Diversity and distribution of seagrasses as related to salinity, temperature, and availability of light in the Indian River Lagoon, Florida

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Abstract Seven species of seagrass have been found in the Indian River Lagoon (IRL), making it an unusually diverse location at the global scale. From 1994 to 2019, the lagoon-wide distribution of these species reflected variations in temperature, salinity, and the availability of light at depth, which were related to latitudinal differences in hydrology and hydrodynamics along the IRL. In general, species richness was higher near the four southern inlets, and fewer species were found in areas with longer residence times for water. At a finer scale, the distribution of species varied among depths, with the greatest number of species found at mid-depths ($\sim$0.4–0.9 m). Prior to 2011, these patterns remained relatively consistent for $\sim$ 40 years, but several, intense and prolonged phytoplankton blooms disrupted them. The areal extent of all seagrasses decreased by over 50%, the offshore ends of canopies moved shoreward and shallower, distributions of species along gradients of latitude and depth were disrupted, and mean percent cover decreased. Major changes in distribution and abundance of seagrasses arose when salinity, temperature, and availability of light at depth exceeded limits derived for each species. These substantial and widespread changes engendered concerns for recovery or rehabilitation of seagrasses in the lagoon.

Introduction

Globally, seagrass meadows deliver thousands of dollars of ecosystem services per hectare annually, but these vital habitats are being lost at an alarming rate (Barbier et al. 2011). For example, declines in biomass and density have been reported for many seagrass beds throughout the United States since the middle 1900s (Waycott et al. 2009, Orth et al. 2010). In many cases, these losses are attributed to human activities, such as the creation of excess loads of nutrients that result in blooms of phytoplankton and reduced light availability (Duarte 1991, 1995, Lee et al. 2007) or changes in hydrology that alter salinities or temperatures (Doering et al. 2002). In fact, reducing anthropogenic loads of nutrients has led to recovery in some estuaries, such as Chesapeake, Tampa and Sarasota bays (Lefcheck et al. 2018, Handley and Lockwood 2020). Unfortunately, relatively long residence times made

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the Indian River Lagoon (IRL) in Florida more vulnerable to the global trends of degraded water quality and loss of seagrass, with recent changes being substantial (Morris et al. 2018, Kahn 2019).

Water quality in the IRL has been impaired by excessive loads of nitrogen and phosphorus for decades (Steward et al. 2003, Steward and Green 2007). Planning to reduce these loads was underway (Gao 2009, Banana River Lagoon Stakeholders 2013, Central Indian River Lagoon Stakeholders 2013, North Indian River Lagoon Stakeholders 2013) and seagrasses were expanding their areal extent, when conditions changed dramatically in 2011 (Phlips et al. 2015). A series of phytoplankton blooms in 2011, 2016, and 2017–2018 decreased light penetration, and this shading contributed to a 50% reduction in the 32,000 ha of seagrass present in 2007 (Morris et al. 2018). The unusual blooms had concentrations of chlorophyll-a that were ~2x higher than 99% of the values recorded in the preceding 15 years (over 100 µg/L) and concentrations > 30 µg/L that persisted for up to 13 months. The reduced footprint of seagrass was expected to yield a loss of ecosystem services potentially exacerbated by a loss of diversity and the resilience it provides (Collier et al. 2020).

When conditions were not so extreme, the IRL supported seven species of seagrass, which were *Halodule wrightii* (Hw)*, Syringodium filiforme* (Sf)*, Thalassia testudinum* (Tt)*, Ruppia maritima* (Rm)*, Halophila engelmannii* (He)*, Halophila johnsonii* (Hj)*, and Halophila decipiens* (Hd) in order of decreasing areal extent and percent cover. In large part, this diversity has been attributed to temperature, salinity, and light availability that vary and interact in space and through time (Zimmerman et al. 1971, Fong and Harwell 1994, Fletcher and Fletcher 1995, Ralph 1999). For example, ecologically important differences in temperature exist between the southern and northern IRL because the 260-km long lagoon spans tropical and warm temperate waters (Gilmore 1995). In addition, salinities are affected by spatiotemporal variation in exchange with the coastal ocean and delivery of fresh water. Oceanic exchange occurs primarily through five inlets, with residence times for water increasing farther from the inlets, especially in the northern region where the two adjacent inlets are separated by approximately 150 km (Smith 1993, Steward and Green 2007). In combination with varying freshwater inputs, this configuration results in a range of salinities that persist for different periods. For example, southern Mosquito Lagoon, Banana River Lagoon, and the northern IRL are far from inlets and have limited freshwater inputs from small watersheds resulting in residence times upwards of one year; therefore, salinities can become and remain either high or low for extended periods depending on the balance between freshwater inputs and evaporation (Steward et al. 2005, 2006). In contrast, the central IRL receives fresh water from a greater number of creeks, rivers, and canals draining larger areas of land, resulting in lower and more temporally variable salinities (Woodward and Clyde 1994). Relatively large freshwater inputs also enter the southern IRL, but oceanic exchange through three inlets delivers water with higher salinities and lowers residence times so conditions tend to be more stable (Woodward and Clyde 1994).

In combination, these factors help determine the latitudinal distribution of species of seagrass along the IRL. For example, surveys in 1976 documented an increase in cover for Sf from south of Merritt Island to Fort Pierce and a concurrent decrease in the density of Hw shoots (Thompson 1978). Subsequent surveys indicated that all seven species were found within 3 km of Sebastian Inlet, but the more tropical species, Tt, Hd, and Hj, typically were found south of Sebastian Inlet (Dawes et al. 1995, Virnstein 1995). In fact, the IRL has been established as the northern limit of the distribution of Sf, Tt, He, Hj, and Hd, whereas Hw and Rm extend as far as North Carolina and Nova Scotia, respectively (den Hartog 1970). Furthermore, the more ephemeral species, Rm and He, were rarely found south of Fort Pierce Inlet and St. Lucie Inlet, respectively (Dawes et al. 1995, Virnstein 1995).

To augment such historical information, this paper evaluated recent changes in the distribution and abundance of the seven species of seagrass using data collected at two scales: mapping from aerial photography and monitoring of fixed transects. The goals were to 1) establish the overall context for species-specific changes by examining changes in areal extent of all seagrasses; 2) identify spatiotemporal patterns in the distances seagrasses extended from shore, the percent occurrence and cover of species, and water depths where cover was most stable; and 3) explore spatiotemporal variation in temperature, salinity, and the availability of light at depth as explanatory factors for changes in seagrasses.

Materials and Methods

For this paper, the IRL was subdivided into smaller areas labeled reaches (Figure 1). The reaches were delineated by evaluating similarities in time series of water quality parameters (St. Johns River Water Management District, unpublished data). The first six reaches were within the St. Johns River Water Management District (SJRWMD). The remainder were within the boundary of the South Florida Water Management District (SFWMD), and they included reaches 7, 8, and 9 in the southern IRL from just north of Fort Pierce Inlet to Jupiter Inlet. For analyses relying on depth and monthly data, reaches 7, 8, and 9 were not included because those data were unavailable.

Across and within the reaches, seagrass was monitored at two scales: lagoon-wide mapping from aerial photography and monitoring of fixed transects that were approximately 20–1,800 m long and separated by 400–14,000 m. Mapping did not detect changes in the distribution or abundance of species, but the lagoon-wide data on areal extent provided a valuable context for measurements taken along transects. In contrast, monitoring of fixed transects supported rapid, repeated, reliable, and non-destructive detection of small-scale changes in distribution, abundance, and species composition at selected locations and depths over time (Morris et al. 2000). Because each transect extended to the offshore end of the bed, expansions or contractions of the bed can be detected and related to changing water quality conditions.

Mapping was recommended to occur every 2–3 years according to the Surface Water Improvement and Management (SWIM) Plan for the entire IRL (Steward et al. 1994). In actuality, SJRWMD, SFWMD, and the Florida Department of Environmental Protection produced maps spanning the whole lagoon for 1943, 1992, 1994, 1996, 1999, and every two years from 2003 to 2019.

Mapping was based on visual interpretation of aerial photographs, primarily at a 1:24,000 scale but in some cases at a 1:10,000 scale. Features on the aerial photographs were identified with the aid of stereoscopic analysis, photo-interpretation keys, and ground truthing. Features were classified according to Florida Land Use, Cover and Forms Classification System (FLUCCS) codes (Florida Department of Transportation 1999) as modified by the SJRWMD and SFWMD. Features were delineated, and the
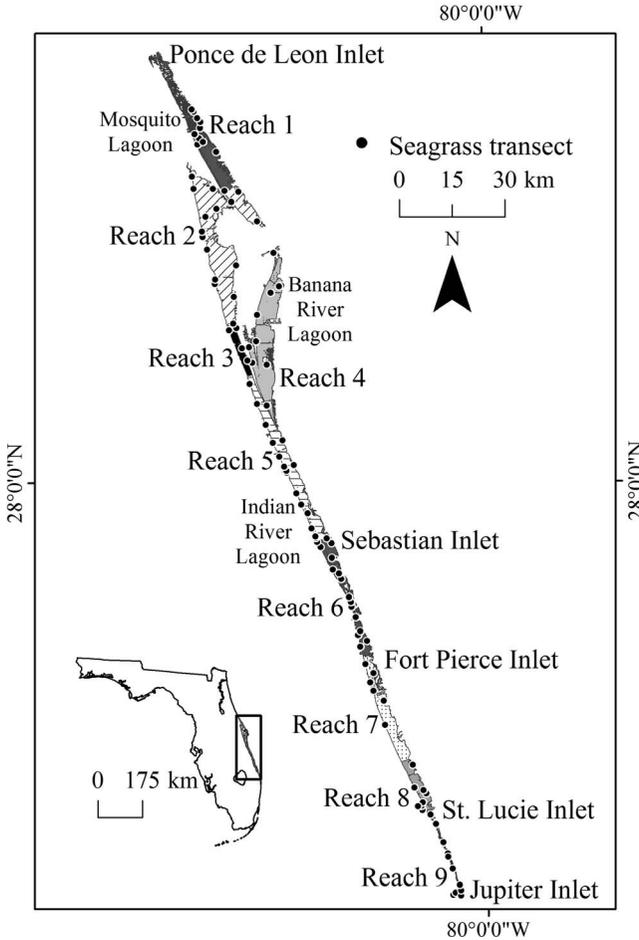
Figure 1. Map showing the location of the Indian River Lagoon and five inlets, nine reaches, and transects where seagrass was surveyed.

resulting polygons were connected to create a GIS data layer for the areal extent of seagrass. The accuracy of classifications was evaluated from 1999 onward, and it was at least 80%.

Starting in 1994, seagrasses in the IRL also were surveyed along fixed transects at least twice a year (summer and winter) approximating times of annual maximum and minimum abundance (Virnstein and Morris 1996). The location of each transect was marked with poles, and the path to be surveyed was delineated by a graduated line extending perpendicular to the shoreline from the shore out to the deep end of the seagrass canopy (EOC). For consistency with mapping, the EOC was designated only for Hw, Sf, Tt, and Rm because the three *Halophila* species were small, ephemeral, and difficult to map accurately from aerial images. The EOC was demarcated when percent cover in 1-m^2 quadrats dropped to zero or remained < 1% for 30 m. However, surveys always extended at least 30 m beyond the EOC so that *Halophila* spp. could be detected.

At pre-designated points along transects, a suite of standardized, non-destructive measurements were made within a 1-m^2 quadrat divided by strings into 100 cells, each 10 cm by 10 cm. Relevant measurements were: 1) percent occurrence for each species based on the number of cells in the quadrat

containing one or more shoots, 2) a visual estimate of percent cover for individual species starting in 1998; 3) water depths at points along transects; and 4) total transect length from the shore to the EOC (Morris et al. 2001).

In order to standardize data among years where the cover of individual species was recorded, i.e., 1998–2019, records were adjusted to yield equal lengths for each transect across all years. This goal was achieved by adding cover values of zero beyond the EOC to the maximum distance measured across all years.

Seagrasses required light to survive and grow, and light availability was affected by depth. For this study, depths measured in the field were adjusted to depths below mean water level (MWL) using bathymetric data collected by Coastal Planning & Engineering (1997). Depth soundings were taken throughout the IRL at 15.2 m intervals along east-west tracks that were spaced approximately 150–300 m apart. This bathymetric survey resulted in over 230,000 depths that were referenced to North American Vertical Datum of 1988 (NAVD88) and adjusted to depth below MWL. These data yielded isobaths that were used to adjust depths measured in the field by calculating the difference between the measured depth and the 0.75-m isobath for each transect and using the resulting constants to correct all field measurements for that sampling event. This process was repeated for all transects and all years. The resulting depths below MWL were rounded to the nearest 0.1 m.

In addition to the availability of light at depth, the distributions of seagrasses were influenced by physical and chemical conditions. Therefore, data on water temperatures, salinities, and attenuation of photosynthetically active radiation (PAR, wavelengths of 400–700 nm) were extracted from monthly data collected at nearby, fixed stations.

Water temperatures and salinities were measured in the field using multiparameter instruments equipped with the relevant probes. The instruments were calibrated and verified using standards and procedure that agree with state guidelines.

The coefficient of attenuation for PAR (K_d) was determined by applying Beer's Law to simultaneous readings recorded by three spherical quantum sensors. Two of the sensors were held at 0.2 m and 0.5 m below the water's surface, and the third was held 0.3 m from the bottom in water $\leq$ 1.8 m deep or at 1.5 m from the surface in deeper water (Morris et al. 2001).

Areal extents in hectares in each of nine reaches for the 14 years with maps were used in two analyses. Bray-Curtis distance measures calculated with raw data were used in a permutation analysis of variance (PERMANOVA; Anderson et al. 2008). The model treated reaches as a fixed factor and years of mapping as repeated measures nested within reaches. Furthermore, a hierarchical cluster analysis based on Bray-Curtis distances and single linkage clustering was used to identify groups of years with similar extents of seagrasses across all reaches.

Transects provided depths at the EOCs corrected in MWL, which represented another means of estimating changes in the extent of seagrass. These depths measured along transects in the northern six reaches over 26 years (1994–2019) were analyzed with a PERMANOVA. The analysis was based on Bray-Curtis distance measures calculated with raw data. The model treated the northern six reaches as a fixed factor, with years nested within reach to account for repeated measures along the fixed transects.

Mean percent cover values from the summers of 22 years (1998–2019) for 7 species found in 9 reaches were used in a PERMANOVA. The analysis was based on Bray-Curtis distance measures calculated with raw data. The model treated species and reach as fixed factors, with years nested within the interaction between these factors to account for repeated measures along the fixed transects.

The hierarchical clustering based on areal extent of seagrasses was designed to identify years with generally suitable conditions for seagrasses. Data on percent cover from suitable years were assigned to one of nine depth zones based on the associated depths below MWL, i.e., depth < 0.1 m, 0.1 $\leq$ depth < 0.4 m, 0.4 $\leq$ depth < 0.5 m, 0.5 $\leq$ depth < 0.6 m, 0.6 $\leq$ depth < 0.7 m, 0.7 $\leq$ depth < 0.8 m, 0.8 $\leq$ depth < 0.9 m, 0.9 $\leq$ depth < 1.0 m, and $\geq$ 1.0 m. For each of the seven species, mean percent cover values for each combination of year, one of the six reaches, and depth zone were calculated and then examined with boundary analyses (Ludwig and Tongway 1995). The analyses involved 1) ranking percent covers in order of depth, 2) bracketing contiguous sets of percent covers in a window of preassigned width (4, 6, or 8 datapoints), 3) halving each window (two sets of 2, 3, or 4 datapoints), 4)
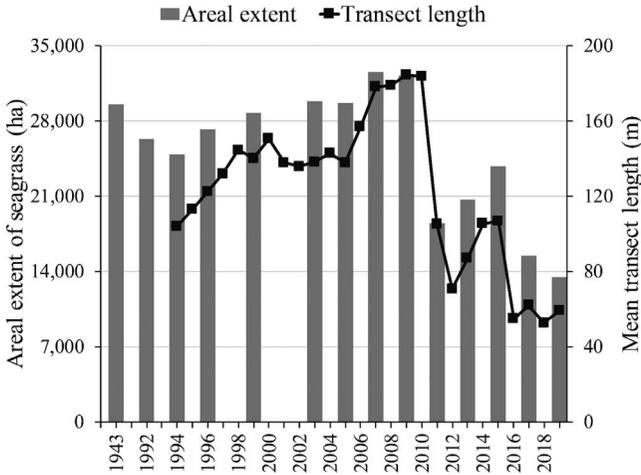
Figure 2. Areal extent of seagrass in maps derived from aerial photography and mean distances to the deep ends of the seagrass canopies or mean length of transects versus years. grey bars = seagrass extent in ha, black line = mean transect length in m

averaging the percent covers in the two groups (μ_1 and μ_2), 5) computing a squared Euclidean distance [SED = $(\mu_1 - \mu_2)^2$], 6) moving the window one position further along the ordered series of percent covers, 7) computing another SED, 8) repeating this process for the entire dataset, and 9) examining the SEDs to identify a depth zone where cover increased or decreased. The goal of these analyses was to identify a depth zone most suitable for examining the importance of light attenuation.

In addition, mean percent cover values from summer and winter surveys in the nine reaches during years with conditions generally suitable for seagrass were combined with mean metrics characterizing water quality in the same reaches and subjected to a series of boundary analyses (Ludwig and Tongway 1995). For each combination of year and reach, the analyses paired the appropriate mean percent covers with mean temperatures, mean salinities, or mean proportions of incident light reaching the maximum depth of the zone deemed most suitable for seagrass. Wherever possible, values for water quality parameters associated with increases or decreases in the mean percent cover of species of seagrass were identified as those values associated with the first large increase or the last large decrease in the relevant SED. To confirm that these limits were consistent, percent covers equal to and above or below the limits were compared to percent covers between the limits with a Student's t-test that accounted for unequal variances.

The confirmed limits were applied to a time series of monthly water quality data collected at fixed stations distributed throughout the northern six reaches of the lagoon. The numbers of consecutive months that were more extreme than the limits were calculated for each species in each reach. The distributions of these values were used to explain spatiotemporal changes in cover of the species of seagrass.

Results

Approximately 5,000 ha of seagrass were lost between 1943 and 1994 (Figure 2), with losses likely occurring after 1976 given that Thompson (1978) found no detectable losses in photos from 1945, 1954, and 1976. By 2009, the extent of all seagrasses reached over 32,000 ha, which exceeded the 1943 coverage. Unfortunately, by 2011, the areal extent of seagrasses had decreased by approximately 14,000 ha. The resilience of seagrasses was illustrated by the slight
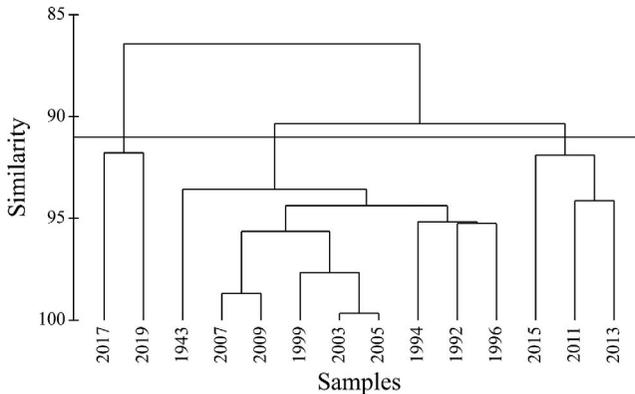
Figure 3. Results of a hierarchical cluster analysis based on areal extent of seagrass in nine reaches. horizontal line = delineates three periods of time at 91% similarity

increase in areal extent in 2013 and 2015. Regrettably, these gains were not sustained, with the areal extent of seagrasses decreasing to 58% of the 2009 value by 2019.

The hierarchical cluster analysis indicated three groups of years with similarities of 91% (Figure 3). The years before 2011 formed one group; 2011, 2013, and 2015 formed a second group; and 2017 and 2019 formed a third group. These groups tracked the lagoon-wide increase in extent from 1943 to 2009, the initial decrease in extent in 2011, and the second decrease in extent in 2017.

The lagoon-wide changes in seagrass areal extent were not consistent among reaches according to the PERMANOVA ($F_{8;117} = 40.26$, $p < 0.001$; Figure 4). In reaches 2, 4, 5, 6, and 7, the extent of seagrass decreased in 2011, increased slightly in 2013 and 2015, and decreased again in 2017 and 2019. Of the reaches displaying this pattern, reach 4 exhibited the largest loss of seagrass in 2011, over 8,000 ha. In contrast to this pattern, the extent of seagrass in reach 3 decreased in 2011 and remained low through 2019, and the extent of seagrass in reaches 1, 8, and 9 remained relatively stable until a decrease in 2017.

Additional evidence of changes in areal extent came from evaluating the distance to the EOC for each transect, which was measured during every sampling event. At the scale of the lagoon, hectares of seagrass in maps and mean distances to the EOC were highly correlated, which provided confidence in using changes in these distances as proxies for changes in the areal extent of seagrass between maps (Figure 2). Mean distances to the EOC increased in parallel to areal extents from 1994 through 2010. They also declined beginning in 2011 and continued to decline in 2012. There were slight increases in distances to the EOC from 2013 to 2015; however, those gains were lost again in 2016 and mean distances to the EOCs remained around 60 m through 2019.

Along with decreases in distances to the EOC across all reaches, the EOCs moved into shallower water at different times according to a significant PERMANOVA examining depths at the EOC for combinations of years and
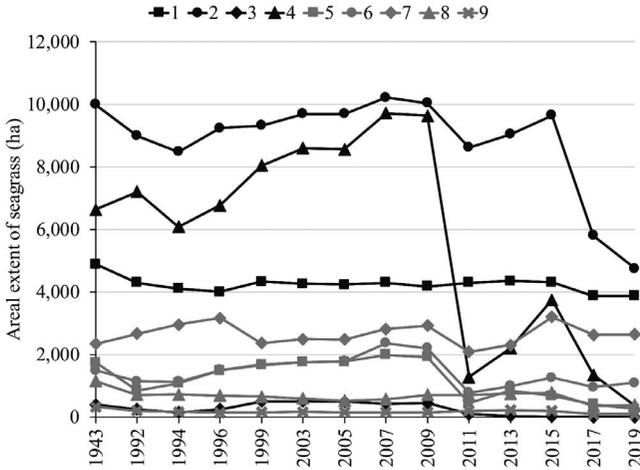
Figure 4. Mean areal extents of seagrass in nine reaches versus years when maps were made. black squares = reach 1, black circles = reach 2, black diamonds = reach 3, black triangles = reach 4, grey squares = reach 5, grey circles = reach 6, grey diamonds = reach 7, grey triangles = reach 8, grey Xs = reach 9

reaches ($F_{150;1,448} = 7.99$, p < 0.001; Figure 5). The EOCs in all reaches were deepest in 2006, 2007, or 2009, with the ends being 0.1–0.7 m shallower in 2008. In reaches 3, 4, 5, and 6, the EOCs became 0.4–0.7 m shallower in either 2011 or 2012, whereas the EOCs in reaches 1 and 2 did not change as much at that time. The EOCs in all six reaches extended further offshore and 0.2–0.6 m deeper in
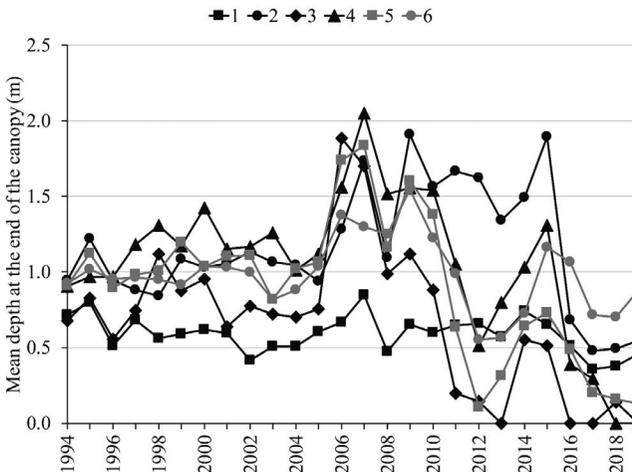

Figure 5. Mean depths at the deep ends of canopies in six reaches versus years when surveys were conducted. black squares = reach 1, black circles = reach 2, black diamonds = reach 3, black triangles = reach 4, grey squares = reach 5, grey circles = reach 6
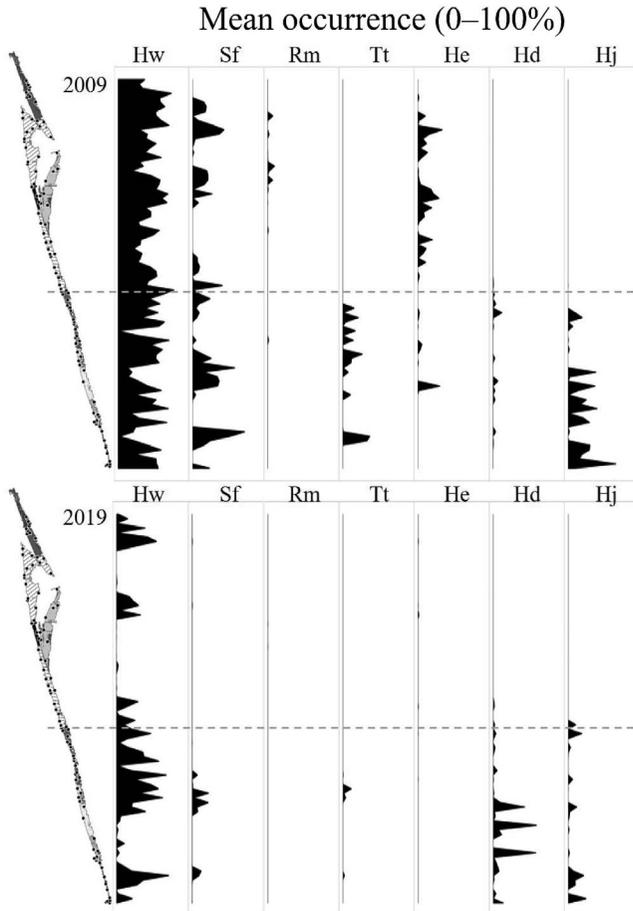
Figure 6. Latitudinal patterns of mean percent occurrence for seven species of seagrass in a year with extensive seagrass (2009) and a year with reduced seagrass (2019). black circles = transects surveyed to yield mean percent occurrences, dashed line marks the boundary between temperate and subtropical waters near Sebastian Inlet, Hw = *Halodule wrightii*, Sf = *Syringodium filiforme*, Tt = *Thalassia testudinum*, Rm = *Ruppia maritima*, He = *Halophila engelmannii*, Hj = *Halophila johnsonii*, Hd = *Halophila decipiens*

2013–2015, moved nearer the shore and 0.4–1.5 m shallower by 2016–2017, and remained at similar distances offshore and depths in 2018–2019.

In addition to changes in areal extent and depths, measures of percent occurrence in quadrats surveyed along transects revealed that the seven species of seagrasses were not distributed uniformly from north to south, with the distributions in 2009 and 2019 presented as examples of these results (Figure 6). In 2009 and earlier years, Hw and Sf were the most widespread and dominant species, although Rm and He sometimes expanded their typical distribution south of reach 7. The species with tropical distributions, Tt, Hd, and Hj, were found south of Sebastian
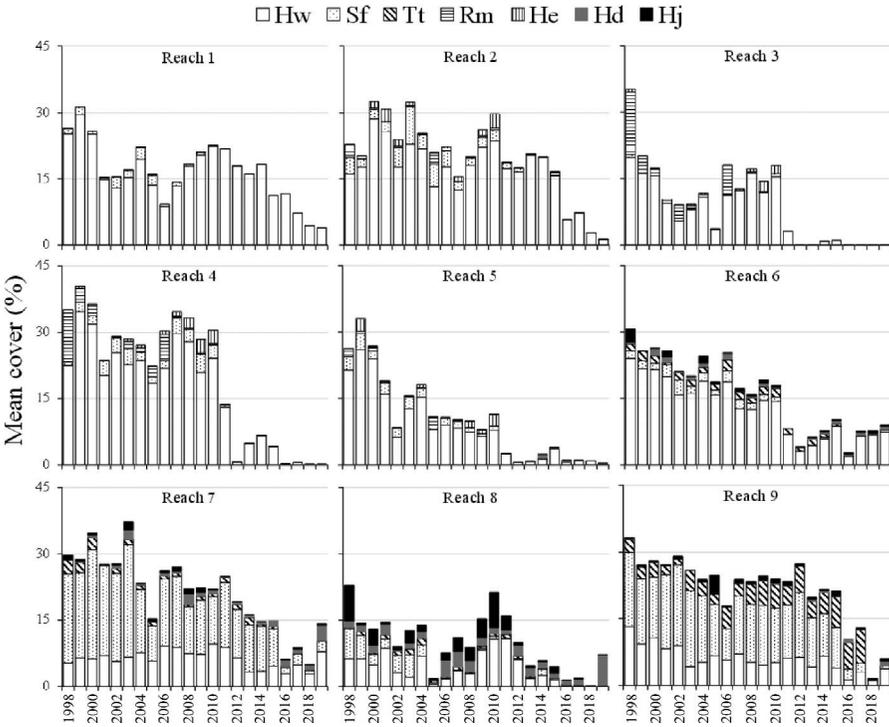
Figure 7. Mean percent cover of seven species of seagrass in nines reaches versus years when surveys were conducted. Hw = *Halodule wrightii*, Sf = *Syringodium filiforme*, Tt = *Thalassia testudinum*, Rm = *Ruppia maritima*, He = *Halophila engelmannii*, Hj = *Halophila johnsonii*, Hd = *Halophila decipiens*

Inlet in 2009 and other years. In terms of species richness, reaches 1–5 had up to four species, i.e., Hw, Sf, Rm, and He. South of Sebastian Inlet, all seven species were recorded in reaches 6 and 7, and five species typically were recorded in reaches 8 and 9 due to the scarcity of Rm and He. After 2011, species richness decreased (Figure 6). By 2019, Hw occurred in fewer reaches and was almost completely absent from reaches 3 and 4. In addition, Sf was lost in reaches 1–6 and only remained near the inlets in reaches 7 and 8. *Ruppia maritima* and He essentially disappeared, and Tt was present only near Fort Pierce Inlet. In contrast, Hd and Hj exhibited sporadic losses and gains across the range they had occupied in 2009, which emphasized their ephemeral nature. Interestingly, Hd and Hj extended northward into reach 5 in 2019, which was last documented in 2007 (Virnstein and Hall 2009).

Within transects, the mean percent cover for each of the seven species of seagrass varied significantly among combinations of years and reaches according to a significant PERMANOVA ($F_{1,323;9,856} = 3.38$, $p = 0.010$; Figure 7). In reaches 3–6, mean percent cover of most species decreased in 2011 or 2012 and remained relatively low thereafter. In the other reaches, i.e., 1, 2, 7, 8, and 9, mean percent cover remained relatively low after decreases in 2016 or 2017. In terms of patterns
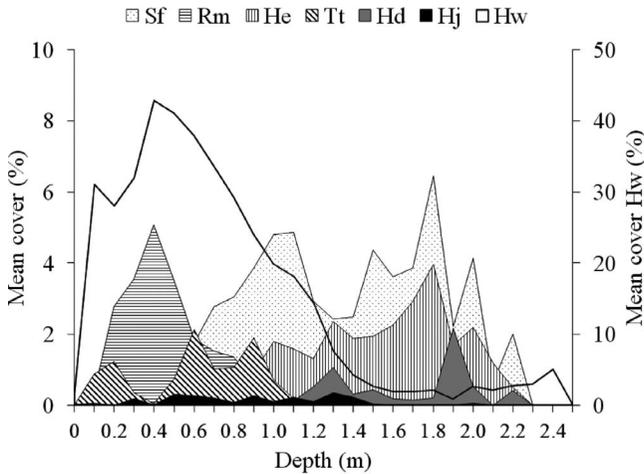
Figure 8. Mean percent cover for seven species of seagrass in six reaches calculated from surveys during 1998–2010 versus depths corrected to depth below mean low water. Sf = *Syringodium filiforme*, Rm = *Ruppia maritima*, He = *Halophila engelmannii*, Tt = *Thalassia testudinum*, Hd = *Halophila decipiens*, Hj = *Halophila johnsonii*, Hw = *Halodule wrightii* shown as the black line with cover on the righthand axis

for species, Hw remained the most abundant and widespread seagrass, having appeared along every transect at least once, averaging approximately 20% cover across all transects, and reaching 35% cover in some years. In the northern reaches (1–6), other species exhibited some interesting patterns. The next most abundant seagrasses were Sf and Rm, with mean percent covers as high as 25% and 14%, respectively, and higher mean percent covers in different years, such as between 2004 and 2008. Furthermore, percent cover of He increased from 2008–2010 in reaches 2–5. In reaches 7 and 9, Sf had higher percent cover than Hw, Tt, He, Hj and Hd through 2015, with a decrease in mean percent cover in 2005 following landfalls of two hurricanes south of Fort Pierce in 2004. Six species were recorded in reach 8 at mean percent covers less than 12%. Cover for all species fell below 3% in 2015–2018, with Hd rebounding to 8% cover in 2019.

In addition to latitudinal variation, each species tended to be found at certain depths, although vacant patches at any depth typically were colonized by smaller species (Figure 8). In waters of < 1 m, Hw had a mean percent cover that was ≥ 5× that of the other 6 species, and mean cover of Tt and Rm reached 2% and 5%, respectively. From 1–2 m, Sf and He attained mean percent covers of 4–7%. At depths > 1 m, Hd achieved ∼3% cover near the inlets in reaches 5–6. At depths > 1.8 m, Hw and He were recorded in the northern IRL and Hd was paired with either Hw or Sf further south.

The depths at which the mean percent cover of each species of seagrass remained relatively high across all years in all reaches were consistent (Table 1). Key depth zones ranged from 0.1 m to either 0.9 m or deeper. Given these results, 0.9 m was used as the target depth when analyzing changes in light availability

Table 1. Depths with stable percent cover of seagrasses from 1998 to 2010.

Species	Start depth (m)	End depth (m)
Halodule wrightii	0.1	< 1.0
Syringodium filiforme	0.4	< 0.9
Thalassia testudinum	0.1	> 1.0
Ruppia maritima	0.1	< 0.9
Halophila engelmannii	0.6	> 1.0
Halophila decipiens	0.9	> 1.0
Halophila johnsonii	0.1	> 1.0

because it captured conditions at the deeper and more vulnerable portion of the bed, and it included the depth ranges for three of the four species that form canopies.

Patterns in mean percent cover related to salinity, temperature, and percent of incident light at 0.9 m were elucidated by boundary analyses using data from all nine reaches, which improved estimates of limits for the species primarily found in the southern lagoon (Table 2). For salinity, the limits with statistically significant consistency ranged from 18 to 35 psu. For temperature, the limits ranged from 18 °C to 30 °C. For light available at 0.9 m, six species exhibited significant lower limits, Hj was nearly significant, and He exhibited a significant upper limit. The lower limits varied from 18% of incident light to 38% of incident light, and the upper limit was 53% of incident light. These limits reflected physiological tolerances to salinity, temperature, and light availability, but they also reflected responses to combinations of these factors and the results of intraspecific and

Table 2. Results of boundary analyses to identify lower and upper limits for environmental conditions where percent cover of seagrasses was higher during 1998–2010.

	Parameter limit (p-value for t-test)					
	Salinity (psu)		Temperature (°C)		Incident light at 0.9 m (%)	
Species	Lo	Hi	Lo	Hi	Lo	Hi
Halodule wrightii	18 (0.323)	NA	20 (< 0.001)	NA	18 (0.020)	NA
Syringodium filiforme	28 (< 0.001)	NA	20 (< 0.001)	NA	38 (< 0.001)	NA
Thalassia testudinum	24 (< 0.001)	NA	19 (< 0.001)	NA	25 (0.030)	NA
Ruppia maritima	NA (NA)	18 (0.006)	20 (< 0.001)	29 (< 0.001)	33 (< 0.001)	NA
Halophila engelmannii	20 (< 0.001)	35 (< 0.001)	19 (< 0.001)	29 (< 0.001)	28 (0.002)	53 (0.001)
Halophila johnsonii	19 (< 0.001)	35 (0.070)	18 (< 0.001)	NA	23 (0.058)	NA
Halophila decipiens	26 (< 0.001)	35 (< 0.001)	20 (< 0.001)	30 (< 0.001)	24 (0.029)	NA

NA = not applicable

interspecific interactions. In addition, the limits were estimated without explicit consideration of interactions or delayed effects, and the data on seagrasses were collected twice per year. Thus, the benefit of matching mean percent cover and water quality conditions lay mainly in exploring influences generating larger changes in cover for abundant species in reaches 1–6 where monthly water quality data were available.

Four key patterns in mean percent cover were identified, and influential relationships were explored using species-specific limits (Table 2) and documented salinities, temperatures, and light regimes. From 2010 onward in reaches 1–6, the mean percent cover of Hw decreased. A combination of light availability and temperature may have affected this change because there were periods of 3–6 months when these parameters exceeded the lower limit estimated for Hw. Starting in 2016, mean percent cover decreased for essentially all species in reaches 1–6. Salinities were within the estimated limits for all but Rm, temperatures were below the lower limit for only 1–2 months (i.e., during the winter), and light availability fell below the lower limits for all species for 6–12 months. Thus, a degraded light regime was the most likely influence on percent cover. In contrast to these widespread patterns, individual species exhibited their own patterns. For example, mean percent cover of Rm in reach 3 was relatively high during 1998 and 2005–2007. During those times, salinities seldom rose above the estimated limit of 18 psu, and temperatures and light availability were above the relevant limits for Rm for $\geq$ 9 months. Lastly, mean percent cover of He in reaches 2–5 rose in 2009–2010. Antecedent salinities were generally between the high and low limits, with low salinities for up to 8 months in reaches 4–5 and high salinities for 3–5 months in reach 2. Temperatures exceeded the estimated high and low limits for $\leq$ 4 months in all reaches, light availability was below the lower limit for $\leq$ 2 months across all reaches, and light availability was above the upper limit for up to 4 months in reaches 2 and 3 and up to 7 months in reach 4. It appeared that high light did not inhibit He, which suggested that the upper limit may have been related to interactions with other species that become dominant when light is available.

Discussion

Over two decades of data from mapping and surveying fixed transects yielded valuable insights into the distribution and abundance of seven species of seagrass in the IRL. Firstly, the seven species exhibited consistent spatial patterns along gradients of latitude and depth. Secondly, evaluation of those patterns in conjunction with data on water quality identified limits related to salinity, temperature, and availability of light. Thirdly, the resulting limits yielded insights into major influences on the areal extent, distance to the EOC, and percent cover of the seven species of seagrass.

In terms of spatial patterns, five of the seven species of seagrasses in the IRL were at the northern limit of their distributions, with Hw and Rm extending as far as North Carolina and Nova Scotia, respectively (den Hartog 1970). Prior to 2011, data indicated that the latitudinal distribution of the seven species had not changed since 1976, and Tt, Hd, and Hj still were found predominantly south of Sebastian

Inlet (Thompson 1978). In addition to confirming differences along the lagoon, the data also confirmed differences in the composition of beds along depth gradients. Prior to 2011, Hw was found across the widest range of depths, Sf and Tt were mixed with Hw at intermediate depths, Sf became more prevalent at depths ≥ 1 m, Rm was more prevalent in shallower water, He and Hd were found in deeper water although He was found in mixed beds, and Hj typically grew in either shallow or deep water (Phillips 1960, Eiseman 1974, Eiseman and McMillan 1980, Kenworthy 1992, Virnstein et al. 2009).

Distributions of seagrasses across latitudes and depths were controlled, in part, by species-specific, physiological responses to a combination of environmental conditions, including salinity, temperature, and availability of light (Duarte 1995, Kenworthy and Fonseca 1996, Fourqurean et al. 2003, Steward et al. 2005, Fredley et al. 2019). The results of this study confirmed previous work that documented species-specific responses to variation in environmental conditions (Choice et al. 2014). In fact, the limits estimated by boundary analyses fell within previously reported ranges, even though these limits were based on a combination of physiological tolerances and intraspecific and interspecific interactions. For example, latitudinal distributions of species were influenced by temperature, with Tt, Hd, and Hj found in the warmer waters south of Sebastian Inlet (Thompson 1978). Distributions among reaches also were influenced by salinities, because reaches differ in the amount of fresh water and oceanic water they receive via tributaries, canals, and inlets. In fact, Hw, the most widely distributed seagrass in the IRL, has been shown to tolerate 5–80 psu (Phillips 1960, Montague and Ley 1993, Lirman and Cropper 2003), whereas Tt and Sf, which occupied the reaches affected by inlets, have been reported to grow best in stable salinities of 20–60 psu (Zieman 1982, Lewis et al. 1985, Montague 1989, Tomasko and Hall 1999, Irlandi et al. 2002). Distributions among reaches were less likely to be influenced by light availability, but this parameter strongly influenced distributions along depth gradients. For example, studies conducted elsewhere showed that Hw, the seagrass that grew across the depth gradient in the IRL, only required 10–20% of incident light to maintain a positive net carbon budget (Fourqurean and Zieman 1991, Kenworthy and Haunert 1991), whereas Tt that grew in water < 1 m deep required 22–23% of incident light to support growth and maintenance (Dixon and Leverone 1995).

Beyond influencing the long-term distribution and abundance of the seven species among reaches, salinity, temperature, and light availability also affected responses to variations in water quality through time. Most notably, decreases in the distribution and abundance of multiple species of seagrass in the northern reaches of the IRL followed reduced light availability at depth during an unprecedented bloom of phytoplankton in 2010–2011, with seagrasses recovering slightly in 2013–2015 and those gains erased following more shading by blooms of phytoplankton in 2016 and 2017–2018. In addition, suitable salinities, temperatures, and light availability influenced increases in the abundance of Rm in 1998 and 2005–2007 and He in 2009–2010. In the past, salinity also influenced the distribution and abundance of seagrasses in Banana River Lagoon

between 1994 and 1995, with a decline in Sf and an increase in Rm associated with heavy rainfall and persistently low salinity (Provancha and Scheidt 2000, Hanisak 2002). Furthermore, rainfall from hurricanes in 2004 and 2005 led to a 50% loss of Hw and an increase of Rm in the northern IRL (Steward et al. 2006), and decreased light availability and lowered salinities following storms led to losses of Sf in the southern IRL (Buzzelli et al. 2012). The influence of light also was confirmed by estimates that showed the median percent of incident light needed to support healthy seagrass at the deepest EOC recorded in the IRL was 33%, with a minimum of 20% of incident light required for maintenance (Steward et al. 2005).

Overall, the loss of thousands of hectares of seagrass and the reduction in species richness in multiple reaches raised concerns for the future of the IRL. For example, less seagrass has been shown to lead to conditions unfavorable for recovery due to increased turbidity and decreased light availability arising from resuspension of particles, with inorganic, suspended solids accounting for up to 80% of the attenuation of submarine light (McPherson and Miller 1994, Gallegos and Kenworthy 1996, Christian and Sheng 2003). Furthermore, the scarcity of ephemeral, fast-growing species of seagrass in the northern IRL engendered concerns about recovery based on dispersal and colonization by these species with a subsequent transition to seagrass beds that characterized the lagoon before 2011. In fact, the widespread losses led to an interest in rehabilitation via planting and a recognition that such projects must consider the composition of the resulting assemblage at spatial scales that range from meters to hectares if the result is to be resilient (Virnstein 1995). Perhaps, the key messages derived from recent events is that a hectare of seagrass in the IRL today lacks the species richness and percent cover that it had prior to 2011 and recovering those characteristics will be challenging.

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