



# Status and Trajectories of Soft-Bottom Benthic Communities of the South Florida Seascape Revealed by 25 Years of Seagrass and Water Quality Monitoring

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## Abstract

Although seagrass ecosystems are valued for the services they provide, anthropogenic impacts have led to global declines in seagrass area. South Florida harbors one of the most extensive and iconic seagrass landscapes in the world, but historic seagrass losses appeared to threaten their integrity. The establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1995 created a benthic community and water quality monitoring network to aid management efforts. With this study, we report on the status and trajectories of benthic communities in South Florida using 25 years of monitoring data. Overall, most of our permanent monitoring sites maintained stable benthic communities over the period of observation. However, for areas that did experience decline, we identified mechanisms for loss of the climax seagrass *Thalassia testudinum* in the FKNMS with no or only partial recovery over decadal timescales. We observed a shift towards fast-growing *Halodule wrightii* meadows at anthropogenically nutrient-enriched nearshore sites along the Florida Keys. In addition, we describe almost complete loss of seagrass meadows at some exposed, back-reef sites offshore from the Florida Keys resulting from physical disturbance by major hurricanes. This study demonstrates the utility of long-term monitoring programs for the identification of benthic community trajectories and their putative drivers on the seascape scale, offering valuable lessons for the design of future seagrass monitoring programs.

**Keywords** Seagrass · Monitoring · Disturbance · Hurricane · Nutrient enrichment · Calcareous green algae

## Introduction

Globally, seagrass ecosystems have been in decline since at least the early twentieth century. The current extent of seagrasses is at most 80% of historical values, and seagrass losses continue at rates of up to 2% year<sup>-1</sup> in most bioregions (Dunic et al. 2021). Seagrass losses have been primarily driven by anthropogenic deterioration of water quality

resulting in increased turbidity and nutrient pollution, as well as destructive demersal fishing practices and coastal urbanization (Turschwell et al. 2021). Seagrasses require relatively high light to thrive, so they are very sensitive to decreases in water clarity (Duarte 1995), which is often caused by eutrophication and poor management of runoff from urban and agricultural watersheds (Short and Wyllie-Echeverria 1996). Seagrasses provide many ecological goods and services, including (1) provisioning ecosystems and human populations; (2) providing habitat for commercially, ecologically important, and endangered species; (3) regulating water quality; and (4) protecting human environments from erosion and storm damage, making them among the most valued and valuable of earth's ecosystems (Costanza et al. 1997, 2017).

South Florida harbors one of the most extensive and iconic seagrass landscapes in the world, centered around the Florida Keys, but historic seagrass losses appeared to threaten their integrity (Kruczynski and Fletcher 2012).

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The Florida Keys are a chain of small islands stretching ca. 150 km along a northeast to southwest line extending from the southern tip of the Florida Peninsula, surrounded by seagrass meadows, and lined with a coral reef to their seaward side. Archeological evidence suggests humans first colonized the Florida Keys about 1000 BCE (Kruczynski and Fletcher 2012). These Native American people were hunter-gatherers who derived much of their resources from the sea, but Europeans replaced them in the eighteenth century through settlement and warfare. By the late 1800s, Key West had become the largest and richest city in the new State of Florida, with a population of about 18,000. The construction of the overseas railroad and overseas highway in the early twentieth century sets the stage for more rapid population growth, which accelerated after World War II when aggressive development of waterfront residential property was accomplished through the construction of hundreds of residential canals. By 1970, the population had grown to over 52,000 residents plus a substantial transient population of visitors, and the toll that this rapid development was taking on the once-clear tropical waters of the Keys was becoming apparent.

The State of Florida stopped the construction of new residential canal systems in the Florida Keys in 1970 because of water quality concerns (Kruczynski 1999). In 1987, an unprecedented die-off of seagrasses began in Florida Bay to the north of the Keys that affected over 23,000 ha of dense turtle grass (*Thalassia testudinum*) meadows (Robblee et al. 1991). Subsequent to the initial die-off, the area experienced a decade of decreased water quality and phytoplankton blooms (Fourqurean and Robblee 1999; Hall et al. 1999, 2021). Concerns about water quality in the region prompted the designation of the Florida Keys National Marine Sanctuary (FKNMS) by the US Congress (US Public Law 101-605) in 1990. This law directed the creation of a comprehensive water quality monitoring program to “(i) determine the sources of pollution causing or contributing to existing or anticipated pollution problems in the Sanctuary, (ii) evaluate the effectiveness of efforts to reduce or eliminate those sources of pollution, and (iii) evaluate progress towards achieving and maintaining water quality standards and towards protecting and restoring the coral reefs and other living marine resources of the Sanctuary.”

Until the turn of the twenty-first century, almost all sewage produced in the Florida Keys was disposed of in ineffective, shallow onsite sewage disposal systems (cesspits, septic tanks or shallow injection wells), and nutrients, toxins, and fecal contaminants discarded this way migrated from the subsurface to the ocean (reviewed in Kruczynski 1999). Continued deterioration of nearshore water quality in

the Florida Keys led to the 1999 legislation by the State of Florida (House Bill No. 1993) mandating the replacement of these onsite sewage disposal systems with regional sewage collection systems and centralized treatment and disposal of effluent. This conversion was begun in 2000 and was substantially completed in 2017.

In response to the creation of the FKNMS, a Water Quality Protection Program was established in 1995 in order to measure water quality directly (Boyer and Jones 2002), as well as the impacts that water quality has on the important seagrass (Fourqurean et al. 2002; Fourqurean and Rutten 2003) and coral reef (Porter et al. 2002) habitats of the Sanctuary. An important goal of monitoring is to generate signals useful to managers for taking action to avert unwanted impacts. Monitoring programs that only report on the spatial extent of a habitat may not provide the information necessary to understand the drivers of change and therefore to inform management action to alter the trajectory of the status and health of the ecosystem.

For seagrass ecosystems, species composition, tissue elemental stoichiometry, stable isotope composition, and shoot morphology have all been identified as indicators linked to known stressors (Fourqurean et al. 2019; Fourqurean and Rutten 2003). Specifically, when nutrient availability increases, (1) the species composition of seagrass meadows shifts to faster-growing taxa; (2) seagrass plant morphology changes as individual shoots get wider and longer; (3) internal concentrations of important elements like N and P increase and the stoichiometry of the elemental content of seagrass leaves approaches a species-specific “Redfield Ratio”; and (4) the abundance of  $^{13}\text{C}$  relative to  $^{12}\text{C}$  (expressed as  $\delta^{13}\text{C}$ ) decreases as plants become light-limited. Further, as nutrient sources can have distinct abundance of  $^{15}\text{N}$  relative to  $^{14}\text{N}$  (expressed as  $\delta^{15}\text{N}$ ), changes in  $\delta^{15}\text{N}$  can also indicate changes in the importance of different nutrient sources for the seagrasses.

Because anthropogenic impacts on coastal oceans threaten valuable seagrass ecosystems globally (Turschwell et al. 2021), monitoring programs are needed to assess the status and trajectories of seagrass meadows and to facilitate their management (Duffy et al. 2019). With this study, we take advantage of 25 years of benthic monitoring data from South Florida to detect habitat change and evaluate anthropogenic and other drivers of seagrass meadow trajectories. Here, we characterize the benthic communities present in the South Florida seascape and examine their long-term changes over the 25-year period from 1995 to 2020. We explore whether spatial or qualitative patterns of benthic community changes exist and identify water quality metrics and benthic community parameters that predict seagrass condition to attribute the driving forces behind observed changes.

## Methods

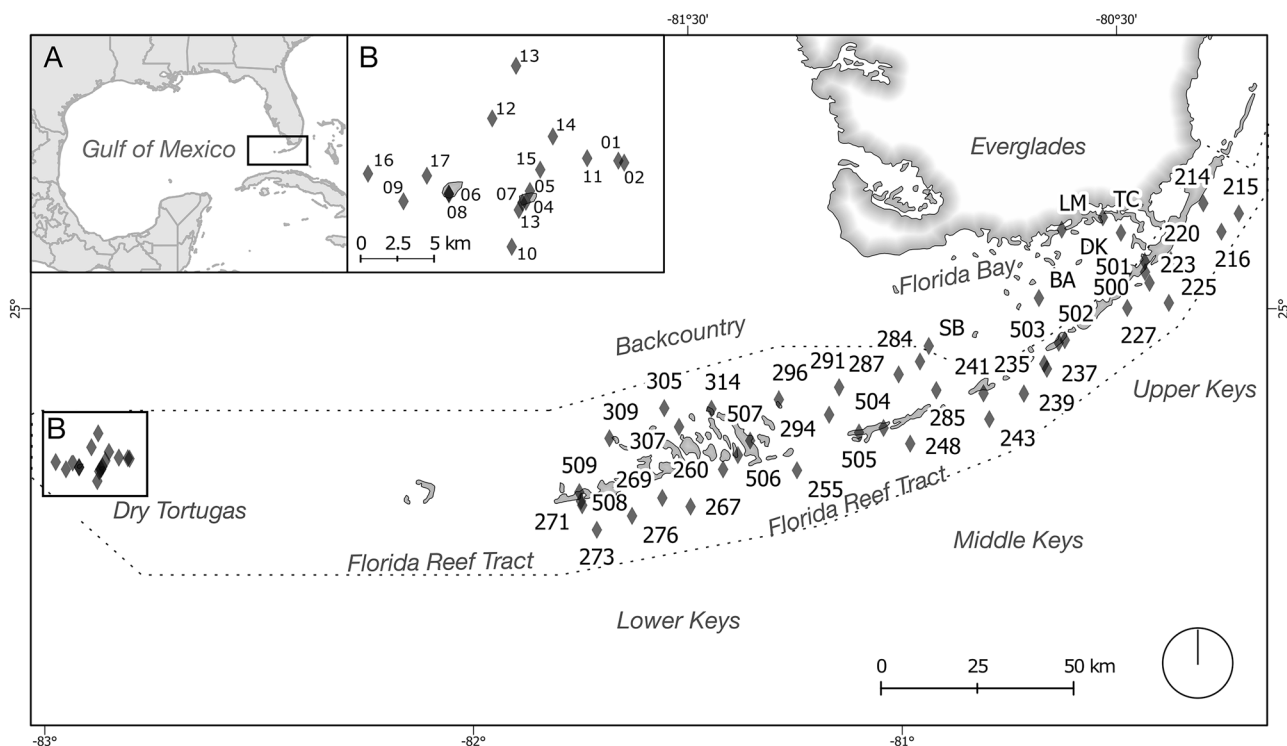
### Site Selection

Thirty sites within the FKNMS were originally established in 1995 using a stratified-random approach, with two random locations being chosen within three strata (inshore, offshore, and intermediate) in each of the defined segments of the Sanctuary (Fourqurean et al. 2001; Klein and Orlando 1994) to be monitored for water quality and benthic community composition (Fig. 1). Five more sites were established in Florida Bay in 2000 as part of the Florida Coastal Everglades Long-term Ecological Research (LTER) Program (<https://fcelter.fiu.edu>). An additional 17 sites were established in the Dry Tortugas National Park in 2011. In 2012, ten additional nearshore sites were added to the program by choosing five pairs of monitoring sites within 500 m of shoreline, one north of the Florida Keys chain of islands and one south, from sites that had already been monitored for water quality since 1995 (Boyer and Jones 2002). These pairs of stations were distributed quasi-evenly along the extent of the Florida Keys (Fig. 1). Note that our benthic monitoring sites in the FKNMS were a subset of a larger network of water quality monitoring sites (Boyer and Jones 2002).

Data on ambient water quality and seagrass community characteristics were routinely collected from each site. Benthic community species composition and relative abundance of conspicuous sessile organisms and the elemental and isotopic composition of seagrasses at the FKNMS permanent sites were collected four times per year during the period December 1995–January 2011 and two times per year (winter/summer) from 2011. LTER sites in Florida Bay were sampled roughly six times per year beginning in September 2000. Sites in Dry Tortugas National Park were sampled annually in the summer beginning in 2011.

### Water Quality Sampling

Beginning in 1995, water quality samples were also collected quarterly at all the seagrass monitoring sites within the FKNMS and 6 times per year at the LTER sites (Boyer and Jones 2002; Briceño et al. 2013). At the Dry Tortugas, water quality was only sampled in the vicinity of three sites close to the park boundary. Sample analyses included field measurements of surface and bottom salinity, temperature, dissolved oxygen (DO), water clarity ( $k_d$ ), and turbidity. Unfiltered surface water samples (10–50 cm depth) were analyzed for total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and chlorophyll *a* (CHL*a*).



**Fig. 1** Permanent monitoring sites in the Florida Keys National Marine Sanctuary (dashed line), Florida Bay, and the Dry Tortugas (diamonds), labeled with site identifiers. Inset panels show **A** the regional context and **B** a larger scale map of the monitoring sites in Dry Tortugas National Park

Additionally, filtered surface water samples were analyzed for dissolved nutrients, including nitrate + nitrite ( $\text{NO}_x^-$ ), nitrite ( $\text{NO}_2^-$ ), ammonium ( $\text{NH}_4^+$ ), soluble reactive phosphate (SRP), and silica ( $\text{SiO}_2$ ). Some parameters were not measured directly but were calculated by difference. Nitrate ( $\text{NO}_3^-$ ) was calculated as  $\text{NO}_x^- - \text{NO}_2^-$ , and dissolved inorganic nitrogen (DIN) was calculated as  $\text{NO}_x^- + \text{NH}_4^+$ . Details of sampling methodology and laboratory analysis have been described elsewhere (Boyer and Jones 2002). Data were downloaded from Florida International University's water quality monitoring database (<http://serc.fiu.edu/wqmnetwork/>).

### Benthic Community Data Collection

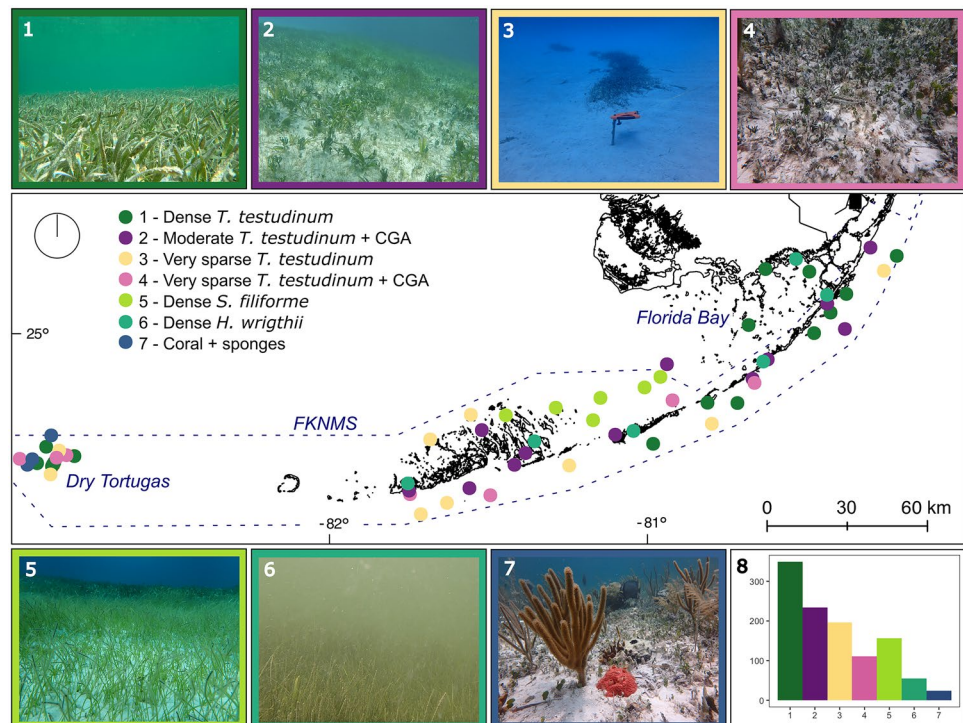
At each monitoring site, divers stretched a 50-m transect tape between two permanent site markers (located with permanent steel rods hammered into the bottom at the site). At 10 pre-determined random distances along each transect, a 0.25 m<sup>2</sup> quadrat was placed on the benthos, and all conspicuous sessile taxa (including seagrasses, macroalgae, sponges, and corals) were identified and assigned a cover-abundance score using a modified Braun-Blanquet protocol (Braun-Blanquet 1972; Kenworthy et al. 1993), with 0 = absent, 0.1 = less than 5% cover by a single individual or short shoot, 1 = < 5% cover with many individuals/shoots, 2 = > 5 to 25% cover, 3 = > 25 to 50% cover, 4 = > 50 to 75% cover, and 5 = > 75 to 100% cover. Data were summarized on each transect by calculating taxon-specific Braun-Blanquet

frequency, abundance, and density values, as described in Fourqurean et al. (2001).

During each sampling visit, seagrass samples were collected for the determination of plant morphology, elemental (C, N, and P) content, and stable isotope ratios of carbon and nitrogen. In order to provide enough biomass for chemical analyses, 7 intact short shoots of *Thalassia testudinum*, 30 short shoots of *Syringodium filiforme*, 40 short shoots of *Halodule wrightii*, and ca. 300 leaflets of any *Halophila* species were haphazardly collected from a 10 m<sup>2</sup> area near the site when the species were present. These samples were returned to the lab, and the number of leaves per short shoot, and the length of all leaves on each shoot, were measured for the three dominant seagrass species (*T. testudinum*, *S. filiforme*, and *H. wrightii*). For *T. testudinum*, leaf widths were also measured, while leaf widths of *S. filiforme* and *H. wrightii* were assumed to always be 1 mm. All attached green leaves were cut from the short shoots and cleaned of adhering epiphytes by gently scraping with a razor blade.

All leaves from a species at a site were pooled and dried at 60 °C. Dried leaves were ground to a fine powder using a motorized ball mill. Powdered samples were analyzed in duplicate for C and N content using a CHN analyzer (Fisons NA1500 or Thermo Flash EA 1112). P content was determined by a dry oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al. 1992) using Shimadzu spectrophotometers (various models). Elemental content was calculated on a dry weight basis, and elemental ratios

**Fig. 2** Map of all permanent sampling sites in the FKNMS (dashed line), Florida Bay, and the Dry Tortugas. The benthic community type at each site for the majority of years is shown by point colors. Representative pictures of community types are shown in panels 1–7. Panel 8 shows a histogram of cluster assignments to annual monitoring data ( $n = 1124$ ). All images courtesy of the FIU Seagrass Ecosystems Research Lab



were calculated on a mole:mole basis. Stable isotopes of C and N were determined using standard elemental analyzer/isotope ratio mass spectrometer (EAIRMS) procedures. The samples' isotopic ratios are reported in the standard delta notation ( $\delta$ , ‰), presented with respect to the international standards of atmospheric N (AIR, N<sub>2</sub>) and Vienna Pee Dee belemnite (V-PDB) for C. Analytical reproducibility of the reported  $\delta$  values, based on sample replicates, was better than 0.2‰ for  $\delta^{15}\text{N}$  and 0.08‰ for  $\delta^{13}\text{C}$ .

**Data Analyses**

To characterize south Florida benthic communities and identify spatiotemporal patterns of change, we used spatiotemporally explicit data to identify groups of similar benthic community composition. To this end, we performed cluster analysis of datasets containing yearly mean Braun-Blanquet density scores of seagrasses and other benthic species at each site, as well as the abiotic site characteristics depth, sediment type, and canopy height (for a total of 34 community characteristics for each site per year, Table S2). After identifying the ideal number of clusters by examining elbow

and silhouette plots as well as gap statistics (Figs. S1, S2, S3), yearly site averages were assigned to seven clusters using the “partition around medoids” clustering algorithm implemented in the R package “cluster” (Maechler et al. 2021). These clustering procedures identified seven groups of benthic community “archetypes.”

Next, we characterized each cluster by examining their associated benthic vegetation densities, seagrass tissue stoichiometry, seagrass morphology, and water quality parameters. Although Braun-Blanquet scores are inherently non-linear, they were found to produce accurate results when subjected to parametric statistical analysis (Furman et al. 2018). However, due to largely non-normal distributions of predictor variables in our dataset, we used Kruskal–Wallis tests to identify significant differences between clusters. For post-hoc analysis, we used Dunn’s test with Bonferroni adjustment of the *p* value for multiple comparisons. All variable means with standard deviations, results from multiple comparison tests, and effect sizes ( $\eta^2$ ) are listed in supplementary Table S1.

For each permanent monitoring site, a dominant cluster identity was determined as the majority cluster identity

**Table 1** Transition matrix of cluster identities

		From						
		Cluster 1 • Dense Tt	Cluster 2 • Mixed Tt + CGA	Cluster 3 • Very sparse Tt	Cluster 4 • Very sparse Tt + CGA	Cluster 5 • Dense Sf	Cluster 6 • Dense Hw	Cluster 7 • Coral + Sponges
To	Cluster 1 • Dense Tt	270	28	16	5	5	4	0
	Cluster 2 • Mixed Tt + CGA	25	165	6	17	6	0	1
	Cluster 3 • Very sparse Tt	25	2	142	12	1	0	5
	Cluster 4 • Very sparse Tt + CGA	3	22	11	71	1	0	0
	Cluster 5 • Dense Sf	5	6	2	1	134	2	0
	Cluster 6 • Dense Hw	7	0	0	0	2	40	0
	Cluster 7 • Coral + Sponges	0	1	7	0	0	0	14
Stability Index		4.2	2.8	3.4	2.0	8.9	6.7	2.3

Every year-to-year cluster change (or lack thereof) was tallied, with the top panel indicating the starting cluster. A stability index was calculated as the number of times a site maintained the same cluster identity, divided by the number of instances that a site changed to a different cluster. Higher values are indicative of more stable benthic community types, while lower values indicate frequent changes in cluster identity

Tt *T. testudinum*, Sf *S. filiforme*, Hw *H. wrightii*, CGA calcareous green algae

over all years of data collection at that site. The dominant cluster identity was mapped to identify spatial pattern in the distribution of benthic communities (Fig. 2). Furthermore, the cluster identity of each site was plotted for subsequent years, and a transition matrix was created to identify common trajectories of change and temporal variability of benthic communities at a given site (Table 1). To compare the tendency of clusters to transition or remain stable, we calculated a “Stability Index.” This metric was calculated as the number of times a site maintained the same cluster identity, divided by the number of instances that a site changed to a different cluster (Table 1). Higher values are indicative of more stable benthic community types, while lower values signal frequent changes in cluster identity.

Finally, we employed random forest modeling to predict density of the three most common seagrasses of the South Florida seascape, *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*, using the full dataset of water quality parameters, seagrass morphology, and tissue stoichiometry, as well as benthic macroalgae abundance and frequency scores. Using the R package “randomForest” (Liaw and Wiener 2002), we generated random forest regression models averaging the predictions of 1000 decision trees, with 10 randomly selected predictor variables tested at each node and trained on 70% of total data. Model performance was tested on the remaining 30% of data and reported as RMSE of predicted BB scores as well as % variance explained (% of target variance explained by out-of-bag predictions). To address the issue of missing data, we excluded all predictor variables with < 50% completeness

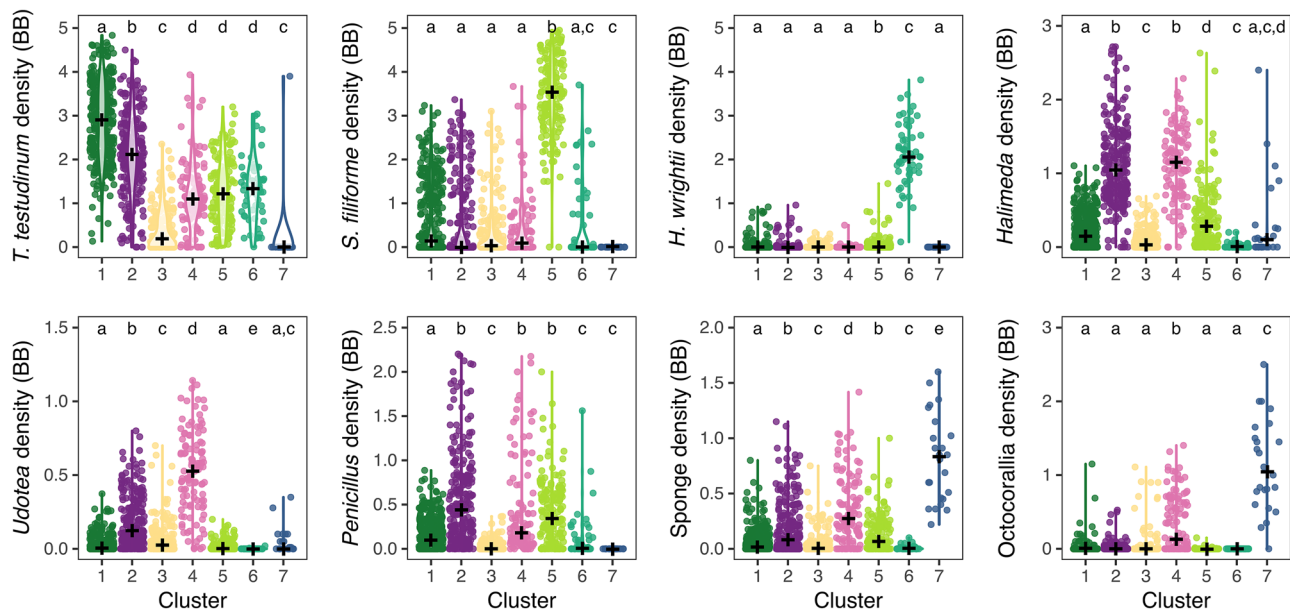
and imputed the remaining missing values using the R package missForest (Stekhoven and Buehlmann 2012). We did not perform additional pre-processing steps such as feature selection or feature engineering, because random forest methods are relatively robust towards redundancy of predictor variables since feature selection is inherent in its architecture, and because we do not aim to generate predictions outside our dataset. To identify the drivers of seagrass density, we assessed the relative importance of predictors for model performance as the average increase in squared out-of-bag residuals when the predictor variable was permuted. All data analyses were performed in the computational environment R version 4.1.1.

## Results

### Benthic Community Types

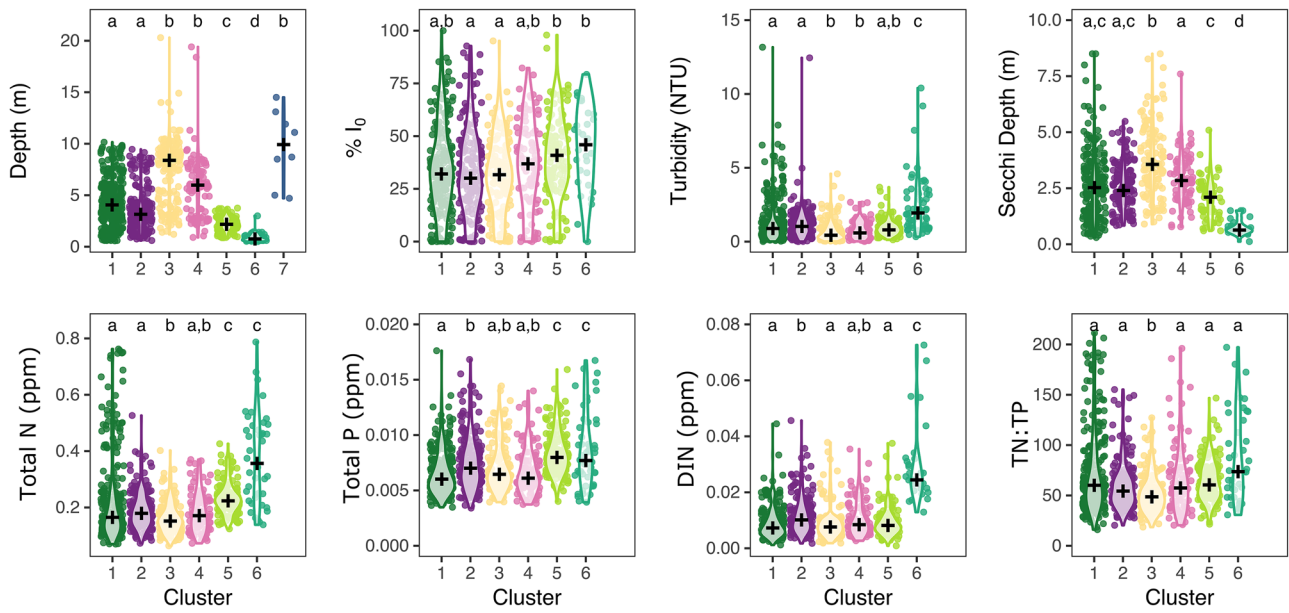
We identified seven clusters representative of distinct benthic community types (Fig. 2). By assessing water quality, community composition, seagrass tissue nutrient, and morphological data for each cluster, we characterized the benthic community types to aid interpretation of any spatiotemporal trends in cluster identity over the course of the monitoring program (Figs. 3, 4, and 5).

Cluster 1 (“Dense *T. testudinum*”) was characterized by dense *T. testudinum* cover (mean BB density score of 2.88), but sparse *S. filiforme* may occur (Fig. 3). Calcareous green algae (CGA), sponges, and coral were largely absent



**Fig. 3** Yearly mean Braun-Blanquet density scores for the seagrasses *T. testudinum*, *S. filiforme*, *H. wrightii*, and the calcareous green algae of genera *Halimeda*, *Udotea* and *Penicillus*, all sponges, and octocor-

als, by cluster. Medians (black cross) and distributions (colored violin plots) are shown. Letters indicate homogenous subsets of clusters derived from Dunn's post-hoc test

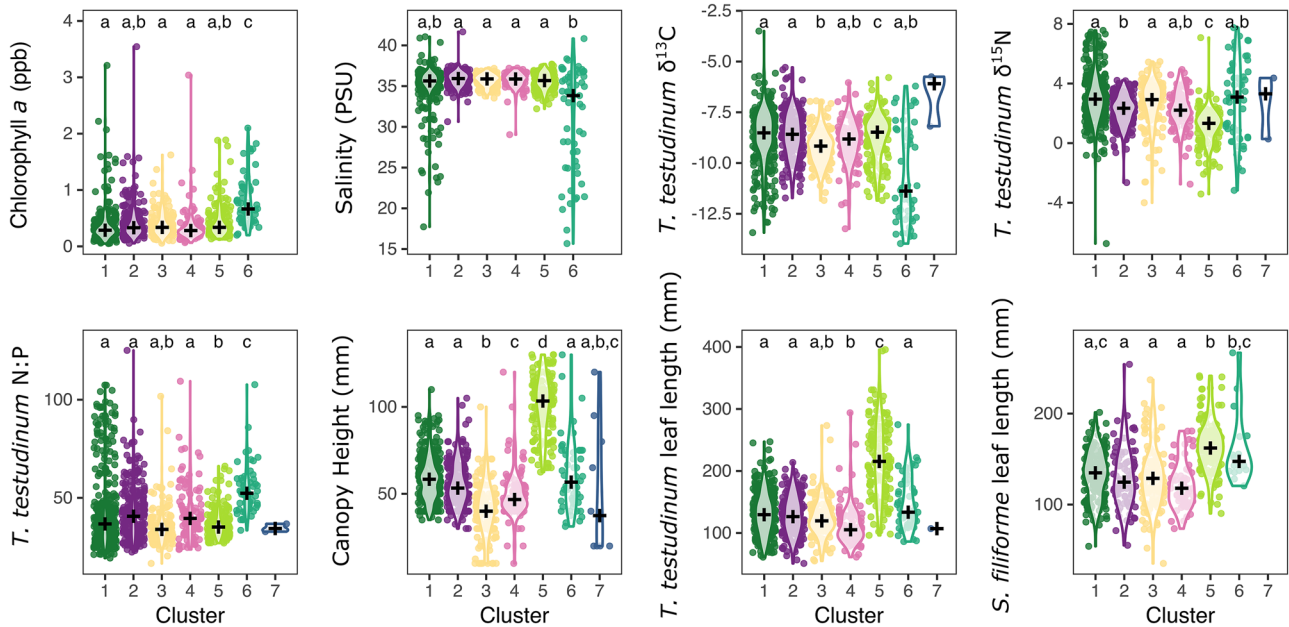


**Fig. 4** Yearly means of site depth (m), irradiance at the top of the seagrass canopy (% of surface irradiance), turbidity (NTU), Secchi depth (m), total nitrogen (ppm), total phosphorus (ppm), dissolved inorganic nitrogen (ppm), and TN:TP (molar), by cluster. Medians

(black cross) and distributions (colored violin plots) are shown. Letters indicate homogenous subsets of clusters derived from Dunn's post-hoc test

(Fig. 3). Water quality of this cluster was characterized by low CHL<sub>a</sub> levels (0.38 ppb, Fig. 5) and irradiance at the top of the seagrass canopy (34%, Fig. 4). Some cluster 1 sites experienced occasional freshwater runoff as indicated by reduced salinity at times (Fig. 5). The sediment grain

size was typically between muddy sand and sandy mud. The average depth was 4.29 m. This community type was found throughout the monitoring network, with locations on the reef side of the Upper and Middle Keys, in Florida Bay, and at the Dry Tortugas (Fig. 2).



**Fig. 5** Yearly means of water quality parameters chlorophyll a concentration (ppb) and salinity (PSU), as well as *T. testudinum* tissue stable isotope ratios (C, N), tissue C:N, seagrass canopy height (mm), *T. testudinum* leaf length (mm), and *S. filiforme* leaf length (mm), by

cluster. Medians (black cross) and distributions (colored violin plots) are shown. Letters indicate homogenous subsets of clusters derived from Dunn's post-hoc test

Cluster 2 (“Mixed *T. testudinum* + Calcareous green algae”) typically featured *T. testudinum* at moderate density (mean BB score of 2.1) and CGA of the genera *Halimeda*, *Udotea*, and *Penicillus*, among others (Fig. 3). Sparse *S. filiforme* occurred at some sites (Fig. 3). Sediment grain size was between muddy sand and sandy mud, and the average depth was 3.64 m. Turbidity and irradiance at the top of the seagrass canopy were varied, but Secchi depth did not exceed 5.5 m. *T. testudinum* tissue  $\delta^{15}\text{N}$  was never larger than 4‰ (Fig. 5). Typical sites were located close to shore from the Upper to the Lower Florida Keys (Fig. 2).

Cluster 3 (“Very sparse *T. testudinum*”) was characterized by largely absent seagrass cover; however, short (Fig. 5) and sparse *T. testudinum* and *S. filiforme* may occur (BB score of 0.39 and 0.34, respectively) (Fig. 3). Sites of this cluster also featured the lowest densities of CGA and sponges (Fig. 3). Low turbidity (0.71 NTU) and high Secchi depths (3.79 m) indicated high levels of light penetration, but the relatively large water depths (2 to 12 m, 7.25 m on average) resulted in one of the lowest irradiances of all clusters (31%, Fig. 4). CGA were typically absent (Fig. 3), and the seagrass canopy height was lower than at sites of other clusters (41 mm, Fig. 5). Typical sites were located farthest from shore in the FKNMS, with most sites in the Lower Keys (Fig. 2).

Cluster 4 (“Very sparse *T. testudinum* + Calcareous green algae”) had very sparse cover of *T. testudinum* (BB score of 1.18) but among the highest densities of CGA, sponges, and octocoral (Fig. 3). Depths ranged from 2 to 10 m. Here, the overall canopy height was low (50 mm), and *T. testudinum* leaves were particularly short (114 mm) (Fig. 4). Only four sites were assigned this community type consistently throughout the monitoring period, and they were scattered along the FKNMS, with additional sites at the Dry Tortugas (Fig. 2).

Cluster 5 (“Dense *S. filiforme*”) featured dense *S. filiforme* (BB score of 3.45) co-occurring with CGA belonging to the genera *Penicillus* and *Halimeda*, as well as sparse *T. testudinum* (1.23, Fig. 3). Here, *T. testudinum* leaves were almost twice as long compared to other clusters (217 mm), contributing to the largest canopy height of all clusters (101 mm) (Fig. 5). Water quality was characterized by higher TP (84 ppb) and TN (230 ppb) with a smaller range (Fig. 4), and the sediments were muddy. Despite their low Secchi depth (2.05 m), irradiance at the top of the seagrass canopy at these sites was typically higher compared to sites of other benthic community types (40%) (Fig. 4), likely due to their shallow position with a mean depth of 2.23 m. Here, *T. Testudinum* tissue showed the lowest  $\delta^{15}\text{N}$  (1.12‰, Fig. 5), and *S. filiforme* tissue had the highest N:P and most depleted  $\delta^{15}\text{N}$  values (data not shown). Sites typical for this cluster were all located in the backcountry, west of the Middle Keys (Fig. 2).

Cluster 6 (“Dense *H. wrightii*”) was characterized by the presence of *H. wrightii* (2.13), and sparse *T. testudinum* typically also occurred (1.3) (Fig. 3). Water quality was

characterized by the highest nutrient concentrations in form of TP (86 ppb), TN (370 ppb), and DIN (297 ppb) (Fig. 4). Water temperature was typically higher than at other clusters, and freshwater inputs could reduce the salinity considerably (Fig. 5). Sediments were mostly muddy. Sites were very shallow (average 0.88 m), and consequently, irradiance at the top of the seagrass canopy was relatively high (Fig. 4). This cluster showed the highest CHL *a* levels (0.8 ppb) and turbidity (2.52 NTU) of all clusters (Figs. 4, 5). Here, *T. testudinum* tissues were depleted in  $\delta^{13}\text{C}$  (− 10.67‰) and N:P was elevated (81, Fig. 5). These sites were located closest to shore in the Keys and in Florida Bay (Fig. 2).

Cluster 7 (“Coral + sponges”) was distinguished from the other groups by a benthic community dominated by coral and sponges instead of seagrasses or CGA (Fig. 3). It had the largest sediment grain size and an average depth of 9.69 m. The only sites of the monitoring network featuring this benthic community type were found exclusively in the Dry Tortugas (Fig. 2).

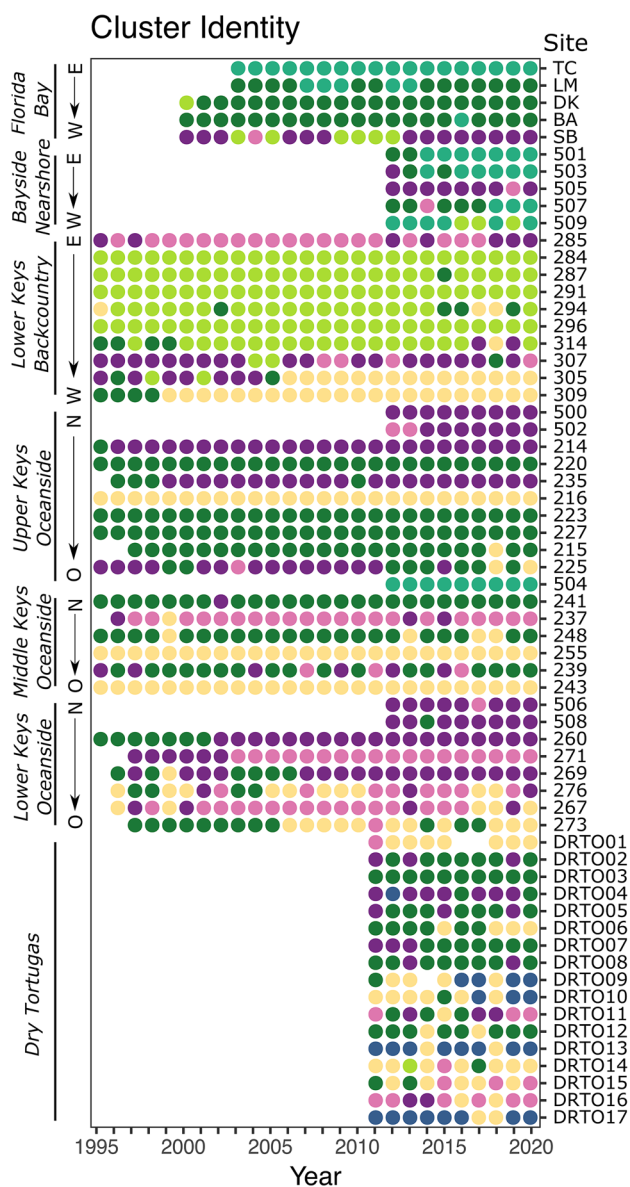
### Temporal Benthic Community Trajectories

As each combination of monitoring site and year was assigned to one of the seven clusters, long-term change in benthic community assemblage could be discerned by tracking the cluster identity of each site over time (Fig. 6). While some sites were consistently assigned to the same cluster, other sites changed cluster identity over time. Common cluster transitions were identified by use of a transition matrix (Table 1). Overall, it was most common for benthic communities at a given site to remain similar from year to year. However, if changes did occur, they followed one of several trajectories. For example, a dense *T. testudinum* meadow (cluster 1) commonly transitioned to mixed *T. testudinum* with CGA (cluster 2) and vice versa (Table 1). However, a near-total loss of *T. testudinum* (cluster 3 following an assignment of cluster 1) was observed just as frequently (Fig. 6, Table 1). The opposite direction of change, from very sparse to dense *T. testudinum* (cluster 3 to 1), did not occur as often.

When the starting benthic community was that of a mixed *T. testudinum* meadow with CGA (cluster 2), a transition to sparse *T. testudinum* and CGA (cluster 4) occurred frequently. This trajectory also represents a loss of seagrass and occurred more often over the period of monitoring compared to a *T. testudinum* density increase (cluster 4 to 2) (Table 1).

A transition of the benthic community towards *H. wrightii* dominance (cluster 6) was observed only rarely, but once this type of benthic community was established, it was unlikely to change. This is illustrated by a high “stability index” for cluster 6 (Table 1). The most stable benthic community type was the dense *S. filiforme* meadow (cluster 5), which rarely changed to a different community type. At the other extreme





**Fig. 6** Benthic community type at each permanent monitoring site over the 25-year period of monitoring. Each colored dot indicates the cluster identity for a given site and year. Sites are first sorted by region, and within region, from east (E) to west (W) or nearshore (N) to oceanside (O). Site identifiers are listed on the right. Figure 1 provides a reference for the location of each site within the monitoring network

were the very sparse *T. testudinum* + CGA communities (cluster 4), which tended not to persist over multiple years and instead transitioned to either denser *T. testudinum* (cluster 2) or a further loss of CGA (cluster 3) (Table 1).

### Predictors of Seagrass Density

We used random forest modeling to predict the density of seagrass species *T. testudinum*, *S. filiforme*, and *H. wrightii* and determined the relative importance of water quality,

seagrass morphology, tissue stoichiometry, and benthic species density metrics for model performance (Fig. 7). Overall, the machine learning method employed herein allowed for the prediction of seagrass density, explaining 52–71% of the variability in the data with root mean squared errors of 0.35 to 0.85 (BB score) (Table 2).

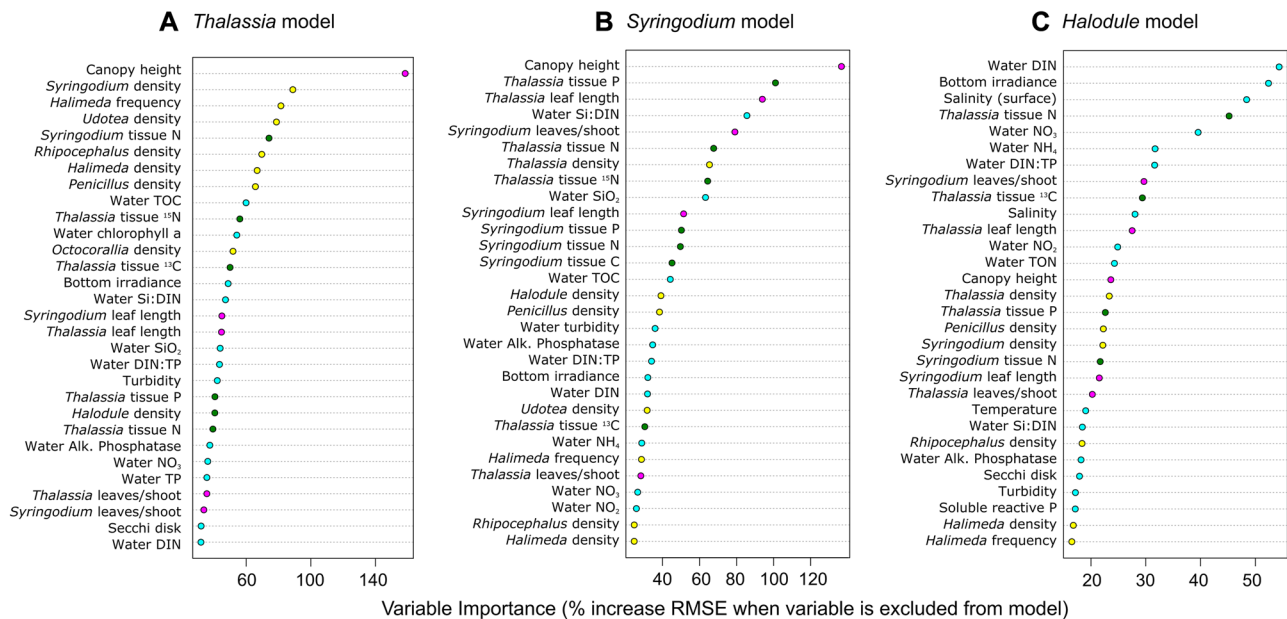
The most successful model predicted *H. wrightii* density (RMSE = 0.35, 63% var.). The best predictors of *H. wrightii* density were water quality parameters DIN, NO<sub>3</sub>, and NH<sub>4</sub>, as well as salinity and irradiance (Fig. 7). The model predicting *S. filiforme* density captured most of the variability in the data (RMSE = 0.64, 71% var.) (Table 2). Important predictors were overall canopy height and *T. testudinum* leaf length. In contrast to the other two seagrasses, *S. filiforme* density was predicted by silicate concentrations in the water (Fig. 7). Lastly, *T. testudinum* density was predicted with least accuracy (RMSE = 0.85, 52% var.) (Table 2). The most important predictors were related to the density of other benthic species, with CGA featuring prominently (Fig. 7).

### Discussion

This study synthesized data from 25 years of soft-bottom benthic community and water quality monitoring to describe the status and trends of seagrasses and other macrophytes in the South Florida seascape. The monitoring program was established in response to the perceived threat that deteriorating water quality could pose to the health of an iconic seagrass landscape and its associated ecosystem services. Although we did identify shifts in benthic community assemblages, it is notable that most sites showed remarkable stability over the entire 25-year monitoring period, despite increasing anthropogenic pressures on the system. However, we acknowledge that changes might have occurred prior to the monitoring period, and these would not be covered in this study. In the following paragraphs, we discuss instances of nutrient enrichment that led to shifts in benthic community assemblages. We further report observations of instantaneous seagrass loss from physical disturbance following the passage of major hurricanes and the associated impact to benthic communities at over 10% of our monitoring sites. We close with recommendations for future monitoring-based evaluations of benthic communities globally and provide lessons for the design of seagrass monitoring programs more broadly.

### Intra-Site Benthic Community Transitions Associated with Changes in Nutrient Availability

In the largely oligotrophic South Florida seascape, *T. testudinum* is considered the successional endpoint and dominant primary producer in climax seagrass communities (den



**Fig. 7** The most important predictor variables for each of the three random forest models. Point fill color indicates predictor variable type (blue = water quality, pink = seagrass morphology, yellow = benthic cover BB scores, dark green = seagrass tissue stoichiometry). Vari-

able importance was assessed by calculating the increase in root mean squared error of the model if a particular variable was removed from the model, all else equal

Hartog 1967). We found dense *T. testudinum* meadows to be widespread throughout the monitoring network and prevalent over the 25-year monitoring period at sites in Florida Bay, the Dry Tortugas, as well as the Upper and Middle Keys (Fig. 5). Even though this benthic community type was relatively stable in the South Florida seascape, we frequently observed transitions towards either mixed *T. testudinum* and CGA, very sparse *T. testudinum*, or less frequently to dense *H. wrightii* meadows (Table 1).

In the oligotrophic waters of the region, growth rates and therefore competitive potential of benthic primary producers are limited by the availability of light, nitrogen, or phosphorus, depending on location within the seascape (Fourqurean and Rutten 2003; Fourqurean and Zieman 2002; Ferdie and Fourqurean 2004). Macroalgae, which have higher relative growth rates than seagrasses, can outcompete slower-growing seagrasses when nutrient supply is relatively high (Davis and Fourqurean 2001). Further, increased densities of CGA are associated with areas of higher water column

concentrations of nutrients, and especially N, in the FKNMS (Collado-Vides et al. 2007). However, the simple correlation between macroalgal abundance and water column N concentration does not prove that water column N concentrations drive increases in abundance, especially at nearshore sites since they tend to be areas of severe P-limitation (Fourqurean and Zieman 2002). Rather, the rapid assimilation of any P in nutrient loadings into primary producers and biofilms in these P-limited environments strips P out of the water column (Frankovich and Fourqurean 1997), driving correlations of the residual water-column N with CGA abundances.

Nonetheless, it is clear that increased nutrient supply can favor macroalgal dominance over seagrasses. This competitive dynamic may be reflected in the transitions at some sites through time between dense *T. testudinum* and mixed *T. testudinum* and CGA meadows. We found the latter benthic community type to occur predominantly at nearshore sites (Figs. 2, 6), which receive higher overall nutrient inputs (Ferdie and Fourqurean 2004). Further, CGA densities were

**Table 2** Random Forest model characteristics for three models predicting the density of *T. testudinum*, *S. filiforme*, and *H. wrightii*

	Thalassia model	Syringodium model	Halodule model
Response	<i>T. testudinum</i> density	<i>S. filiforme</i> density	<i>H. wrightii</i> density
% var	52	71	63
RMSE (training)	0.34	0.29	0.12
RMSE (validation)	0.85	0.64	0.35

Root mean squared error of model prediction (RMSE) was computed over the training dataset (70% of data) and validation dataset (the remaining 30%)

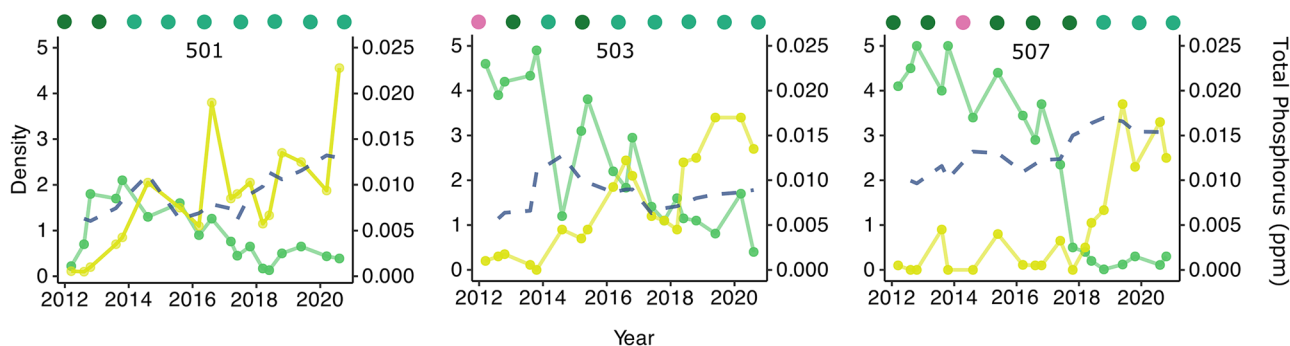
among the best predictors of *T. testudinum* density across the entire monitoring network (Fig. 7), highlighting the importance of their competitive relationship. Occasionally, CGA appear to outcompete *T. testudinum*, indicated by a collapse of seagrass densities, coinciding with the benthic community becoming dominated by CGA. This is illustrated by transitions from mixed *T. testudinum* and CGA communities to very sparse *T. testudinum* and CGA (Table 1, Fig. 6). However, this benthic community type does not typically persist over several years and frequently transitions back to a mixed community with moderate seagrass densities (Table 1, Fig. 6); this could be interpreted as interannual variation in the nutrient supply at sites that support near competitive balance between *T. testudinum* and CGA.

Previous investigations suggested that the slow-growing *T. testudinum* outcompetes normal early-successional seagrasses *H. wrightii* and *S. filiforme* in nutrient-limited conditions (Fourqurean et al. 1995). Fertilization experiments in Florida Bay demonstrate that, if nutrient limitation is lifted, normal early-successional seagrass species can dominate even decades after nutrient addition ceased (Fourqurean et al. 1995; Herbert and Fourqurean 2008, Howard et al. 2016). Therefore, changes in the dominant seagrass species at a given site can be indicative of historic nutrient loadings as well as current nutrient enrichment. Our results suggest that a replacement of dense *T. testudinum* by dense *H. wrightii* meadows has occurred in nearshore sites in the FKNMS (Fig. 6). Specifically at sites immediately abutting the shoreline, a replacement of *T. testudinum* by *H. wrightii* coincided with increases in TP concentrations in the water column (Fig. 8). We found that *H. wrightii*-dominated sites have elevated TN, TP, and DIN concentrations compared to other benthic communities (Fig. 4), and across the entire monitoring network, water DIN was the best predictor of *H. wrightii* density (Fig. 7). However, similar to our conclusions for macroalgae and water column TN above, the simple correlation between *H. wrightii* abundance and water column TN does not imply that N-loading

is driving the replacement of *T. testudinum* by *H. wrightii* in the very nearshore regions of our study area. These sites are found in areas of severe P-limitation (Fourqurean and Zieman 2002), and it is therefore likely that increased availability of P drives the observed changes in benthic community composition. Dense *H. wrightii* meadows were found in places that experience freshwater runoff (Fig. 4) and likely nutrient loading, as indicated by increased concentrations of TN and TP in the water column. These sites exhibited seagrass N:P ratios well above 30:1 (Fig. 5), indicative of P-limitation, not N-limitation (Fourqurean and Rutten 2003). At these sites, water clarity is reduced, Secchi depth is low, and turbidity as well as chlorophyll *a* concentrations are elevated relative to other sites, indicating increased productivity in the water column (Fig. 4). However, irradiance reaching the top of the seagrass canopy remains high due to the shallow depth of these sites (Fig. 4). Nevertheless, *T. testudinum* appears to be light limited, as indicated by reduced tissue  $\delta^{13}\text{C}$  (Fig. 5), which might be caused by self-shading in very dense meadows or by competition for light with *H. wrightii*. Corroborating earlier reports of nutrient enrichment promoting long-lasting changes in benthic community composition (Howard et al. 2016), we found dense *H. wrightii* meadows to persist, once established at our monitoring sites (Table 1, Fig. 6). Considering that the efforts to reduce nutrient inputs to the FKNMS by upgrading wastewater treatment were largely completed in 2017, it is concerning that several of our nearshore monitoring sites transitioned towards a nutrient-enriched, *H. wrightii*-dominated state in recent years (Fig. 8).

### Intra-Site Benthic Community Transitions Associated with Hurricane Disturbance

An alternative trajectory of dense *T. testudinum* meadows that occurs independently of competition with other macrophytes is that of catastrophic seagrass loss, where sites



**Fig. 8** Timeseries of *T. testudinum* (green) and *H. wrightii* (yellow) densities (BB score) at nearshore monitoring sites that transitioned to become *H. wrightii*-dominated. Blue, dashed lines are total phosphorus concentrations (ppm) in instantaneous water samples. Colored dots on top of each panel indicate cluster membership for each year

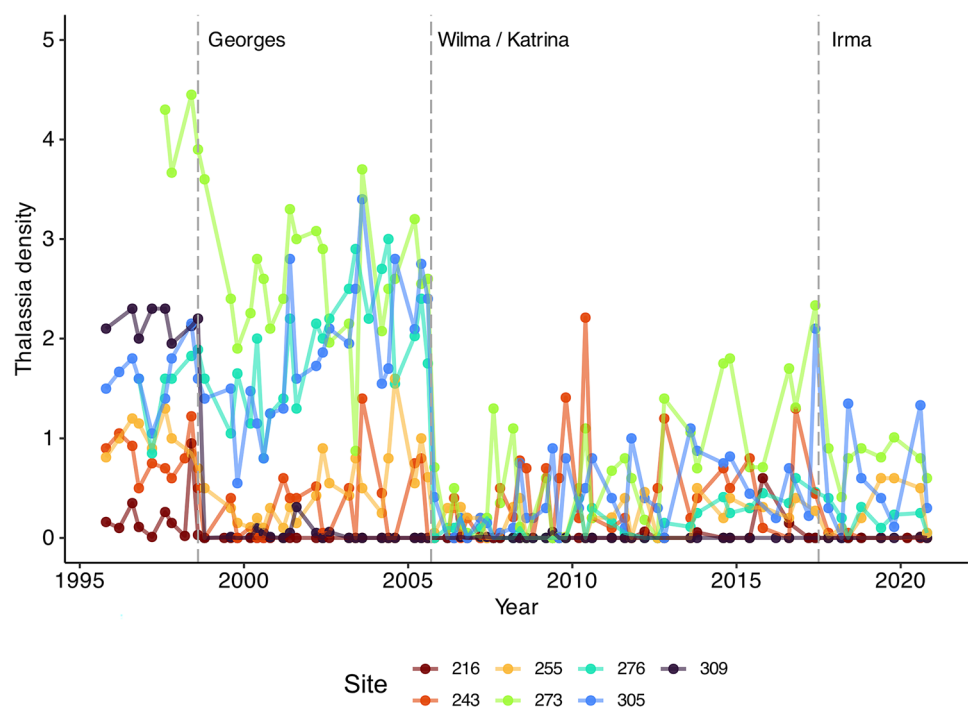
phorus concentrations (ppm) in instantaneous water samples. Colored dots on top of each panel indicate cluster membership for each year

transition towards very sparse *T. testudinum* meadows in the wake of major hurricanes. Previous research described direct physical damage to the benthos of the FKNMS in the wake of hurricanes Irma in 2017 (Wilson et al. 2020) and George in 1998 (Fourqurean and Rutten 2004), emphasizing the spatial heterogeneity of seagrass loss. We report the loss of dense *T. testudinum* meadows at several of our more exposed monitoring sites near the Florida reef tract (Figs. 6 and 9). These declines in seagrass cover occur suddenly after major storm events and are believed to be the direct result of wave-induced erosion of the surface sediment layer including seagrass rhizomes, leaving unvegetated depressions in the seascape. These bare patches are termed “blowouts” and were previously reported from Barbados and Carriacou (Patriquin 1975) and Western Australia (Kirkman and Kirkman 2000). It was posited that blowouts migrate through a continuous process of erosion and infill, promoting revegetation by fast-growing pioneer species and increasing overall species diversity in the seagrass landscape (Kirkman 1985). These primary successional dynamics were found to unfold over time periods from a few years to decades, depending on the blowout size and the disturbance regime (Bell et al. 2007; Walker et al. 2007; Duarte et al. 2007). At the FKNMS however, we did not find evidence for succession of seagrass species at sites of blowouts. If fast-growing pioneering seagrasses were to capitalize on a competitive advantage over the slow-growing climax species *T. testudinum* in blowout areas, we would expect to see increases in *H. wrightii* or *S. filiforme* post-disturbance at these sites, which is not the case. To the

contrary, at hurricane-impacted sites with presence of *S. filiforme*, this seagrass was impacted much like *T. testudinum*, with similar magnitude and rate of decline and only partial recovery of the two seagrass species. This finding supports earlier research reporting higher loss rates of lightly-rooted CGA, *S. filiforme* and *H. wrightii* following the passage of hurricane George in the Florida Keys, where recolonization was driven by CGA instead of supposed “pioneering” seagrasses (Fourqurean and Rutten 2004). In fact, none of our permanent monitoring sites impacted by hurricane-induced erosion showed a full revegetation with seagrasses over the 25-year period of this study (Figs. 6 and 9).

Several factors may explain the lack of revegetation and succession in our observations. First, the size of blowouts was previously related to their likelihood of revegetation, with bare patches larger than 20 m remaining unvegetated for over 50 years at Rottneest Island, Western Australia (Hastings et al. 1995). The blowouts we describe in the FKNMS are typically larger than 20 m, often exceeding the length of our 50-m transects, which may preclude a comprehensive re-establishment of seagrass meadows. Second, the period of monitoring post-disturbance may be insufficient to capture revegetation dynamics. Although Patriquin (1975) estimates revegetation after 5 to 15 years in Barbados and Carter et al. (2022) found 10-year cycles of loss and recovery at the Great Barrier Reef, other studies suggest this process can take considerably longer (Hastings et al. 1995; Kirkman and Kirkman 2000). Third, our fixed transects may not intersect the location of the blowout at which revegetation occurs. This last point portrays an important

**Fig. 9** Timeseries of *T. testudinum* density at seven monitoring sites that were classified as very sparse *T. testudinum* meadows for most monitoring years. Vertical dashed lines indicate the occurrence of major hurricanes that impacted the Florida Keys in 1998 (Georges), 2005 (Wilma, Katrina), and 2017 (Irma)



limitation of this monitoring program regarding the detection of post-disturbance recovery dynamics. Since the main motivation for the program was to monitor the status of soft-bottom benthic communities in relation to water quality, all permanent monitoring sites were set up in existing seagrass meadows. Therefore, we can detect the loss of such meadows and changes towards benthic communities not dominated by seagrasses. However, the lack of monitoring transects established at sites where seagrasses were absent limits our ability to describe recovery dynamics, which we can only describe for our sites that lost seagrass cover over the 25-year monitoring period. In either case, this study documents catastrophic and enduring loss of seagrass cover at our fixed monitoring sites furthest offshore, highlighting the importance of storm events for the distribution of benthic community types in the south Florida seascape.

The most stable benthic community type throughout our monitoring network was characterized by dense *S. filiforme* cover (Table 1). Monitoring sites with dense *S. filiforme* meadows are largely constrained to the backcountry and sluiceway north of the Middle and Lower Keys (Fig. 2). Here, the concentrations of TN and TP are elevated compared to *T. testudinum*-dominated sites (Fig. 4), and the density of *S. filiforme* is well-predicted by water SiO<sub>2</sub> concentrations and the Si:DIN ratio (Fig. 7), suggesting the influence of a distant, riverine water source supplying nutrient-replete waters to this part of the FKNMS. These dense *S. filiforme* meadows are located adjacent to the West Florida shelf, where episodic upwelling supplies nutrient-rich waters from the Gulf of Mexico (Weisberg et al. 2016). Ferdie and Fourqurean (2004) propose a mode of competition where fast-growing *S. filiforme* assimilates nutrients quickly and maintains a competitive advantage over *T. testudinum* through shading. Accordingly, we found the longest *S. filiforme* and *T. testudinum* leaves, as well as the tallest seagrass canopy heights at these sites with dense *S. filiforme* communities (Fig. 5). However, growth rates of *T. testudinum* may be reduced compared to sites without dense *S. filiforme*, as indicated by more depleted *T. testudinum* tissue  $\delta^{15}\text{N}$  (Fig. 5) and *T. testudinum* densities remain low (Fig. 3). This competition between the two seagrass species is also illustrated by the importance of canopy height as a predictor of both *T. testudinum* and *S. filiforme* densities, as well as the importance of *S. filiforme* density as a predictor of *T. testudinum* density (Fig. 7). Even though these findings indicate ongoing competition for available nutrients, the conditions favoring *S. filiforme* appear to be largely consistent over the 25-year monitoring period, resulting in few changes of benthic community assemblage in this part of the FKNMS (Figs. 1 and 5). The exception may be sites adjacent to the backcountry, such as the Florida Bay site “SB” and the Lower Keys sites “305” and “307,” which occasionally become dominated by dense *S. filiforme* (Fig. 5).

This could be explained by stochastic effects of sampling 10 random quadrats along particularly heterogeneous transects. Alternatively, these benthic community changes may be caused by temporal variability in the delivery of the nutrient-rich waters described above and potentially point towards regional climatic patterns driving benthic community composition in the backcountry region of the FKNMS. Future studies should evaluate these hypotheses by investigating synchronicity of water column nutrient concentrations and seagrass abundance.

## Lessons Learned

This study demonstrates the value of long-term benthic monitoring programs because succession and recovery dynamics in seagrass meadows can operate on decadal timescales (Walker et al. 2007; Carter et al. 2022). For example, at sites impacted by disturbance events such as hurricanes, *T. testudinum* density recovers only slowly, typically remaining below pre-disturbance levels over our 25-year monitoring period (Fig. 9). We found other inter-species dynamics to occur on somewhat shorter timescales, with a replacement of *T. testudinum* by *H. wrightii* at sites with rising nutrient concentrations over the course of 3 to 5 years (Fig. 8). However, decadal timescales for *T. testudinum* to *H. wrightii* transition were recently reported for Florida Bay (Hall et al. 2021).

This monitoring program was designed to make use of permanent, fixed transects. While this design facilitates detailed studies of the benthic community composition and condition at specific sites, the methodology does not necessarily allow for the evaluation of seagrass condition in a spatially comprehensive way. For example, even though we describe seagrass loss from storm impacts at several of our monitoring sites (Fig. 9), we cannot confidently report on the net balance of localized seagrass loss and potential (re)vegetation of bare sediment elsewhere. To evaluate how well our monitoring sites represent seagrass cover trends of the entire system, future studies should contrast transect-derived trends with remote sensing products. This issue is of particular concern when fixed transects were established only at locations where seagrass meadows were in good state at the beginning of the monitoring period, because the resulting trends in seagrass cover can be expected to be biased towards decline. We therefore recommend complementing in situ benthic monitoring at specific sites with remote sensing techniques that enable spatially comprehensive assessments on the seascape scale where feasible, following the hierarchical system of tiered monitoring outlined in Neckles et al. (2012).

It is notable that our monitoring network did not detect the kinds of massive (ca. 40 km<sup>2</sup>) seagrass die-offs that were documented in Florida Bay in 1987–1991 (Robblee et al. 1991; Fourqurean and Robblee 1999; Hall et al. 2021)

before the program was established or that re-occurred in Florida Bay in 2015 (Hall et al. 2016). These events were ultimately caused by sulfide toxicity driven by water column hypoxia (Borum et al. 2005) as a result of multi-year droughts and above normal temperatures (Hall et al. 2021). Our program had very few monitoring sites in Florida Bay, and none in the subbasins affected by the 2015 seagrass die-off event (see Fredley et al. 2019), largely because Florida Bay is well-covered by another monitoring program (Hall et al. 2021). Further, since the impetus of our monitoring program was to detect nutrient-driven water quality changes and their effect on the region's seagrasses, the largely oligotrophic Florida Bay region, which receives very little anthropogenically influenced runoff (Nuttall et al. 2000; Fourqurean et al. 1993), was not the focus of our program. This underscores an important limitation of any monitoring program: its design in anticipation of specific conditions and stressors determines the scope of insights that can be gained from monitoring. While the perceived value of monitoring datasets increases the longer the monitoring period lasts, it can be beneficial to re-evaluate and adapt monitoring locations and protocols to accommodate shifting priorities. This is illustrated by the 2012 addition of nearshore sites to this monitoring program, facilitating the observation of secondary succession dynamics that were not captured by the initial monitoring network.

## Future Outlook

We demonstrate that benthic communities typical of South Florida and other tropical shallow seascapes are dynamic and can change on timescales from years to decades. The seagrass trajectories we describe are likely the result of disturbance and recovery dynamics, with both press (e.g., nutrient enrichment) and pulse disturbances (e.g., hurricane impacts) causing long-term change in seagrass density and meadow composition. The likelihood of extreme Atlantic hurricane seasons is increasing with climate change (Pfleiderer et al. 2022). Already, the periodicity of hurricane impacts can be shorter than recovery time, preventing the revegetation of *T. testudinum* at some of our monitoring sites (273 and 305, Fig. 9). In the future, reduced intervals between erosion events could further hinder seagrass revegetation and prevent seagrass meadow recovery, particularly at exposed sites near the reef tract. For seagrass meadows in these locations, long recovery times after perturbations may signal that the system is close to a “bifurcation point”; i.e., the system may be close to a shift to an alternative stable state (Scheffer et al. 2009). It is conceivable that the back-reef environment at the FKNMS, which was historically dominated by *T. testudinum* meadows, will not sustain climax seagrass meadows in a future with more frequent high-intensity storm events. However, as noted above, monitoring data from fixed transects do not

necessarily represent the net balance of seagrass loss and recovery for the entire FKNMS.

While storm severity cannot be directly reduced through management action, it may be possible to counteract the impact of nutrient pollution on South Florida seagrass meadows. We demonstrate that the composition of seagrass meadows exposed to high nutrient concentrations shifted from *T. testudinum* towards dominance of *H. wrightii* at nearshore sites in the FKNMS. Once this shift occurred, the *H. wrightii* communities were relatively stable (Table 1), and a reduction in nutrient delivery is unlikely to have immediate effects on benthic community composition since P, the limiting nutrient, is efficiently retained within the benthos (Herbert and Fourqurean 2008; Howard et al. 2016). Therefore, it is paramount that nutrient concentrations are managed before this shift occurs at sites where *T. testudinum* meadows are the target community of management actions. However, targeted management in form of the conversion of the geographically expansive and modestly populated Florida Keys municipalities from septic to centralized sewer has not appeared to yield substantive results to date, perhaps indicating a slow response of the system to reductions in nutrient delivery. It is also possible that the current sewage disposal wells do not effectively remove sewage nutrients from the nearshore marine system.

What are the consequences of changes in the benthic community composition and dominance of different seagrass species for the ecosystem services provided by South Florida seagrass meadows? For example, the ecosystem service of sedimentary carbon storage may be unaffected by shifts from *T. testudinum* to *H. wrightii* (Howard et al. 2016), but commercially valuable fish are thought to prefer mixed-species meadows over monospecific *T. testudinum* (Chester and Thayer 1990). In an expert and literature-driven review, seagrasses of the genus *Thalassia* were found to provide more ecosystem services than seagrasses belonging to *Halodule* and *Syringodium* (Mtwana Nordlund et al. 2016). Several ecosystem services appear to vary with the size of seagrass shoots, so that larger genera such as *Thalassia* are more effective at sediment stabilization, shoreline protection, and food provisioning than small seagrass genera like *Halodule* (Mtwana Nordlund et al. 2016). However, we found that nutrient-enriched waters not only support the growth of *Halodule* and *Syringodium*, but can also be associated with increased canopy height and leaf length of *Thalassia* in our study system, thereby potentially enhancing ecosystem services associated with seagrass size and density. From this service-centered perspective, there is still much to be learned about the consequences of shifts in the dominance of specific seagrass species in South Florida and beyond. Ultimately, management and potential restoration targets are set by governmental agencies, and in the case of South Florida, the current policy prescribes that all change from

the historic baseline be avoided. Our findings of changes to benthic communities therefore represent needs for management action and call for efforts to minimize nutrient enrichment of nearshore sites within the FKNMS.

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**Author Contribution** Study design: JF, JB, HB; Data collection: JK, CL, SW, HB; Data analysis: JK; Interpretation of results: JF, JK, CL, SW; Initial manuscript: JF, JK; Manuscript edits: JF, JK, CL, SW, HB, JB.

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**Data Availability** All data that form the basis of our analysis are available at <https://seagrass.fiu.edu/data.htm>.

## Declarations

**Conflict of Interest** The authors declare no competing interests.

## References

- Bell, S.S., M.S. Fonseca, and N.B. Stafford. 2007. Seagrass ecology: new contributions from a landscape perspective. In *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer. [https://doi.org/10.1007/978-1-4020-2983-7\\_26](https://doi.org/10.1007/978-1-4020-2983-7_26).
- Borum, J., O. Pedersen, T.M. Greve, T.A. Frankovich, J.C. Zieman, J.W. Fourqurean, and C.J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology* 93: 148–158. <https://doi.org/10.1111/j.1365-2745.2004.00943.x>.
- Boyer, J.N., and R.D. Jones. 2002. View from the bridge: External and internal forces affecting the ambient water quality of the Florida Keys National Marine Sanctuary. In *The Everglades, Florida Bay, and coral reefs of the Florida Keys*, ed. J.W. Porter and K.G. Porter, 609–628. Boca Raton: CRC Press.
- Braun-Blanquet, J. 1972. *Plant sociology: The study of plant communities*. New York: Hafner Publishing Company.
- Briceño, H.O., J.N. Boyer, J. Castro, and P. Harlem. 2013. Biogeochemical classification of South Florida's estuarine and coastal waters. *Marine Pollution Bulletin* 75: 187–204. <https://doi.org/10.1016/j.marpolbul.2013.07.034>.
- Carter, A.B., C. Collier, R. Coles, E. Lawrence, and M.A. Rasheed. 2022. Community-specific “desired” states for seagrasses through cycles of loss and recovery. *Journal of Environmental Management* 314: 115059. <https://doi.org/10.1016/j.jenvman.2022.115059>.
- Chester, A.J., and G.W. Thayer. 1990. Distribution of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) juveniles in seagrass habitats of western Florida Bay. *Bulletin of Marine Science* 46: 13.
- Collado-Vides, L., V.G. Caccia, J.N. Boyer, and J.W. Fourqurean. 2007. Tropical seagrass-associated macroalgae distributions and trends relative to water quality. *Estuarine, Coastal and Shelf Science* 73: 680–694. <https://doi.org/10.1016/j.ecss.2007.03.009>.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260. <https://doi.org/10.1038/387253a0>.
- Costanza, R., R. de Groot, L. Braat, I. Kubiszewski, L. Fioramonti, P. Sutton, S. Farber, and M. Grasso. 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosystem Services* 28: 1–16. <https://doi.org/10.1016/j.ecoser.2017.09.008>.
- Davis, B.C., and J.W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany* 71: 217–232. [https://doi.org/10.1016/S0304-3770\(01\)00179-6](https://doi.org/10.1016/S0304-3770(01)00179-6).
- den Hartog, C. 1967. The structural aspect in the ecology of sea-grass communities. *Helgolander Wiss Meeresunters* 15: 648–659. <https://doi.org/10.1007/BF01618658>.
- Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112. <https://doi.org/10.1080/00785236.1995.10422039>.
- Duarte, C.M., J.W. Fourqurean, D. Krause-Jensen, and B. Olesen. 2007. Dynamics of seagrass stability and change. In *Seagrasses: Biology, Ecology and Conservation*. Dordrecht: Springer. [https://doi.org/10.1007/978-1-4020-2983-7\\_11](https://doi.org/10.1007/978-1-4020-2983-7_11).
- Duffy, J.E., L. Benedetti-Cecchi, J. Trinanes, F.E. Muller-Karger, R. Ambo-Rappe, C. Boström, A.H. Buschmann, J. Byrnes, R.G. Coles, J. Creed, L.C. Cullen-Unsworth, G. Diaz-Pulido, C.M. Duarte, G.J. Edgar, M. Fortes, G. Goni, C. Hu, X. Huang, C.L. Hurd, C. Johnson, B. Konar, D. Krause-Jensen, K. Krumhansl, P. Macreadie, H. Marsh, L.J. McKenzie, N. Mieszkowska, P. Miloslavich, E. Montes, M. Nakaoka, K.M. Norderhaug, L.M. Norlund, R.J. Orth, A. Prathep, N.F. Putman, J. Samper-Villarreal, E.A. Serrao, F. Short, I.S. Pinto, P. Steinberg, R. Stuart-Smith, R.K.F. Unsworth, M. van Keulen, B.I. van Tussenbroek, M. Wang, M. Waycott, L.V. Weatherdon, T. Wernberg, and S.M. Yaakub. 2019. Toward a coordinated global observing system for seagrasses and marine macroalgae. *Frontiers in Marine Science* 6: 317. <https://doi.org/10.3389/fmars.2019.00317>.
- Dunic, J.C., C.J. Brown, R.M. Connolly, M.P. Turschwell, and I.M. Côté. 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Global Change Biology* 27: 4096–4109. <https://doi.org/10.1111/gcb.15684>.

- Ferdie, M., and J.W. Fourqurean. 2004. Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. *Limnology and Oceanography* 49: 2082–2094. <https://doi.org/10.4319/lo.2004.49.6.2082>.
- Fourqurean, J.W., and M.B. Robblee. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22: 345–357. <https://doi.org/10.2307/1353203>.
- Fourqurean, J.W., and L.M. Rutten. 2003. Competing goals of spatial and temporal resolution: Monitoring seagrass communities on a regional scale. In *Monitoring ecosystem initiatives: Interdisciplinary approaches for evaluating ecoregional initiatives*, ed. D.E. Busch and J.C. Trexler, 257–288. Washington, D. C.: Island Press.
- Fourqurean, J.W., and L.M. Rutten. 2004. The impact of hurricane Georges on soft-bottom, back reef communities: Site- and species-specific effects in south Florida seagrass beds. *Bulletin of Marine Science* 75: 20.
- Fourqurean, J.W., and J.C. Zieman. 2002. Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys, USA. *Biogeochemistry* 61: 229–245. <https://doi.org/10.1023/A:1020293503405>.
- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from the C:N: P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162–171. <https://doi.org/10.4319/lo.1992.37.1.0162>.
- Fourqurean, J.W., R.D. Jones, and J.C. Zieman. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. *Estuarine, Coastal and Shelf Science* 36: 295–314. <https://doi.org/10.1006/ecss.1993.1018>.
- Fourqurean, J.W., G.V.N. Powell, W.J. Kenworthy, and J.C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349. <https://doi.org/10.2307/3546120>.
- Fourqurean, J.W., A.W. Willisie, C.D. Rose, and L.M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* 138: 341–354. <https://doi.org/10.1007/s002270000448>.
- Fourqurean, J.W., M.J. Durako, M.O. Hall, and L.N. Hefty. 2002. Seagrass distribution in south Florida: a multi-agency coordinated monitoring program. In *The Everglades, Florida Bay, and the coral reefs of the Florida Keys*, ed. J.W. Porter and K.G. Porter, 497–522. Boca Raton: CRC Press. <https://doi.org/10.1201/9781420039412-22>.
- Fourqurean, J.W., S.A. Manuel, K.A. Coates, S.C. Massey, and W.J. Kenworthy. 2019. Decadal monitoring in Bermuda shows a widespread loss of seagrasses attributable to overgrazing by the green sea turtle *Chelonia mydas*. *Estuaries and Coasts: Journal of the Estuarine Research Federation* 42: 1524–1540. <https://doi.org/10.1007/s12237-019-00587-1>.
- Frankovich, T., and J. Fourqurean. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159: 37–50. <https://doi.org/10.3354/meps159037>.
- Fredley, J., M.J. Durako, and M.O. Hall. 2019. Multivariate analyses link macrophyte and water quality indicators to seagrass die-off in Florida Bay. *Ecological Indicators* 101: 692–701. <https://doi.org/10.1016/j.ecolind.2019.01.074>.
- Furman, B., E. Leone, S. Bell, M. Durako, and M. Hall. 2018. Braun-Blanquet data in ANOVA designs: Comparisons with percent cover and transformations using simulated data. *Marine Ecology Progress Series* 597: 13–22. <https://doi.org/10.3354/meps12604>.
- Hall, M.O., M.J. Durako, J.W. Fourqurean, and J.C. Zieman. 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22: 445–459. <https://doi.org/10.2307/1353210>.
- Hall, M.O., B.T. Furman, M. Merello, and M.J. Durako. 2016. Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: Initial observations. *Marine Ecology Progress Series* 560: 243–249. <https://doi.org/10.3354/meps11923>.
- Hall, M.O., S.S. Bell, B.T. Furman, and M.J. Durako. 2021. Natural recovery of a marine foundation species emerges decades after landscape-scale mortality. *Science and Reports* 11: 6973. <https://doi.org/10.1038/s41598-021-86160-y>.
- Hastings, K., P. Hesp, and G.A. Kendrick. 1995. Seagrass loss associated with boat moorings at Rottnest Island, Western Australia. *Ocean & Coastal Management* 26: 225–246. [https://doi.org/10.1016/0964-5691\(95\)00012-Q](https://doi.org/10.1016/0964-5691(95)00012-Q).
- Herbert, D.A., and J.W. Fourqurean. 2008. Ecosystem structure and function still altered two decades after short-term fertilization of a seagrass meadow. *Ecosystems* 11: 688–700. <https://doi.org/10.1007/s10021-008-9151-2>.
- Howard, J.L., A. Perez, C.C. Lopes, and J.W. Fourqurean. 2016. Fertilization changes seagrass community structure but not blue carbon storage: Results from a 30-year field experiment. *Estuaries and Coasts* 39: 1422–1434. <https://doi.org/10.1007/s12237-016-0085-1>.
- Kenworthy, W.J., M.J. Durako, S.M.R. Fatemy, H. Valavi, and G.W. Thayer. 1993. Ecology of seagrasses in Northern Saudi Arabia one year after the Gulf War oil spill. *Marine Pollution Bulletin* 27: 213–222. [https://doi.org/10.1016/0025-326X\(93\)90027-H](https://doi.org/10.1016/0025-326X(93)90027-H).
- Kirkman, H. 1985. Community structure in seagrasses in southern western Australia. *Aquatic Botany* 21: 363–375. [https://doi.org/10.1016/0304-3770\(85\)90077-4](https://doi.org/10.1016/0304-3770(85)90077-4).
- Kirkman, H., and J. Kirkman. 2000. Long-term seagrass meadow monitoring near Perth, Western Australia. *Aquatic Botany* 67: 319–332. [https://doi.org/10.1016/S0304-3770\(00\)00097-8](https://doi.org/10.1016/S0304-3770(00)00097-8).
- Klein, C.J.I., and S.P.J. Orlando. 1994. A spatial framework for water-quality management in the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* 54: 1036–1044.
- Kruczynski, W.L. 1999. *Water quality concerns in the Florida Keys: sources, effects and solutions*, vol. 90. United States Environmental Protection Agency.
- Kruczynski, W.L., and P.J. Fletcher. 2012. *Tropical connections: South Florida's marine environment*, 492. Cambridge, MD: IAN Press.
- Liaw, A., and M. Wiener. 2002. Classification and regression by random forest. *R News* 2 (3): 18–22. <https://CRAN.R-project.org/doc/Rnews/>. Accessed 1 Dec 2022.
- Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2021. *cluster: Cluster Analysis Basics and Extensions*. R Package version 2.1.2.
- Mtwana Nordlund, L., E.W. Koch, E.B. Barbier, and J.C. Creed. 2016. Seagrass Ecosystem services and their variability across genera and geographical regions. *PLoS ONE* 11: e0163091. <https://doi.org/10.1371/journal.pone.0163091>.
- Neckles, H.A., B.S. Kopp, B.J. Peterson, and P.S. Pooler. 2012. Integrating scales of seagrass monitoring to meet conservation needs. *Estuaries and Coasts: Journal of the Estuarine Research Federation* 35: 23–46. <https://doi.org/10.1007/s12237-011-9410-x>.
- Nuttle, W.K., J.W. Fourqurean, B.J. Cosby, J.C. Zieman, and M.B. Robblee. 2000. Influence of net freshwater supply on salinity in Florida Bay. *Water Resources Research* 36: 1805–1822. <https://doi.org/10.1029/1999WR900352>.
- Patriquin, D.G. 1975. “Migration” of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. *Aquatic Botany* 1: 163–189. [https://doi.org/10.1016/0304-3770\(75\)90021-2](https://doi.org/10.1016/0304-3770(75)90021-2).



- Pfleiderer, P., S. Nath, and C.-F. Schleussner. 2022. Extreme Atlantic hurricane seasons made twice as likely by ocean warming. *Weather and Climate Dynamics* 3: 471–482. <https://doi.org/10.5194/wcd-3-471-2022>.
- Porter, J.W., V.N. Kosmynin, K.L. Patterson, K.G. Porter, W.C. Jaap, J. Wheaton, K. Hackett, M. Lybolt, C.P. Tsokos, G.P. Yanev, D. Marcinek, J. Dotten, D. Eaken, M. Patterson, O.W. Meier, M. Brill, and P.A. Dustan. 2002. Detection of coral reef change by the florida keys coral reef monitoring project. In *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An ecosystem sourcebook*, ed. J.W. Porter and K.G. Porter, 750–769. Boca Raton: CRC Press.
- Robblee, M.B., T.R. Barber, P.R. Carlson, M.J. Durako, J.W. Fourqurean, L.K. Muehlstein, D. Porter, L.A. Yarbrow, R.T. Zieman, and J.C. Zieman. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71: 297–299. <https://doi.org/10.3354/meps071297>.
- Scheffer, M., J. Bascompte, W.A. Brock, V. Brovkin, S.R. Carpenter, V. Dakos, H. Held, E.H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. *Nature* 461: 53–59. <https://doi.org/10.1038/nature08227>.
- Short, F.T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27. <https://doi.org/10.1017/S0376892900038212>.
- Stekhoven, D.J., and P. Buehlmann. 2012. MissForest - non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28 (1): 112–118. <https://doi.org/10.1093/bioinformatics/btr597>.
- Turschwell, M.P., R.M. Connolly, J.C. Dunic, M. Sievers, C.A. Buelow, R.M. Pearson, V.J.D. Tulloch, I.M. Côté, R.K.F. Unsworth, C.J. Collier, and C.J. Brown. 2021. Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale. *Proceedings of the National Academy of Sciences* 118: e2110802118. <https://doi.org/10.1073/pnas.2110802118>.
- Walker, D., G. Kendrick, A. McComb, A. Larkum, R. Orth, and C. Duarte. 2007. Decline and recovery of seagrass ecosystems—the dynamics of change. In *Seagrasses: Biology, Ecology and Conservation*, 551–565. Dordrecht: Springer. [https://doi.org/10.1007/978-1-4020-2983-7\\_23](https://doi.org/10.1007/978-1-4020-2983-7_23).
- Weisberg, R.H., L. Zheng, and Y. Liu. 2016. West Florida shelf upwelling: Origins and pathways. *Journal of Geophysical Research: Oceans* 121: 5672–5681. <https://doi.org/10.1002/2015JC011384>.
- Wilson, S.S., B.T. Furman, M.O. Hall, and J.W. Fourqurean. 2020. Assessment of Hurricane Irma impacts on south florida seagrass communities using long-term monitoring programs. *Estuaries and Coasts: Journal of the Estuarine Research Federation* 43: 1119–1132. <https://doi.org/10.1007/s12237-019-00623-0>.

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