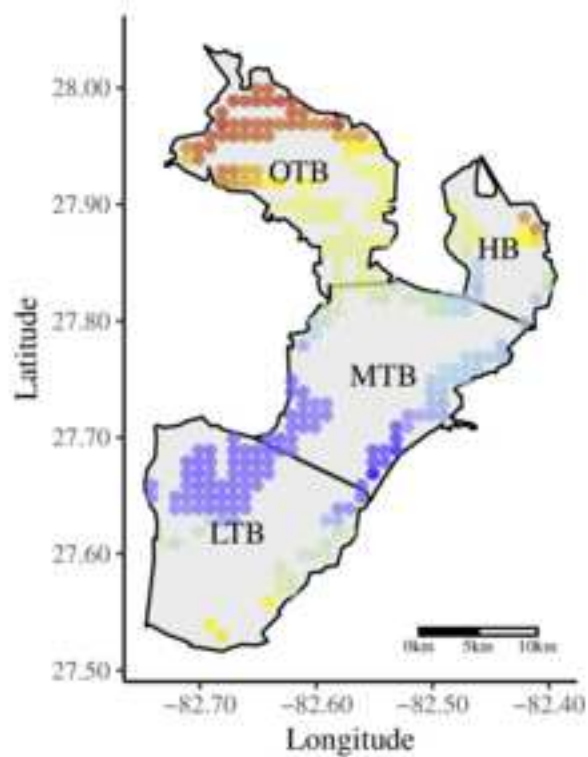
(a) Uncorrected satellite estimates and stations for *in situ* data

(b) Example of satellite correction

FigS3

FigS5