Ecological Indicators 156 (2023) 111090

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Common ecological indicators identify changes in seagrass condition following disturbances in the Gulf of Mexico

Victoria M. Congdon [a,b,*], Margaret O. Hall [b], Bradley T. Furman [b], Justin E. Campbell [c], Michael J. Durako [d], Kathleen L. Goodin [e], Kenneth H. Dunton [a]

[a] University of Texas at Austin Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA
[b] Florida Fish Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 Eighth Avenue, Southeast, St. Petersburg, FL 33701, USA
[c] Institute of Environment, Coastlines and Oceans Division, Department of Biological Sciences, Florida International University, 11200 SW 8th St., Miami, FL 33199, USA
[d] University of North Carolina at Wilmington, Department of Biology and Marine Biology, Center for Marine Science, 5600 Marvin Moss Ln., Wilmington, NC 28409, USA
[e] NatureServe, Arlington, VA, USA

ARTICLE INFO

Keywords:
Bioindicator
Morphometric
Texas
Florida Bay
Florida Keys National Marine Sanctuary
Disturbance

ABSTRACT

Seagrasses are long-lived, clonal plants that can integrate fluctuations in environmental conditions over a range of temporal scales, from days to years, and can act as barometers of coastal change. There are many estimated seagrass traits and ecosystem parameters that have the potential to reflect ecosystem status, linking seagrass condition to natural and anthropogenic drivers of change. We identified five seagrass indicators and seven metrics that are suitable, affordable and frequently measured by 38 monitoring programs across the Gulf of Mexico (GoM). A specific set of ratings and assessment points were formulated for each measurable metric. We determined metric ratings (Acceptable, Concerning, Alarming) and validated assessment points using long-term monitoring data from Texas and Florida, coupled with existing literature and input from a panel of seagrass biologists. We reported scores using a blue-gray-orange (Acceptable-Concerning-Alarming) scale to summarize information in a format accessible to the public, resource managers, stakeholders, and policymakers. Seagrass percent cover, shoot allometry and species composition were sensitive indicators of large-scale climatic disturbances (droughts, hurricanes). Severe drought led to reductions in total seagrass cover and leaf length in Upper Laguna Madre, Texas, and Florida Bay; however, *Syringodium filiforme* was disproportionally affected in Texas while *Thalassia testudinum* beds responded strongly to drought impacts in Florida. Hurricanes Harvey (TX) and Irma (FL) also resulted in loss of seagrass cover and diminished leaf length in the Texas Coastal Bend and Florida Keys; both storms largely impacted *T. testudinum* and to a lesser extent, *S. filiforme*. Many of the metrics within these affected bays and basins received either a “Concerning” or “Alarming” rating, driven by the impacts of these disturbances. Our proposed indicators serve as a tool to evaluate seagrass condition at the bay or basin scale. Moreover, the indicators, metrics, and assessment points are amenable to large-scale evaluations of ecosystem condition because they are economically feasible. This framework may provide the foundation for a comprehensive assessment of seagrass status and trends across the entire GoM.

1. Introduction

Seagrasses are marine flowering plants that form vast underwater meadows along coastlines worldwide. They provide food and critical habitat for many commercially and recreationally fished species, protect coastlines from erosion, mitigate climate change (Costanza et al. 1997; Barbier et al. 2011) via carbon uptake and storage (Fourqurean et al., 2002; Duarte et al. 2013; Marbà et al. 2015), and act as buffers to ocean acidification (Hendriks et al. 2014). However, studies estimate seagrass loss at 1 to 7 % per year (Waycott et al. 2009; Dunic et al. 2021). Drivers of seagrass loss include anthropogenic impacts such as coastal development, impaired water quality (Orth et al. 2006), and climatic disturbances such as marine heatwaves (Marbà and Duarte 2010; Arias-Ortiz et al. 2018; Kendrick et al. 2019; Sen Gupta et al. 2020), droughts (Hall et al. 2016; Wilson and Dunton 2018) and storms (Gera et al. 2014). To reverse trajectories of habitat degradation and loss,

* Corresponding author at: 100 Eighth Avenue, Southeast, St. Petersburg, FL 33701, USA.
E-mail address: victoria.congdon@myfwc.com (V.M. Congdon).

https://doi.org/10.1016/j.ecolind.2023.111090
Received 17 May 2023; Received in revised form 27 September 2023; Accepted 12 October 2023
Available online 21 October 2023

resource managers have focused efforts on seagrass conservation. Important components of this process include societal awareness, strengthened through public outreach and education campaigns, and information on ecosystem status and trends informed by long-term and often coordinated monitoring programs (Fourqurean et al. 2002; Unsworth et al. 2018). Yet, spatial and temporal measurements of seagrass abundance and distribution remain patchy and, in some regions, scarce.

Sustained monitoring, coupled with more widespread assessments of seagrass condition, can detect seagrass trajectories, and allow implementation of actions to reverse habitat degradation (Unsworth et al. 2018). As changes in abundance and distribution often signify environmental perturbations (Orth et al. 2006; Orth et al. 2017), a plethora of indicators are used to identify changes in condition and assess seagrass ecosystem status (Martínez-Crego et al. 2008; Madden et al. 2009; van Katwijk et al. 2011; Marbà et al. 2013; McMahon et al. 2013; Collier et al. 2016; Roca et al. 2016). However, indicator selection, monitoring frequency, and spatial grain (resolution) often differ among programs, limiting their applicability for regional assessment (Roca et al. 2016). Regardless, the monitoring of seagrass indicators helps us better understand and identify factors that influence seagrass abundance, composition, and distribution through time and space (Orth et al. 2017). This is becoming increasingly important, particularly in the context of extreme disturbances (i.e., marine heatwaves, El Niño–Southern Oscillation, storms) which further exacerbate seagrass loss. Unfortunately, these types of disturbances have led to large declines in foundation seagrass species (Marbà and Duarte 2010; Gera et al. 2014), affecting seagrass coverage and diversity in many places throughout the world (Arias-Ortiz et al. 2018; Kendrick et al. 2019).

Seagrass coverage within the Gulf of Mexico (GoM) comprises nearly 50 % of the total seagrass extent in the U.S. (Green and Short, 2003). Previous estimates of seagrass areal extent within the GoM range from ~17,000–19,000 km^2 (Handley et al. 2007). The largest, most contiguous beds are located along the south Florida and Texas coasts (Mendelssohn et al. 2017). Approximately 94 % of seagrasses in Texas are located within the Coastal Bend and Laguna Madre (Dunton et al. 2011), and more than 50 % of Florida seagrasses are in south Florida (Yarbro and Carlson 2011). Although six species are found in the GoM, the dominant species include *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*. *T. testudinum* and *H. wrightii* tend to dominate seagrass communities in Florida Bay and Texas, respectively. However, all three species form mixed assemblages with composition largely dictated by water quality and successional state (*H. wrightii* (pioneer) < *S. filiforme* < *T. testudinum* (climax); Zieman et al. 1989).

Exceptional drought conditions plagued much of Texas from 2011 to 2012 (Seager et al. 2014) and persisted until 2015. South Texas estuaries are prone to periods of hypersalinity due to long residence times, minimal freshwater inputs, and high net evaporation (Solis and Powell 1999). Wilson and Dunton (2018) identified a significant decline in *S. filiforme* cover due to prolonged hypersalinity (50–70) in Upper Laguna Madre from September 2012 to October 2013. In August 2017, Hurricane Harvey (a category 4 storm) struck the Coastal Bend, shearing blades and removing patches of *T. testudinum* (Congdon et al. 2019). Coincidentally, seagrass meadows in Florida Bay and the Florida Keys exhibited the same types of disturbances during a similar timeframe. By 2015, drought conditions led to hypersalinity (15-year highs, exceeding 50–60) and bottom-water anoxia which resulted in the loss of *T. testudinum* (Hall et al. 2016; Hall et al. 2021). Shortly after, Hurricane Irma crossed the Florida Keys as a category 4 storm in September 2017. Wilson et al. (2020) attributed significant decreases in total seagrass density to erosion (north of Lower Keys), and low salinities and dissolved oxygen from storm water runoff (northern coastal basins of Florida Bay).

Although stochastic events are unpredictable, indicators may provide an early warning of seagrass collapse. Changes in plant abundance, composition, blade morphology and/or elemental constituents may signal a system that is responding to physical or environmental stressors that threaten ecological stability and resilience, defined as "the capacity to undergo disturbance without permanent loss of key ecological structures and functions" (*sensu* Holling 1973). Studies have shown that biochemical and physiological responses such as alterations in the expression of stress-related genes (i.e., photosynthetic and carbon metabolism) and leaf phenolics (Ceccherelli et al. 2018), and photosynthesis/respiration (i.e., photosynthetic efficiency (α), chlorophylls *a* and *b*; Marín-Guirao et al. 2022) presaged seagrass collapse from eutrophication, burial or light reduction. Increases in the recovery time from local perturbations may signify that an ecosystem is approaching a change in community structure (Dakos et al. 2015; van de Leemput et al. 2018). Additionally, increased variability in plant characteristics (i.e., abundance, morphology) may immediately precede a regime shift (Brock and Carpenter 2006; Carpenter and Brock 2006; Dakos et al. 2015). However, some changes in the system-state prior to a transition are less conspicuous (Scheffer et al. 2009), making the identification of tipping points challenging (Petraitis et al. 2009).

What indicators help us better understand factors affecting seagrass resiliency? Which indicators can be used to evaluate seagrass ecosystem status? In 1992, an ecological indicator working group proposed a variety of response (e.g., abundance and plant constituents, such as ratios of carbon (C), nitrogen (N), phosphorus (P)) and exposure (e.g., light, nutrients) indicators for adoption by the Environmental Monitoring and Assessment Program (Neckles, 1994). Furthermore, the participants recommended that this program increase sampling density, expand the sampling spatial footprint, and include permanent stations (Neckles, 1994); participants also recognized the need for other long-term monitoring programs to incorporate these recommendations as well. Since then, monitoring programs have multiplied across the GoM (see Goodin et al. 2018), increasing the breadth and scope of substantial long-term data sets. Moreover, there has been a resurgence in efforts to develop a Gulf-wide framework for assessing ecosystem condition (Goodin et al. 2018; Harwell et al. 2019; Handley and Lockwood, 2020), but selecting the appropriate indicators, metrics and meaningful quantitative thresholds has posed a challenge. To effectively work towards a global coordinated effort for assessing seagrass condition, Duffy et al. (2019) proposed that monitoring networks identify a core set of common metrics, practice comparable sampling methodologies (i.e., field measurements) and follow similar study designs using a tiered approach, such as those presented in Neckles et al. (2012).

The monitoring data from long-term programs in Florida and Texas provide a unique opportunity to re-examine the question proposed in the 1992 Indicator Development workshop (Neckles, 1994). Our goal was to distill a comprehensive list of indicators into a select set of common indicators and metrics at a regional scale. Here, we adopt the operational definition of "an indicator in ecology and environmental planning [as] a component or a measure of environmentally relevant phenomena used to depict or evaluate environmental conditions or changes, or to set environmental goals" (Heink and Kowarik 2010), to which metrics, measures and assessment points can be derived and evaluated. We used two types of natural disturbances, droughts and hurricanes, that impacted seagrass ecosystems in Texas and Florida (Hall et al. 2016; Wilson and Dunton 2018; Congdon et al. 2019; Wilson et al. 2020) in combination with long-term monitoring data to assess the efficacy of our proposed indicators across large spatial scales. Ultimately, we sought to identify indicators that were interpretable and best summarized ecological condition for environmental managers, stakeholders, and the public.

2. Materials and methods

To develop a framework for assessing seagrass condition in the GoM, NatureServe co-facilitated a workshop with partners from The Nature Conservancy, U.S. Geological Survey, Ocean Conservancy, Florida Fish and Wildlife Conservation Commission and the University of Texas Marine Science Institute on October 12–13, 2016. Seagrass habitats were a subset of a more encompassing project that focused on developing ecological indicators for four additional ecosystems (corals, oysters, mangroves, salt marshes) in the GoM (see Goodin et al. 2018 for a description of the indicator, metric, and assessment point selection process). Ecosystem specialist working groups, consisting of researchers, state and federal regulators, and environmental managers, were tasked with curating a list of indicators and metrics, including the development of a quantitative rating system for assessing the condition of seagrass beds.

2.1. Selection process of indicators, metrics, and measures

A seagrass working group composed of seven seagrass biologists developed a list of 20 potential indicators for seagrass ecosystems, which were scored using an evaluation form (adapted from Herrick et al. 2012) on the following scale: 1 = minimally effective, 3 = moderately effective, and 5 = extremely effective (Table S1). We also solicited feedback from five additional seagrass experts to evaluate the proposed indicators using the same scale. The highest performing indicators, i.e., those that met the most criteria and could be effectively managed, were deemed candidate indicators. For each candidate indicator, we selected a quantifiable metric and corresponding measure (see Goodin et al. 2018). Measures were actual values collected in the field and used to calculate the metrics. For example, nitrogen and phosphorus concentrations were considered measures for the metric Nutrient Limitation Index and the indicator Nutrient Content.

Monitoring programs often utilize a hierarchical approach that consists of three tiers which vary in the effort, efficacy and cost of data collection (Bricker and Ruggiero 1998; Neckles et al. 2012). Tiers 1 and 2 are rapid assessments that provide information at the mapping and meadow scale, respectively (e.g., distribution and extent, broad-scale condition). Tier 3 monitoring typically focuses on assessing environmental drivers of change, with more frequent sampling intervals and metrics (e.g., tissue nutrient stoichiometry or stable isotopic composition), but are often labor/time intensive and reduced in spatial scale. Although we attempted to select the most cost-effective, rapid, and

Table 1

Description of seagrass monitoring programs in Texas and Florida, including a summary of the indicators and metrics used in this study. Field measurement data were acquired from three monitoring programs that implemented the methods presented in Durako et al. 2002 (Fisheries Habitat Assessment Program; FHAP); Fourqurean et al. 2002 (Florida Keys National Marine Sanctuary Seagrass Monitoring Program; FKNMS–SMP); Dunton et al. 2011 (Texas Seagrass Monitoring Program; TSMP). Zones and basins included in this study are, for the Texas Coast: CB = Coastal Bend; ULM = Upper Laguna Madre; LLM = Lower Laguna Madre; for Florida Bay: JON = Johnson; RAN = Rankin; RKB = Rabbit Key; TWN = Twin Key; WHP = Whipray; for the Florida Keys: LKB = Lower Keys Bayside; LKO = Lower Keys Oceanside; MKB = Middle Keys Bayside; MKO = Middle Keys Oceanside; UKO = Upper Keys Oceanside.

Disturbance, year, location	Monitoring program	Monitoring years (reference condition)	Zone/Basin (no. of stations)	∑ stations	Season	Indicators assessed	Metrics measured	Case study
Drought, 2013, Texas Coast	Texas Seagrass Monitoring Program (TSMP)	2011 – 2018	CB (138) ULM (144) LLM (285)	567	Summer	Change in cover	Percent cover $\geq$ 50 %	Wilson and Dunton, 2018
						Seagrass species composition	Species Dominance Index	
						Shoot allometry	Leaf length	
						Nutrient content	Nutrient Limitation Index	
						Stable isotope ratios	$\delta^{13}C$, $\delta^{15}N$	
Drought, 2015, Florida Bay	Fisheries Habitat Assessment Program (FHAP)	2006 – 2019	JON (30) RAN (30) RKB (31) TWN (31) WHP (30)	152	Spring	Change in cover	Percent cover < 50 %	Hall et al. 2016
						Seagrass species composition	Species Dominance Index	
						Shoot allometry	Leaf length	
						Shoot allometry	Leaf width	
Hurricane Harvey, 2017, Texas Coast	Texas Seagrass Monitoring Program (TSMP)	2011 – 2018	CB (138) ULM (144) LLM (285)	567	Summer	Change in cover	Percent cover $\geq$ 50 %	Congdon et al. 2019
						Seagrass species composition	Species Dominance Index	
						Shoot allometry	Leaf length	
						Nutrient content	Nutrient Limitation Index	
						Stable isotope ratios	$\delta^{13}C$, $\delta^{15}N$	
Hurricane Irma, 2017, Florida Keys National Marine Sanctuary	Florida Keys National Marine Sanctuary Seagrass Monitoring Program (FKNMS-SMP)	1997 – 2019	LKB (6) LKO (9) MKB (6) MKO (8) UKO (8)	37	Summer	Change in cover	Percent cover < 50 %	Wilson et al. 2020
						Seagrass species composition	Species Dominance Index	
						Shoot allometry	Leaf length	
						Nutrient content	Nutrient Limitation Index	
						Stable isotope ratios	$\delta^{13}C$, $\delta^{15}N$	

widely-monitored indicators and metrics (typically characteristic of Tiers 1 and 2), we did not exclude cost-intensive (Tier 3) indicators; we felt that the limited number of Tier 3 indicators that are currently monitored (only ~8–13 % of programs; see Goodin et al. 2018) highlighted the need for more widespread adoption by monitoring programs throughout the GoM.

2.2. Development of metric ratings and assessment points

For each indicator, we constructed a metric rating by deriving a quantitative value or range of values, referred to as assessment points (Carter and Bennetts 2007). Since these values can vary across landscapes, we sought to develop a set of quantitative metrics and assessment points based on an extensive literature search, knowledge and experience from the panelists, and long-term data (Table 1). For each metric, we generated individualized ratings which were categorized as “Acceptable”, “Concerning” or “Alarming”. To account for regional variation among ecosystems, we crafted two sets of metric ratings and assessment points for some indicators (e.g., different ratings for areas with mean seagrass cover <50 % vs. those with ≥50 % cover).

2.3. Environmental monitoring and long-term data sets

For the case studies, we focused on three management areas identified by their respective monitoring programs: Texas Coast (Texas Seagrass Monitoring Program – TSMP), Florida Bay (Fisheries Habitat Assessment Program – FHAP) and Florida Keys (Florida Keys National Marine Sanctuary Seagrass Monitoring Program – FKNMS-SMP; Table 1; Fig. 1). We acquired seagrass monitoring data from repositories for the TSMP (www.texasseagrass.org), FHAP and FKNMS-SMP (http://seagrass.fiu.edu/data.htm), where all programs follow similar sampling methodologies (Durako et al. 2002; Fourqurean et al. 2002; Dunton et al. 2011; Congdon et al. 2019; Wilson et al. 2020).

The Texas Coast program (total stations, $n = 567$) utilized a restricted random sampling design that generated one random, fixed station within a tessellated hexagon with a 500 m or 750 m edge (Dunton et al. 2011; Neckles et al. 2012; Wilson and Dunton 2018; Congdon et al. 2019). This differed slightly from Florida Bay ($n = 392$), which also visited one station per tessellated hexagon (258–931 m edge), but the station location was randomized annually (Hall et al. 2016). The Florida Keys program ($n = 40$) sampled at 10 pre-determined random points along a 50-m transect at each station (Wilson et al. 2020), where the location of each permanent transect was originally selected within a tessellated hexagon using a stratified-random approach. At each station, seagrass composition by species was visually quantified using 0.25-m^2 quadrats to estimate percent cover by direct calculation (Texas Coast, n = 4) or Braun-Blanquet scores (Florida Bay, n = 8 and Florida Keys, n = 10). Braun-Blanquet scores were converted to ordinal transfer values (OTV) of 1–9 using a “combined transformation” which is a combination of a cover scale in angular transformation with a weighting based on abundance (van der Maarel 1979). Then, OTV was converted to percent cover values using the following equation:

$$\ln C = (OTV - 2)/a \tag{1}$$

where OTV is the ordinal transform value, C is the approximate percent cover and a is a weighting factor which for this study was equal to 1.380 (Table 2; van der Maarel 2007; Furman et al. 2018).

Using the methods of Madden et al. (2009), we determined the relative species composition for the dominant species (RSC_{DOM}) by dividing the mean percent cover of the dominant species (D_{DOM}) by the summed percent cover of all species present at each station, where *Ruppia maritima* (D_{Rm}), *Halophila engelmannii* (D_{He}), *Halodule wrightii* (D_{Hw}), *Syringodium filiforme* (D_{Sf}) or *Thalassia testudinum* (D_{Tt}) is the mean cover by species (Eqs. (2) and (3)):

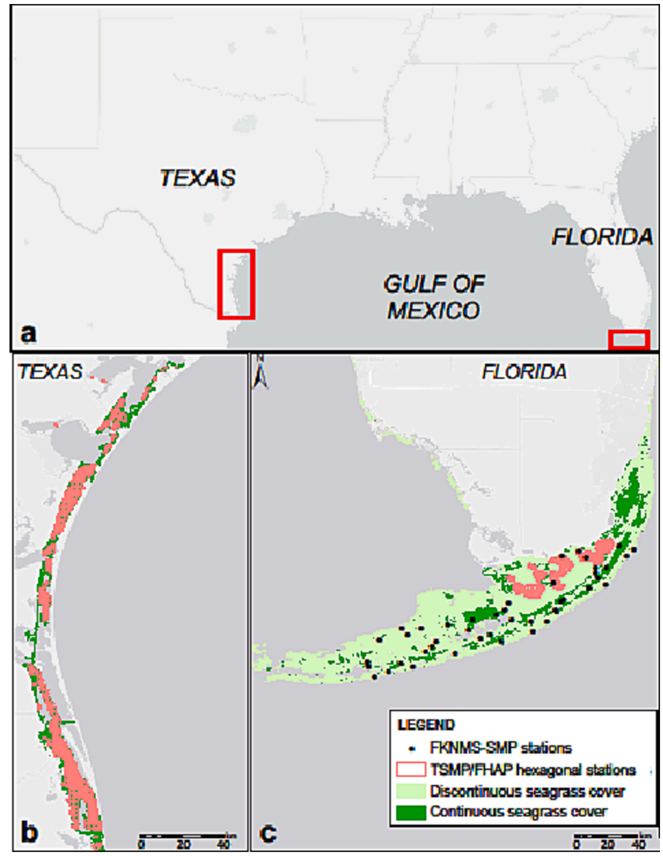

Fig. 1. Map of the study areas of three long-term monitoring programs in Texas and Florida demarcated by red boxes (**a**). Seagrass distribution on the Texas Coast (**b**), and Florida Bay and Keys (**c**). Long-term seagrass monitoring programs include the Texas Seagrass Monitoring Program (TSMP), Fisheries Habitat Assessment Program (FHAP) and Florida Keys National Marine Sanctuary Seagrass Monitoring Program (FKNMS-SMP). Sample stations are denoted by either hexagons (Texas Coast, Florida Bay) or black circles (Florida Keys). Discontinuous and continuous seagrass cover are shown in light and dark green, respectively. We acquired seagrass distribution layers from https://geodata.myfwc.com/. Note, source data recorded as presence/absence or patchy (<40 % cover) were reclassified as discontinuous. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Conversion of raw Braun-Blanquet (BB) scores to percent cover using the ordinal transform values (OTV) of van der Maarel (1979). See text for description of the conversion methods.

Description	BB Score	OTV	% Cover
Absent	0	0	0.23
Single individual present	0.1	1	0.485
Few individuals, < 5 % cover	0.5	2	1
Many individuals, < 5 % cover	1	3	2.064
–	–	4	4.26
5 – 25 % cover	2	5	8.793
–	–	6	18.148
25 – 50 % cover	3	7	37.457
50 – 75 % cover	4	8	77.31
75 – 100 % cover	5	9	159.567

$$RSC_{DOM} = \frac{D_{DOM}}{D_{Hw} + D_{Sf} + D_{Tt}} \quad (2)$$

$$RSC_{DOM} = \frac{D_{DOM}}{D_{Rm} + D_{He} + D_{Hw} + D_{Sf} + D_{Tt}} \quad (3)$$

where the cumulative RSC for each station should sum to 1. We quantified Species Dominance Index (SDI) for each station by applying the RSC value of the dominant species (RSC_{DOM}; Eqs. (4) and (5)):

$$\text{Species Dominance Index (SDI)} = 1.5 \times (1 - RSC_{DOM}) \quad (4)$$

$$\text{Species Dominance Index (SDI)} = 1.25 \times (1 - RSC_{DOM}) \quad (5)$$

with indices on a 0–1 scale. SDI values closer to 0 indicate dominance by a single species and mixed compositions exhibit values near 1. Since Florida Bay and Florida Keys programs reported cover measurements for only *H. wrightii*, *S. filiforme* and *T. testudinum*, we adapted the equation of Madden et al. (2009) to accommodate differences in species data collection (Eqs. (2) and (4)). Moreover, we also adjusted this formula for the Texas Coast to account for the five species reported in Texas (Eqs. (3) and (5)).

Blade lengths were determined as the photosynthetic portion of the longest blade from each random shoot. At each station, 20 shoots were measured for each species (*T. testudinum*, *H. wrightii* and *S. filiforme*) on the Texas Coast, and ten *T. testudinum* shoots were measured in Florida Bay. In the Florida Keys, blade length of the dominant species (*T. testudinum*, *H. wrightii* or *S. filiforme*) was determined within each quadrat per station by categorizing measurements into 5-cm increments for lengths between 5 and 50 cm. For values that fell outside of this range, lengths were classified as 1 cm when less than 5 cm, and 51 cm for all measurements exceeding 50 cm.

Harvested *T. testudinum*, *H. wrightii*, and *S. filiforme* (Florida) shoots were placed on ice and returned to their respective laboratories for the determination of δ^{13}C, δ^{15}N and N:P ratios (Texas Coast and Florida Keys). Briefly, leaves were gently scraped and rinsed in DI or milli-Q water to remove all epibiota. Cleaned seagrass tissues were dried to a constant weight at 60 °C and homogenized by grinding to a fine powder. Tissue samples were analyzed for carbon and nitrogen isotopic values (δ^{13}C and δ^{15}N, respectively) using an Isotope-Ratio Mass Spectrometer. Isotopic ratios (R) were reported in the standard delta notation:

$$\delta\,(‰) = \left[\left(R_{sample}/R_{standard}\right)\right] \times 1000 \quad (6)$$

Carbon and nitrogen content were quantified using a CHN elemental analyzer (Fourqurean et al. 2005; Dunton et al. 2011). Phosphorus content was determined using a general method that involved oxidation and acid hydrolysis as analyzed by the colorimetric methods of Solórzano and Sharp (1980). Elemental ratios (C:N:P) were calculated on a mole:mole basis, and N:P was inserted into the following equation to derive the Nutrient Limitation Index (Campbell and Fourqurean 2009):

$$\text{Nutrient Limitation Index (NLI)} = 30 - N:P \quad (7)$$

where 30 represents the ideal (median) N:P ratio of benthic marine macrophytes (Atkinson and Smith 1983). A negative or positive NLI value implied P or N limitation, respectively. Additionally, larger indices indicated a greater degree of nutrient limitation.

2.4. Evaluating seagrass condition using indicators and metrics

Monitoring programs acquired the data from physical measurements in the field (measures) such as percent cover, leaf length/width, nutrient content and stable isotope ratios. We performed calculations for the metrics percent cover (conversion of BB to percent cover using OTV and Eq. (1)), Species Dominance Index (Eqs. (2) to (5)) and Nutrient Limitation Index (Eq. (7)). Moreover, we determined metric ratings for each zone or basin (Fig. 2) using the assessment points (Table 3) and the multi-year mean derived from the years of monitoring which served as the reference condition. Carter et al. (2022) found that historical data were critical factors for identifying and setting desired states so management could make informed decisions on the current condition of

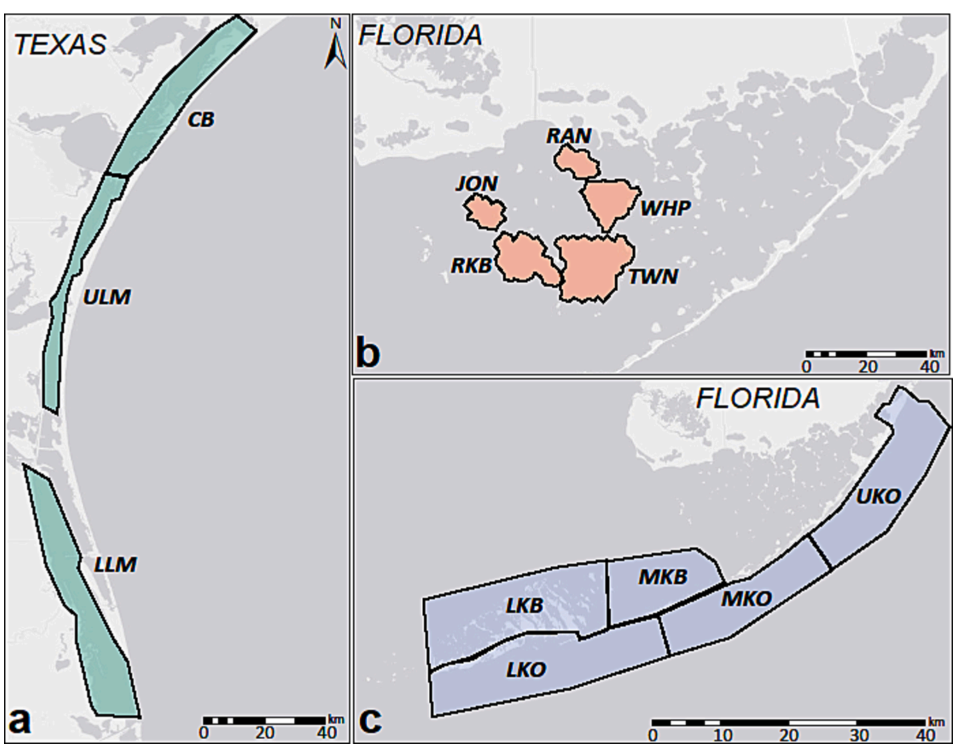

Fig. 2. Zones and basins incorporated in our analyses include, for the Texas Coast (**a**): CB = Coastal Bend; ULM = Upper Laguna Madre; LLM = Lower Laguna Madre; for Florida Bay (**b**): JON = Johnson; RAN = Rankin; RKB = Rabbit Key; TWN = Twin Key; WHP = Whipray; for the Florida Keys (**c**): LKB = Lower Keys Bayside; LKO = Lower Keys Oceanside; MKB = Middle Keys Bayside; MKO = Middle Keys Oceanside; UKO = Upper Keys Oceanside.

Table 3

Summary of selected indicators, metrics, assessment points and metric ratings proposed for seagrass ecosystems across the Gulf of Mexico (GoM). Seagrass-specific indicators in bold and denoted by (*) are presented and assessed within the scope of this paper. Seagrass indicators and metrics were assigned a metric rating (Acceptable, Concerning, Alarming) for each year, determined by the magnitude of change (assessment point) relative to the reference condition. Reference conditions were calculated using the multi-year mean derived from the years of surveying by the respective monitoring program (Texas Seagrass Monitoring Program – TSMP, Fisheries Habitat Assessment Program – FHAP, Florida Keys National Marine Sanctuary – FKNMS-SMP). Note that Phytoplankton Biomass and Change in Cover have two metrics associated with both indicators; the different sets of assessment points were derived to account for regional differences in sediment type and density, respectively. Additional information on abiotic factors, ecosystem function and ecosystem services are presented in the Ecological Resilience Indicators for Five Northern Gulf of Mexico Ecosystems report (Goodin et al. 2018).

MAJOR ECOLOGICAL FACTOR	KEY ECOLOGICAL ATTRIBUTE	INDICATOR	METRIC	METRIC RATINGS AND ASSESSMENT POINTS		
				Acceptable	Concerning	Alarming
Environmental Factors	Water Quality	Transparency	Percent Surface Irradiance	≥ 30%	30 – 20%	≤ 20%
		Phytoplankton Biomass	Chlorophyll *a* concentration			
			Clastic sediments	≤ 10.0 μg L^{-1}	10.0 – 25.0 μg L^{-1}	≥ 25.0 μg L^{-1}
			Carbonate sediments	≤ 1.0 μg L^{-1}	1.0 – 3.0 μg L^{-1}	≥ 3.0 μg L^{-1}
		Sediment Load	Total Suspended Solids	≤ 15 mg L^{-1}	15 – 25 mg L^{-1}	≥ 25 mg L^{-1}
Ecosystem Structure	Abundance	Change in Areal Extent	Areal Extent	0 – 25% increase	< 25% decrease	≥ 25% decrease
		Change in Cover*	Percent Cover			
			≥ 50%	0 – 25% increase	< 25% decrease	≥ 25% decrease
			< 50%	0 – 10% decrease or increase	--	≥ 10% decrease
	Plant Community Structure	**Seagrass Species Composition***	Species Dominance Index	No change or increase	< 25% decrease	≥ 25% decrease
	Morphology	**Shoot Allometry***	Leaf length, Leaf width	≤ 10% change	10 – 25% change	≥ 25% change
	Chemical Constituents	**Nutrient Content***	Nutrient Limitation Index	≤ ±1 change	± 1 to 2.5 change	≥ ± 2.5 change
		Stable Isotope Ratios*	$\delta^{13}C$, $\delta^{15}N$	≤ 0.5 ‰ change	0.5 to 1.0 ‰ change	≥ 1.0 ‰ change
Ecosystem Function	Secondary Production	Scallop Abundance	Scallop Density	≥ 0.4 individuals m^{-2}	0.4 – 0.01 individuals m^{-2}	< 0.01 individuals m^{-2}

seagrasses. We explored if assessment points were effective regardless of species-specific responses by examining measures of total seagrass for each metric (i.e., total seagrass cover). Within a basin or zone, we assigned a metric rating of "Acceptable" (blue), "Concerning" (gray) or "Alarming" (orange) using the designated assessment points for each metric. As an example, for the percent cover metric, mean total seagrass cover from 2011 to 2018 in the Upper Laguna Madre (ULM) was 72.3 %. If cover for any given year ranged between 72.3 % and 90.4 %, or exceeded these values, we assigned an "Acceptable" rating. "Concerning" occurred when mean cover declined to any value between 72.2 % and 54.2 %, and "Alarming" when cover dipped below 54.1 %.

Because the disturbances occurred shortly after spring and summer sampling in Florida, we assessed the impacts from the drought (2015) and Hurricane Irma (2017) the following spring (Florida Bay) or summer (Florida Keys) in 2016 and 2018. For the Texas Coast, we evaluated the impacts for both events during the drought (2013) and immediately following Hurricane Harvey (2017). We visualized multivariate differences across time (before, after, one year) for each disturbance type (drought and hurricane) using nonmetric multidimensional scaling in R (R Core Team, 2021) to identify shifts in the seagrass community.

2.5. Selecting seagrass indicators, metrics and assessment points

Although the seagrass working group identified a total of 10 indicators and 12 metrics, we focused on five seagrass-centric indicators for this study (Table 3). The five seagrass indicators, commonly measured across monitoring programs included: change in cover, seagrass species composition, shoot allometry, nutrient content, and stable carbon and nitrogen isotope ratios. We evaluated five indicators and six metrics for the Texas Coast and Florida Keys, and three indicators and four metrics for Florida Bay (Table 1). We also derived assessment points for each metric (Table 3).

2.6. Rationale for selecting indicators, metrics and assessment points

2.6.1. Change in percent cover

Percent cover is not only an efficient and cost-effective measure of seagrass condition, but is also a sensitive, responsive, and accurate measure of spatial and temporal changes in seagrass abundance (Fourqurean et al. 2001; Neckles et al. 2012). Assessment points for percent cover (Table 3) were separated into two categories (cover ≥50 % and cover <50 %) to account for both continuous meadows and regions composed of sparser seagrass beds (Zieman et al. 1989; Durako 1994; Hall et al. 1999; Fourqurean et al. 2003). We used the minimal detectable change of a Braun-Blanquet (BB) Cover Abundance scale (25 %) as an assessment point for cover ≥50 %; however, when seagrass cover dipped below 50 %, assessment points were set to 10 % to detect change while maintaining sufficient sensitivity in this commonly collected parameter (Braun-Blanquet 1932; Kenworthy et al. 1993).

2.6.2. Seagrass species composition

The Species Dominance Index (SDI; Madden et al. 2009) is a measure of the degree to which a species dominates a specified location. Since productive seagrass beds typically consist of only a few species, "Acceptable" ratings were defined by seagrass meadows that remained relatively stable or approached greater diversity. Seagrass beds with high diversity (genetic and/or multi-species) are likely comprised of individual plants that are better equipped to combat disturbances or facilitate recovery (Hughes and Stachowicz 2004; Duffy 2006). A region that is stable (no change) or increases in diversity is considered "Acceptable" whereas decreases in diversity may reflect the loss of a species and indicate "Concerning" or "Alarming conditions". The difference between "Concerning" and "Alarming" assessment ratings corresponds to the minimal detectable range of a BB score (25 %) (Table 3).

2.6.3. Shoot allometry

Generally, low light availability (i.e., shading) eventually results in decreased leaf length (Dunton 1994; Gordon et al. 1994; Hall et al. 1999) and width (Dunton 1994). Conversely, an increase in leaf length and width may indicate a shift in nutrient availability such as nitrogen enrichment (Powell et al. 1989; Lee and Dunton 2000). Because morphological plasticity is variable by species and in response to changes in environmental conditions (Ralph et al. 2007; McDonald et al. 2016), the associated assessment points (changes ≤10 %, 10–25 %, or ≥25 %; Table 3) were derived from the net extension or reduction in leaf length or width. The basis for assessment points was supported by fertilization experiments from Lee and Dunton (2000); in fertilized plots, *T. testudinum* leaf width significantly increased (>25 % change), but there were no significant differences between treatment and control plots when the change in width was less than 10 %.

2.6.4. Nutrient content

The elemental (C, N, P) and isotopic (δ^{13}C, δ^{15}N) compositions of seagrass tissue is related to nutrient availability and environmental condition (Atkinson and Smith 1983; Fourqurean et al. 2005; Fourqurean et al., 2007). For seagrasses, tissue N:P ratios approaching 30:1 indicate nutrient balance (Atkinson and Smith 1983; Duarte 1990; Fourqurean and Zieman 2002). However, there is interspecific variation in the elemental composition of seagrasses as ratios may vary due to differences in life history traits such as growth rates (Campbell and Fourqurean 2009). Regardless, the degree of deviation from the ideal N:P ratio of 30:1 reflects the extent and type of nutrient limitation. Therefore, the Nutrient Limitation Index (NLI; Eq. (7)) can be used to ascertain whether a plant, representative of a location and time interval, is nutrient limited depending on the sign (+ vs. –) of the index value (Campbell and Fourqurean 2009). Response time is size-dependent and can range 1.4–28 weeks (Roca et al. 2016). Positive or negative indices imply N or P limitation, respectively. Larger index values, those more distant from a N:P ratio of 30:1, indicate greater degrees of nutrient limitation. Assessment points (ratio change of 0 to ±1, ±1 to 2.5, or ≥ ±2.5; Table 3) reflect previous work where N and P enrichment experiments failed to alter seagrass cover or productivity at N:P ratios of 31:1 in *T. testudinum* (Armitage et al. 2005), suggesting a balance with N and P supply and demand (Atkinson and Smith 1983). “Concerning” (±1 to 2.5) and “Alarming” (≥ ±2.5) assessment points were developed using seasonal ranges that occur naturally in seagrass elemental stoichiometry in Florida Bay (Fourqurean et al. 2005). Sources of nutrient enrichment are often determined in combination with shifts in nitrogen isotopic composition.

2.6.5. Stable isotope ratios

Stable isotopic signatures are often employed to identify nutrient sources in ecosystems (Dawson et al. 2002), and frequently used to reconstruct light and water quality conditions that impact seagrass dynamics. Carbon isotope values (δ^{13}C) are controlled by carbon sources and concentrations (Durako and Sackett 1993; Campbell and Fourqurean 2011), irradiance, and temperature (Durako and Hall 1992; Grice et al. 1996). Nitrogen isotope values (δ^{15}N) provide information regarding the source of dissolved inorganic nitrogen, where enriched values have been linked to eutrophic marine ecosystems (McClelland et al. 1997). We used the seasonal sinusoidal relationship (Fourqurean et al. 2005; Campbell and Fourqurean 2009) to develop assessment points for δ^{13}C and δ^{15}N (Table 3) where the amplitude of the sine model (~0.5 ‰) was doubled to provide the boundary between “Concerning” and “Alarming” ratings. “Acceptable” ratings were assigned when changes in δ^{13}C and δ^{15}N were less than the amplitude. Therefore, δ^{13}C and δ^{15}N values outside of this range (>1‰ change) likely reflect an alteration in the assimilation of carbon and/or nitrogen sources. We recognize that physiological differences in carbon acquisition can produce interspecific variation in carbon isotope values of seagrasses (Campbell and Fourqurean 2009), but such responses often occur in conjunction with changes in elemental ratios.

3. Results

3.1. Texas Coast: Drought and Hurricane Harvey

Much of the state of Texas exhibited prolonged severe/exceptional drought conditions from 2011 to 2014 (Seager et al. 2014). Drought can lead to high evaporation rates, and reduced rain and riverine inflow, resulting in hypersaline waters, which can chronically stress seagrasses. Moreover, local geomorphology that restricts water exchange and/or upstream hydrologic alterations can further exacerbate hypersaline

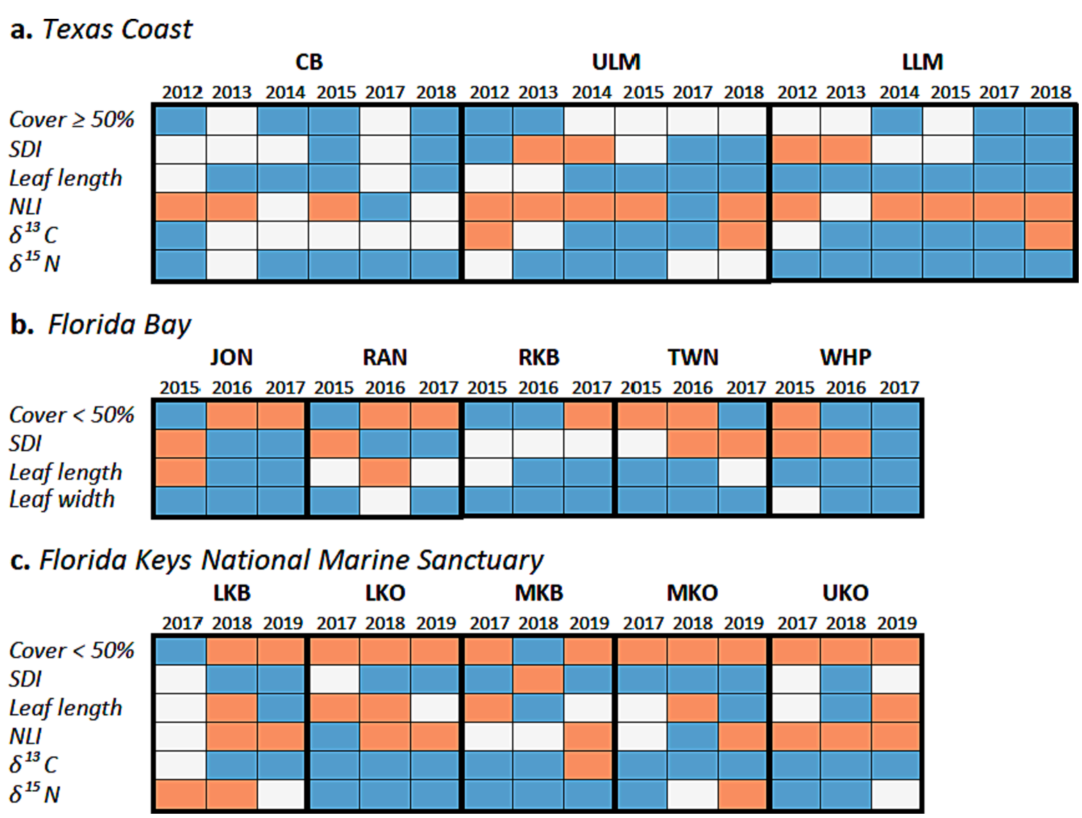

Fig. 3. Ratings were derived using assessment points for each metric across time (before, during and one year after the disturbance) and space (zone or basin) for the Texas Coast (**a**), Florida Bay (**b**) and Florida Keys National Marine Sanctuary (**c**). Ratings were assigned as: ■ = “Acceptable”, □ = “Concerning”, or ■ = “Alarming”. Metrics included cover (≥50 % or < 50 %), Species Dominance Index (SDI), leaf length, leaf width, Nutrient Limitation Index (NLI) and stable isotope ratios (δ^{13}C and δ^{15}N).

conditions. Severe drought conditions in Texas were responsible for "Concerning" and "Alarming" ratings for 50–67 % of metrics in the Upper Laguna Madre (ULM) from 2012 to 2014 (Fig. 3a; Fig. S1a – f). These ratings were primarily due to the loss of *S. filiforme* cover in 2012–2013 (Wilson and Dunton 2018), which ultimately contributed to reductions in leaf length and SDI. The cover metric did not detect this loss as it was almost immediately replaced by *H. wrightii* (Wilson and Dunton 2018). Starting 2014, the ULM was assigned an "Alarming" rating due to declines in total seagrass cover. Interestingly, there was a substantial increase in cover and leaf length in 2012 prior to declining conditions in 2013 (Fig. S1a and c). By 2015, cover, leaf length, δ^{13}C and δ^{15}N metrics reached "Acceptable" status, while SDI improved from "Alarming" to "Concerning" and Nutrient Limitation Index (NLI) remained "Alarming".

In 2017, we observed changes in seagrass condition in the CB following Hurricane Harvey, with 67 % of the metrics assigned as "Concerning" (Fig. 3a; Fig. S1a – f). "Concerning" conditions coincided with decreases in cover, SDI, and leaf length (Fig. 3a; Fig. S1a – c), and slightly more negative δ^{13}C values (Fig. 3a; Fig. S1e). By 2018, cover, SDI and leaf length returned to "Acceptable" conditions (Fig. 3a; Fig. S1a – c). Although "Concerning" ratings endured in the ULM in 2017, these were not directly storm related as Harvey made landfall more than 60 km away (Congdon et al. 2019). A sharp and progressive decline in conditions of Nutrient Limitation Index (NLI), δ^{13}C and δ^{15}N (Fig. S1e and f; Fig. 3a) suggest that other environmental stressors were involved, such as low light conditions. Despite the Lower Laguna Madre (LLM) faring the best of all regions during both disturbances, the drought appeared to have had a greater impact with 50 % of the metrics rated as "Acceptable" relative to 83 % after the hurricane (Fig. 3a; Fig. S1a – f).

3.2. Florida Bay: Drought

Like observations in Texas, drought conditions in Florida preceded seagrass losses in the case studies (Florida Bay: Hall et al. 2016; Texas Coast: Wilson and Dunton 2018). Western Florida Bay has exhibited extensive seagrass die-offs (Robblee et al. 1991; Zieman et al. 1999) and regional drought conditions occurred again in 2014–2015 (Hall et al. 2016; Cole et al. 2018; Johnson et al. 2018; Fredley et al. 2019). Cover appeared to consistently respond across basins where we assigned metric ratings of "Alarming" for Johnson Key (JON), Rankin Lake (RAN), Rabbit Key (RKB), Twin Key (TWN) and Whipray (WHP) before, during and/or one year after the drought (Fig. 3b; Fig. S2a). SDI in JON, RAN, TWN and WHP reached "Alarming" conditions, and "Concerning" at RKB (Fig. 3b; Fig. S2b). "Alarming" and/or "Concerning" conditions for leaf length occurred within JON, RAN and RKB before and during the drought from leaf lengthening (Fig. 3b; Fig. S2c). Leaf width had the greatest proportion of "Acceptable" ratings compared to other metrics, with two basins (RAN, WHP) characterized as "Concerning" due to leaf narrowing (Fig. 3b; Fig. S2d). We observed peak increases in cover and leaf length at JON and RAN in 2015 prior to precipitous declines in 2016 (Fig. 3b; Fig. S2a and c).

3.3. Florida Keys: Hurricane Irma

In 2018, following Hurricane Irma, we detected declines in cover ("Alarming") and leaf length ("Concerning") for Lower Keys Bayside (LKB; Fig. 3c; Fig. S3a and c). Although there were changes in SDI and leaf length at Middle Keys Bayside (MKB) and Middle Keys Oceanside (MKO), respectively, it was likely not storm related at MKB since cover increased and most metrics were assigned as "Acceptable". For MKO, it is possible that "Concerning" and "Alarming" conditions in 2017 exacerbated the impacts of the storm, which resulted in declines in cover and canopy height (Fig. S3a and c). NLI, δ^{13}C and δ^{15}N remained relatively unchanged from the previous year for most zones (Fig. 3c; Fig. S3d – f), except for NLI at Lower Keys Oceanside (LKO) and LKB, which declined to "Alarming" conditions. LKB was most affected by Irma (Wilson et al. 2020), largely due to declines in leaf length and cover. By 2019, one-year after the storm, leaf length recovered to "Acceptable" conditions, but cover remained "Alarming" (Fig. 3c).

4. Discussion

There is no shortage of seagrass indicators in the literature (Martínez-Crego et al. 2008; Madden et al. 2009; Marbà et al. 2013; McMahon et al. 2013; Roca et al. 2016; Yang et al. 2018), which at times may hinder indicator selection and standardization due to variations in their definition, methodology, application, and interpretation across temporal and spatial scales. Even the term "indicator" represents a conceptual challenge as it is both frequently used and variously defined in the science and policy realms. Here, indicator represents an important concept in our hierarchical approach to seagrass status assessment. An indicator should be a measurable ecosystem feature or process that characterizes the condition of an ecosystem. Indicators should consist of an identifiable metric and measure to assess and monitor condition; where metrics are quantified forms of indicators that inform relative condition, while measures are the data measured in the field and used to calculate the metric. An indicator-based approach has the capacity to provide early warnings, particularly when paired with metric ratings and specific assessment points. In addition to being relevant to scientists and resource managers, indicators should be robust, cost-effective, minimally destructive, simple to measure and interpret, and respond in a predictable manner (Dale and Beyeler 2001; Kurtz et al. 2001).

A *meta*-analysis from Marbà et al. (2013) identified an astonishing 49 indicators and 51 metrics measured by 42 seagrass monitoring programs. Shortly thereafter, Roca et al. (2016) contributed 85 indicators that were primarily composed of biochemical and to a lesser extent, morphological and structural measures. These reviews suggest that the most challenging aspect of identifying useful indicators is ensuring applicability across large spatial scales. The distillation of such comprehensive lists is a challenging, yet necessary exercise to identify candidate indicators appropriate for long-term monitoring programs (Borja et al. 2008). Moreover, it is important to have standardized metrics across programs to compare responses, and track status and trends at regional scales (Duffy et al. 2019). Ultimately, resource managers require indicators and metrics that are simple, robust and provide information on ecosystem trajectory and resilience (Unsworth et al. 2015).

Based on these criteria, we selected five widely used indicators and seven metrics that complement recent synthetic reviews of seagrass ecological indicators (e.g., Marbà et al. 2013; Roca et al. 2016), and can serve as robust measures of ecosystem stability and resilience. There are approximately 38 monitoring programs throughout the GoM and many are currently measuring the proposed indicators (see Goodin et al. 2018). The most universally implemented indicators are abundance and plant community structure (79–87 %), followed by water quality (32–45 %), and morphology and plant constituents (8–34 %). We considered environmental variations among seagrass habitats by customizing two sets of metric ratings and assessment points to account for regional differences in seagrass meadow landscapes (i.e., dense vs. sparse cover). Moreover, our indicators and metrics align with seagrass monitoring strategies proposed by Roca et al. (2016) since we blended stress-specific indicators with structural indicators; the proposed set of indicators can be used to assess seagrass trends, identify drivers of change, and evaluate management actions.

4.1. Evaluation of seagrass condition following natural disturbances

4.1.1. Structural and morphological indicators

Our proposed ranges for cover (10–25 % change) detected a response to droughts and align with Collier et al. (2020) who set targets using the maximum values across 3–4 years of the highest biomass, bounded by 95 % confidence intervals. Although variations exist in the response times of structural/morphological (longer) and biochemical (shorter) indicators, we detected changes in seagrass response using percent cover and shoot allometry. In the case of hurricanes Irma and Harvey, the mechanical removal of seagrass (Congdon et al. 2019; Wilson et al. 2020) explained why structural and morphological indicators/metrics (cover and leaf length) responded faster than biochemical processes.

Studies suggest that structural indicators may be inadequate for assessing recovery due to their longer response times (McMahon et al. 2013). Moreover, rates are usually slower for recovery than degradation (Roca et al. 2016) and can vary in trajectory depending on time (i.e., <1 year, 1–5 years, >5 years, etc.) since disturbance (see O'Brien et al. 2018). Cover and leaf length recovered to pre-hurricane conditions the following year in Texas (Fig. 3a, Fig. S1a and c). In contrast, peak cover and leaf length, coupled with regional drought, facilitated extensive die-offs, delaying recovery (1–4 years) of seagrasses in Texas and Florida Bay (Fig. S1a, Fig. S2a).

4.1.2. Biochemical indicators

NLI, δ^{13}C and δ^{15}N metrics provide warning signals of environmental degradation (Martínez-Crego et al. 2008), however, it is strongly recommended that sampling and data comparisons occur during the same season. The values of δ^{13}C and δ^{15}N vary seasonally, peaking in summer (Fourqurean et al. 2005), which can result in misinterpretation if summer values were compared to winter values. Fortuitously, we had the opportunity to compare data during the same seasons across years, documenting decreases in leaf δ^{13}C values within the CB on the Texas Coast beginning 2015 (Fig. S1e). These changes suggest a combined effect of light limitation and the presence of riverine dissolved inorganic carbon (Cuddy 2018) following a major flood event (Reyna et al. 2017). Typically, low light conditions cause narrowing of seagrass blades which may have increased their vulnerability to mechanical damage (de los Santos et al. 2016) from Hurricane Harvey.

In Texas, the ULM has exhibited declines in seagrass biomass resulting from chronic reductions in light availability (e.g., brown tide; Dunton 1994). Sharp changes in δ^{13}C and δ^{15}N from 2015 to 2018 indicated environmental stress via light deprivation reflected in concurrent declines of seagrasses in areas of historically continuous *H. wrightii* beds (https://www.texasseagrass.org). A possible explanation is that water depth has substantially increased (approximately 30 cm) from 2011 to 2020 (V. Congdon, unpublished data), reducing the amount of light reaching the benthic plants, particularly those located in deeper areas within the lagoon (V. Congdon, personal observation; Cuddy and Dunton 2023). This increase in water depth may be a result of relative sea level rise (Liu et al. 2020), long residence times due to limited exchange, and/or large-scale climatic events (e.g., flooding, above average rainfall during El Niño, hurricanes).

4.1.3. Early warnings and recovery

Seagrasses within drought-affected basins may reach critical points of deteriorating condition when high salinities are coupled with seasonally elevated temperatures as noted by Hall et al. (2016) for dense beds of *T. testudinum* in Florida Bay. High temperatures and salinities associated with drought conditions often increase oxygen demands in the plant and sediments despite reduced oxygen solubility in the water column (Borum et al. 2005). By fall, plants downregulate productivity, which supplies less internal oxygen, creating an oxygen imbalance; this imbalance increases the plant's susceptibility to sulfide intrusion, leading to decreases in abundance, and then death (Koch et al. 2007; Koch et al. 2022).

Abundance (i.e., cover, biomass, shoot density) and leaf morphology may serve as precursors of impending susceptibility to mortality via bed overdevelopment (Robblee et al. 1991; Koch et al. 2007). Dense meadows exposed to environmental stressors were more vulnerable to die-off (Zieman et al. 1999) because of higher respiratory demands associated with greater belowground biomass. Generally, increases in density are viewed as a positive response, however, Collier et al. (2014) demonstrated that shoot proliferation preceded plant mortality in response to salinity stress. Although we did not directly measure biomass or shoot density, we observed peak increases in *T. testudinum* leaf length (10–25 %) and cover (>10 %) at JON and RAN (Florida) prior to precipitous declines. Additionally, "Alarming" SDI ratings preceded collapse, which could indicate reduced resiliency (Fig. S2b). Similarly, increases in total seagrass leaf length (10–25 %) and cover (~25 %) occurred prior to declines in cover, leaf length and SDI in the ULM (Texas; Fig. 3a, Fig. S1a and c). Large changes in leaf length prior to cover loss may also serve as an early-warning signal of ecosystem change (Brock and Carpenter, 2006; Carpenter and Brock, 2006; Scheffer et al. 2009).

In many cases, some seagrass indicators may also have value as indicators of recovery. Seagrasses in Texas and Florida appeared to rebound quickly (Congdon et al. 2019) or even resist direct damage (Wilson et al. 2020) from storms. In the CB (Texas), cover and leaf length recovered to pre-disturbance values within a year of Hurricane Harvey (Fig. 3a; Fig. S1a and c), as cropped blades likely regenerated where belowground biomass remained intact (Congdon et al. 2019). Similarly, leaf length conditions improved in affected zones within the Florida Keys following Hurricane Irma (Fig. 3c; Fig. S3c). Interestingly, during the drought in ULM (Texas), leaf length appeared as a leading indicator, followed by changes in SDI, and cover as a trailing indicator. These scenarios highlight the differences in the response time of seagrass indicators to droughts and hurricanes; conditions may not cause immediate mortality pending the plant's plasticity, physiological tolerances, adaptations, and exposure to the disturbance thereby resisting degradation. Recent work identifies the trade-off between ecosystem resistance and resilience, underscoring the vulnerability of coastal habitats (i.e., seagrasses, mangroves) to disturbances (Patrick et al. 2020; Patrick et al. 2022).

Droughts and hurricanes inflicted damage across various spatial and temporal scales. In Texas, drought conditions in the ULM caused an immediate shift in the seagrass community following the event. One-year post-drought, seagrass communities resembled pre-disturbance communities (Fig. 4). In Florida Bay, JON and RAN did not return to pre-drought conditions and remained in this state for at least one year after the disturbance (Fig. 4). Conversely, seagrass communities appear to be quite resistant and resilient to hurricanes. In both Florida (LKB) and Texas (CB North and South), seagrasses exhibited minor shifts in the community after the disturbance (Fig. 5). These findings provide proof-of-concept that the indicators, metrics, and assessment points presented here are scaled appropriately and allow for the detection of changes and recovery within the seagrass community in response to disturbances.

4.2. Moving forward: Things to consider

Seagrass morphometrics (i.e., leaf length, leaf width) and community structure (i.e., cover, species composition) are highly integrative indicators and are effective at tracking environmental degradation as they respond to a broad spectrum of stressors (Roca et al. 2016), whereas biochemical indicators, such as nutrient content and stable isotope ratios, have a greater specificity to a single driver, often shading or nutrients. Regardless of whether an indicator is structural, morphological, or physiological, all can vary in their response time and among species. For example, Collier et al. (2012) found that abundance (e.g., shoot density and biomass), and leaf length and width took months to respond to changes in light availability compared to physiological processes (i.e., leaf extension rates or nutrient concentrations) that took days. Moreover, Roca et al. (2016) found that shading responses were observed within 5–10 weeks for small species but 15–25 weeks for larger species. Meadow-scale characteristics (i.e., cover, species composition) responded most consistently across seagrass species, space, and time in comparison to biochemical indicators (McMahon et al. 2013).

Differences in the specificity and response times of various indicators require monitoring strategies that include measurements of

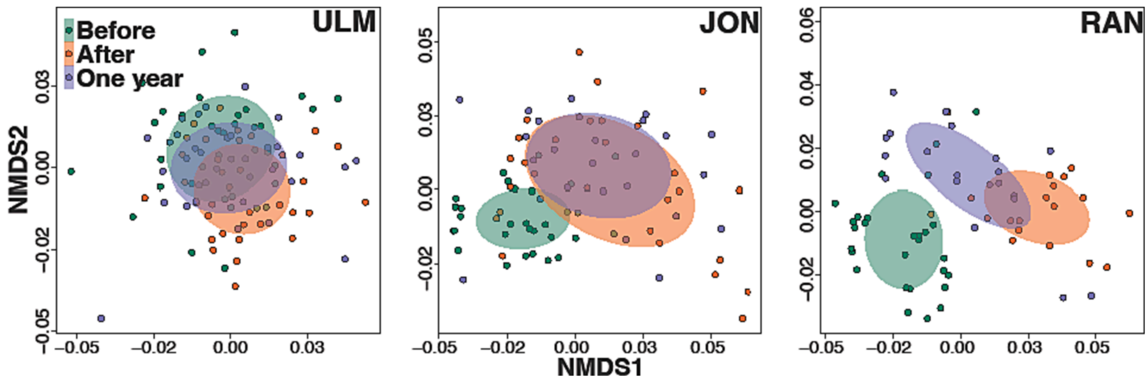

Fig. 4. nMDS plots showing scaled means of seagrass metrics before, after and one year following the droughts within impacted zones/basins for the Texas Coast and Florida Bay (stress < 0.2). The Texas Coast includes Upper Laguna Madre (ULM). Florida Bay basins include Johnson (JON) and Rankin Lake (RAN). Wilson and Dunton (2018) and Hall et al. (2016) reported changes in seagrass communities within these zones/basins following drought conditions.

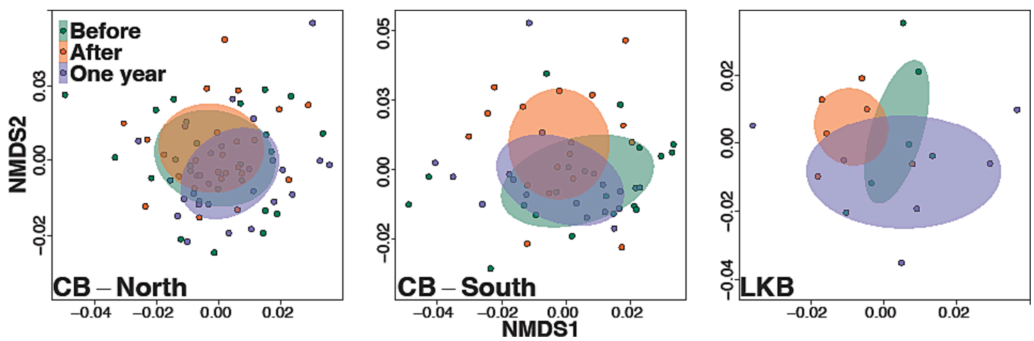

Fig. 5. nMDS plots showing scaled means of seagrass metrics before, after and one year following the hurricanes within impacted zones for the Texas Coast and Florida Keys (stress < 0.2). The Texas Coast includes North and South Coastal Bend (CB). The Florida Key zone includes Lower Key Bayside (LKB). Congdon et al. (2019) and Wilson et al. (2020) reported changes in seagrass communities within these zones following the landfall of hurricanes Harvey and Irma, respectively.

physiological and structural metrics. Although both detect environmental drivers of change, biochemical indicators quickly and reliably pinpoint a specific stressor whereas structural indicators detect generalized degradative processes. Therefore, this overlap affords the opportunity to detect and identify specific stressors (i.e., $\delta^{15}N$ to nutrients and light; Martínez-Crego et al. 2008; Lavery et al. 2009). Ideally, diverse indicators provide an integrative assessment of seagrass ecosystem condition and status. As some indicators have a bi-directional response to stressors (e.g., biochemical, morphology), our framework allows for the inclusion of such indicators because we consider not only the instantaneous value but the change (relative increase and decrease) of an indicator/metric. Ultimately, a monitoring framework that blends both generic and rapid-response indicators would be advantageous and allow management to track a broad range of ecosystem effects.

The use of long-term data is invaluable and provides important context for the natural perturbations that occur within the system. At times, it may be necessary to use expert knowledge to adjust targets or reference conditions as they are often proxies for more latent, site-specific variables. This may also involve decisions regarding data exclusion; for example, an acute disturbance may drastically alter the community and thus, may not reflect 'normal' conditions and desired states (Collier et al. 2020). However, these decisions are not without implications, and can complicate recommendations for specific indicators and syntheses across regions. Additionally, the aggregation of data to provide a comprehensive score may mask specific responses. For example, report cards are popular tools to distill complex scientific information into a more digestible format for diverse, non-technical audiences (Harwell et al. 1999; Dennison et al. 2007; Williams et al. 2009; Orth et al. 2017; Logan et al. 2020; Carter et al. 2023). Although these resources are beneficial to use for the public, the reliance on one or few indicators may not accurately reflect the condition of the ecosystem. For instance, if some indicators are rated "Acceptable" while others suggest "Alarming", an aggregated score may be misleading if it reflects "Acceptable" condition. In this case, the aggregated score reinforces the idea that ecosystem conditions are improving despite other indicators signaling changes within the ecosystem. Therefore, it would be of great value to assess each indicator separately and consider the response times of each indicator when evaluating seagrass ecosystem condition. Ultimately, it is critically important to ensure ratings are provided for each indicator for all types of dissemination strategies so resource managers can make well-informed decisions.

The intrinsic value of indicators is that they can serve as early warning signals of environmental perturbations. However, we used indicators to detect disturbances after the event transpired. In part, this is a result of the disturbance type (hurricane is acute and most likely not predictable by seagrasses), in addition to the differences in response times of the indicators (i.e., biochemical faster response time than structural). Regardless, indicators should have well-documented reactions to disturbances in a system (Dale and Beyeler 2001). Although leading indicators anticipate impending changes in seagrass trajectory, the indicators presented here are reliable trailing indicators of disturbance with the capacity to inform the mechanisms of change. The results yielded from this study can provide actionable intelligence to managers for future decision making and offer the ability to make predictions about recovery potential. A more thorough investigation of leading indicators, particularly biochemical and morphological indicators, coupled with assessment points and metric ratings, may improve predictions of seagrass loss. Here we assessed data from three long-term monitoring programs across the GoM that used different methods, yet the proposed indicator framework was able to identify similar effects of antecedent conditions and coherent responses to common perturbations.

5. Conclusions

Despite a plethora of seagrass indicators (Marbà et al. 2013; McMahon et al. 2013; Roca et al. 2016), the selection of criteria to evaluate seagrass condition is ultimately a cost-benefit analysis. Tier 1 (mapping scale) and Tier 2 (ground-based rapid measurements) indicators and metrics are relatively cost-effective and produce data that are highly replicated; therefore, we recommend that programs incorporate measurements of areal extent (Tier 1) and percent cover, species composition and leaf length (Tier 2). Although Tier 3 indicators are more labor intensive, the incorporation of leaf width, elemental content and isotope ratios into a monitoring framework is necessary to identify the specific stressor(s). Inclusion of structural, morphological, and biochemical indicators within a program's monitoring strategy provides an integrated assessment of seagrass ecosystem condition. The framework proposed here is flexible and adaptable to optimize targets for other regions to meet the needs of resource managers. This methodology could be modified to improve the assessment points, indicators, and metrics for adoption and implementation across monitoring programs within and outside the GoM. Additionally, because seagrasses have not yet captured the public imagination (Unsworth et al. 2018, but see: Courage 2020), distilling information for a broad audience (i.e., public, stakeholders, managers, and policy makers) is imperative to convey their importance. For non-technical audiences, report cards may provide an effective tool informing on the current state and progress towards achieving desired goals (Harwell et al. 1999; Dennison et al. 2007; Williams et al. 2009; Orth et al. 2017; Logan et al. 2020; Carter et al. 2023).

Since resistance, resilience and recovery are important aspects of evaluating ecosystem status, there is great value in assessing how seagrass ecosystems respond to various disturbances (i.e., rapid, one-year recovery, full recovery within 5 years or delayed recovery longer than 5 years; O'Brien et al. 2018). Chronic levels of low stress may provide seagrass meadows with the capacity to recover from more punctuated disturbances (Unsworth et al. 2015). However, when exposed to stressors at levels beyond their physiological and physical limitations, seagrasses can exhibit longer recovery times and reduced resiliency (Scheffer et al. 2009; van de Leemput et al. 2018). The capacity to track ecosystem response across a range of press and pulse perturbation is more important than ever, as an uptick in meteorological disturbances, a changing climate, and increasing human pressures are now reshaping seagrass ecosystems worldwide (Gera et al. 2014; Nowicki et al. 2017; Arias-Ortiz et al. 2018; Kendrick et al. 2019. Conservation efforts require reliable connections between drivers of change and specific organismal and ecosystem responses to disturbance. For seagrasses, such efforts are best achieved through the development of indicators informed by standardized metrics and carefully calibrated assessment points that are based on rigorous data analysis that connect drivers with response variables.

CRediT authorship contribution statement

Victoria M. Congdon: Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – original draft. **Margaret O. Hall:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing. **Bradley T. Furman:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing. **Justin E. Campbell:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing. **Michael J. Durako:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing. **Kathleen L. Goodin:** Conceptualization, Methodology, Writing – review & editing. **Kenneth H. Dunton:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This study was funded by the NOAA RESTORE Science Program to NatureServe [NA15NOS4510227], the University of Texas at Austin [NA15NOS4510234], the U.S. Geological Survey Wetland and Aquatic Research Center [RASP15-18] and supported in part by the U.S. Geological Survey Ecosystems Program. We are deeply appreciative K. Jackson who has led the charge of field and lab work since the infancy of the Texas Seagrass Monitoring Program, in addition to the continued support provided by the Coastal Bend Bays and Estuaries Program (R. Allen; 1610), National Park Service (M. Segura; CESU P16AC01794), and Texas General Land Office (R. Bond; 18-083-000-A592), with in-kind support from the Mission-Aransas National Estuarine Research Reserve (J. Tunnell, Manager). H. Neckles was instrumental in advancing our work, with immeasurable contribution at the workshop and in reviewing of the manuscript, including the pioneer work that is the backbone of this paper. We thank S. Wilson of Florida International University Seagrass Ecosystems Research Lab for providing additional seagrass data. We are also appreciative of assistance from L. Thompson and D. Reed of Florida Fish and Wildlife Conservation Commission for compiling seagrass distribution layers. Funding for Florida Keys National Marine Sanctuary's Water Quality Protection Program seagrass monitoring was provided by Environmental Protection Agency (X7-00D39015). Funding for Florida Bay seagrass monitoring was provided by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research Program (DEB-1237517), and the South Florida Water Management District under the Restoration, Coordination and Verification Program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111090.

References

Arias-Ortiz, A., Serrano, O., Masqué, P., Lavery, P.S., Mueller, U., Kendrick, G.A., Rozaimi, M., Esteban, A., Fourqurean, J.W., Marbà, N., Mateo, M.A., Murray, K., Rule, M.J., Duarte, C.M., 2018. A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. Nat. Clim. Chang. 8, 338. https://doi.org/10.1038/s41558-018-0096-y.

Armitage, A.R., Frankovich, T.A., Heck, K.L., Fourqurean, J.W., 2005. Experimental nutrient enrichment causes complex changes in seagrass, microalgae, and macroalgae community structure in Florida Bay. Estuaries 28, 422–434. https://doi.org/10.1007/BF02693924.

Atkinson, M.J., Smith, S.V., 1983. C-N-P ratios of benthic marine plants. Limnol. Oceanogr. 28, 568–574.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193. https://doi.org/10.1890/10-1510.1.

Borja, Á., Bricker, S.B., Dauer, D.M., Demetriades, N.T., Ferreira, J.G., Forbes, A.T., Hutchings, P., Jia, X., Kenchington, R., Marques, J.C., Zhu, C., 2008. Overview of integrative tools and methods in assessing ecological integrity in estuarine and coastal systems worldwide. Mar. Pollut. Bull. 56, 1519–1537. https://doi.org/10.1016/j.marpolbul.2008.07.005.

Borum, J., Pedersen, O., Greve, T.M., Frankovich, T.A., Zieman, J.C., Fourqurean, J.W., Madden, C.J., 2005. The Potential Role of Plant Oxygen and Sulphide Dynamics in Die-off Events of the Tropical Seagrass, *Thalassia testudinum*. J. Ecol. 93, 148–158. https://doi.org/10.1111/j.1365-2745.2004.00943.x.

Braun-Blanquet, J., 1932. Plant sociology: the study of plant communities. Authorized English translation of Pflanzensoziologie. Translated, revised and edited by GD Fuller and HS Conard. McGraw-Hill, New York, NY.
Bricker, O.P., Ruggiero, M.A., 1998. Toward a national program for monitoring environmental resources. Ecol. Appl. 8, 326–329. https://doi.org/10.1890/1051-0761(1998)008%5B0326:TANPFM%5D2.0.CO;2.
Brock, W.A., Carpenter, S.R., 2006. Variance as a Leading Indicator of Regime Shift in Ecosystem Services. Ecol. Soc. 11, 9. https://doi.org/10.5751/es-01777-110209.
Campbell, J.E., Fourqurean, J.W., 2009. Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. Mar. Ecol. Prog. Ser. 387, 109–123. https://doi.org/10.3354/meps08093.
Campbell, J.E., Fourqurean, J.W., 2011. Novel methodology for in situ carbon dioxide enrichment of benthic ecosystems. Limnol. Oceanogr. Methods 9, 97–109. https://doi.org/10.4319/lom.2011.9.97.
Carpenter, S.R., Brock, W.A., 2006. Rising variance: a leading indicator of ecological transition. Ecol. Lett. 9, 311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x.
Carter, S.L., Bennetts, R.E., 2007. The road to integrating science and management: Planning your next trip using hierarchical objectives and assessment points. The George Wright Forum 24, 78–93.
Carter, A.B., Collier, C., Coles, R., Lawrence, E., Rasheed, M.A., 2022. Community-specific "desired" states for seagrasses through cycles of loss and recovery. J. Environ. Manag. 314 https://doi.org/10.1016/j.jenvman.2022.115059.
Carter, A.B., Coles, R., Jarvis, J.C., Bryant, C.V., Smith, T.M., Rasheed, M.A., 2023. A report card approach to describe temporal and spatial trends in parameters for coastal seagrass habitats. Sci. Rep. 13, 1–14. https://doi.org/10.1038/s41598-023-29147-1.
Ceccherelli, G., Oliva, S., Pinna, S., Piazzi, L., Procaccini, G., Marin-Guirao, L., Dattolo, E., Gallia, R., La Manna, G., Gennaro, P., Costa, M.M., Barrote, I., Silva, J., Bulleri, F., 2018. Seagrass collapse due to synergistic stressors is not anticipated by phenological changes. Oecologia 186, 1137–1152. https://doi.org/10.1007/s00442-018-4075-9.
Cole, A.M., Durako, M.J., Hall, M.O., 2018. Multivariate analysis of water quality and benthic macrophyte communities in Florida Bay, USA reveals hurricane effects and susceptibility to seagrass die-off. Front. Plant Sci. 9, 1–16. https://doi.org/10.3389/fpls.2018.00630.
Collier, C.J., Waycott, M., Ospina, A.G., 2012. Responses of four Indo-West Pacific seagrass species to shading. Mar. Pollut. Bull. 65, 342–354. https://doi.org/10.1016/j.marpolbul.2011.06.017.
Collier, C.J., Villacorta-Rath, C., Van Dijk, K.J., Takahashi, M., Waycott, M., 2014. Seagrass proliferation precedes mortality during hypo-salinity events: A stress-induced morphometric response. PLoS One. https://doi.org/10.1371/journal.pone.0094014.
Collier, C.J., Adams, M.P., Langlois, L., Waycott, M., O'Brien, K.R., Maxwell, P.S., McKenzie, L., 2016. Thresholds for morphological response to light reduction for four tropical seagrass species. Ecol. Indic. 67, 358–366. https://doi.org/10.1016/j.ecolind.2016.02.050.
Collier, C.J., Carter, A.B., Rasheed, M., McKenzie, L., Udy, J., Coles, R., Brodie, J., Waycott, M., O'Brien, K.R., Saunders, M., Adams, M., Martin, K., Honchin, C., Petus, C., Lawrence, E., 2020. An evidence-based approach for setting desired state in a complex Great Barrier Reef seagrass ecosystem: A case study from Cleveland Bay. Environ. Sustain. Indic. 7, 100042 https://doi.org/10.1016/j.indic.2020.100042.
Congdon, V.M., Bonsell, C., Cuddy, M.R., Dunton, K.H., 2019. In the wake of a major hurricane: Differential effects on early vs. late successional seagrass species. Limnol. Oceanogr. Lett. 4, 155–163. https://doi.org/10.1002/lol2.10112.
Costanza, R., Arge, R., Groot, R.D., Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Neill, R.V.O., Paruelo, J., Raskin, R.G., Suttonkk, P., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260. https://doi.org/10.1038/387253a0.
Courage, K.H., 2020. Prairies of the sea. Smithsonian 51 (8), 52–65.
Cuddy, M.R., 2018. Patterns in isoscapes and N: P stoichioscapes of the dominant seagrasses (Halodule wrightii and Thalassia testudinum) in the western Gulf of Mexico. University of Texas, Austin, TX. Masters thesis.
Cuddy, M.R., Dunton, K.H., 2023. Seagrass isoscapes and stoichioscapes reveal linkages to inorganic nitrogen sources in the Lower Laguna Madre, western Gulf of Mexico. Estuaries and Coasts. https://doi.org/10.1007/s12237-023-01206-w.
Dakos, V., Carpenter, S.R., van Nes, E.H., Scheffer, M., 2015. Resilience indicators: Prospects and limitations for early warnings of regime shifts. Philos. Trans. r. Soc. B Biol. Sci. 370, 1–10. https://doi.org/10.1098/rstb.2013.0263.
Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecol. Indic. 1, 3–10. https://doi.org/10.1016/S1470-160X(01)00003-6.
Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annu. Rev. Ecol. Syst. 33, 507–559. https://doi.org/10.1146/annurev.ecolsys.33.020602.095451.
de los Santos, C.B., Onoda, Y., Vergara, J.J., Pérez-Lloréns, J.L., Bouma, T.J., La Nafie, Y. A., Cambridge, M.L., Brun, F.G., 2016. A comprehensive analysis of mechanical and morphological traits in temperate and tropical seagrass species. Mar. Ecol. Prog. Ser. 551, 81–94. https://doi.org/10.3354/meps/11717.
Dennison, W.C., Lookingbill, T.R., Carruthers, T.J.B., Hawkey, J.M., Carter, S.L., 2007. An eye-opening approach to developing and communicating integrated environmental assessments. Front. Ecol. Environ. 5, 307–314. https://doi.org/10.1890/1540-9295(2007)5.
Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. Prog. Ser. 67, 201–207. https://doi.org/10.3354/meps067201.
Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat. Publ. Gr. 3, 961–968. https://doi.org/10.1038/nclimate1970.
Duffy, J.E., 2006. Biodiversity and the functioning of seagrass ecosystems. Mar. Ecol. Prog. Ser. 311, 233–250. https://doi.org/10.3354/meps311233.
Duffy, J.E., Benedetti-Cecchi, L., Trinanes, J., Muller-Karger, F.E., Ambo-Rappe, R., Boström, C., Buschmann, A.H., Byrnes, J., Coles, R.G., Creed, J., Cullen-Unsworth, L. C., Diaz-Pulido, G., Duarte, C.M., Edgar, G.J., Fortes, M., Goni, G., Hu, C., Huang, X., Hurd, C.L., Yaakub, S.M., 2019. Toward a coordinated global observing system for seagrasses and marine macroalgae. Front. Mar. Sci. 6, 317. https://doi.org/10.3389/fmars.2019.00317.
Dunic, J.C., Brown, C.J., Connolly, R.M., Turschwell, M.P., Côté, I.M., 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. Glob. Chang. Biol. 27, 4096–4109. https://doi.org/10.1111/gcb.15684.
Dunton, K.H., 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. Mar. Biol. 120, 479–489.
Dunton, K.H, Pulich, W., Mutchler, T., 2011. A seagrass monitoring program for Texas coastal waters: Multiscale integration of landscape features with plant and water quality indicators. Coastal Bend Bays & Estuaries Program, Corpus Christi, TX. 39 pages.
Durako, M.J., 1994. Seagrass die-off in Florida Bay (USA): changes in shoot demographic characteristics and population dynamics in Thalassia testudinum. Mar. Ecol. Prog. Ser 110, 59–66. https://doi.org/10.3354/meps110059.
Durako, M.J., Hall, M.O., 1992. Effects of light on the stable carbon isotope composition of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 86, 99–101. https://doi.org/10.3354/meps086099.
Durako, M.J., Sackett, W.M., 1993. Effects of CO2(aq) on the carbon isotopic composition of the seagrass Thalassia testudinum Banks ex König (Hydrocharitaceae). J. Exp. Mar. Biol. Ecol. 169, 167–180. https://doi.org/10.1016/0022-0981(93)90192-Q.
Durako, M.J., Hall, M.O., Merello, M., 2002. Patterns of change in the seagrass-dominated Florida Bay hydroscape. In: Porter, J.W., Porter, K.G. (Eds.), Linkages between Ecosystems in the South Florida Hydroscape: the River of Grass Continues. CRC Press, Boca Raton, FL, pp. 515–529.
FIU Seagrass Ecosystems Research Lab. FKNMS and FL Bay Interactive Data Plots and Downloads, Florida International University. http://seagrass.fiu.edu/index.htm (accessed 1 August 2020).
Fourqurean, J.W., Boyer, J.N., Durako, M.J., Hefty, L.N., Peterson, B.J., 2003. Forecasting responses of seagrass distributions to changing water quality using monitoring data. Ecol. Appl. 13, 474–489. https://doi.org/10.1890/1051-0761(2003)013%5B0474:FROSDT%5D2.0.CO;2.
Fourqurean, J.W., Escorcia, S.P., Anderson, W.T., Zieman, J.C., 2005. Spatial and seasonal variability in elemental content, delta C-13, and delta N-15 of *Thalassia testudinum* from South Florida and its implications for ecosystem studies. Estuaries 28, 447–461. https://doi.org/10.1007/BF02693926.
Fourqurean, J.W., Durako, M.J., Hall, M.O., Hefty, L.N., 2002. Seagrass Distribution in South Florida: A Multi-Agency Coordinated Monitoring Program. In The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook, ed. J.W. Porter and K.G. 497–522. CRC Press LLC.
Fourqurean, J.W., Zieman, J.C., 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.
Fourqurean, J.W., Willsie, A., Rose, C.D., Rutten, L.M., 2001. Spatial and temporal pattern in seagrass community composition and productivity in South Florida. Mar. Biol. 138, 341–354. https://doi.org/10.1007/s002270000448.
Fredley, J., Durako, M.J., Hall, M.O., 2019. Multivariate analyses link macrophyte and water quality indicators to seagrass die-off in Florida Bay. Ecol. Indic. 101, 692–701. https://doi.org/10.1016/j.ecolind.2019.01.074.
Furman, B.T., Leone, E.H., Bell, S.S., Durako, M.J., Hall, M.O., 2018. Braun-Blanquet data in ANOVA designs: Comparisons with percent cover and transformations using simulated data. Mar. Ecol. Prog. Ser. 597, 13–22. https://doi.org/10.3354/meps12604.
Gera, A., Pagès, J.F., Arthur, R., Farina, S., Roca, G., Romero, J., Alcoverro, T., 2014. The effect of a centenary storm on the long-lived seagrass *Posidonia oceanica*. Limnol. Oceanogr. 59, 1910–1918. https://doi.org/10.4319/lo.2014.59.6.1910.
Goodin, K.L., Faber-Langendoen, D., Brenner, J., Allen, S.T., Day, R.H., Congdon, V.M., Shepard, C., Cummings, K.E., Stagg, C.L., Gabler, C.A., Osland, M., Dunton, K.H., Ruzicka, R.R., Semon-Lunz, K., Reed, D., Love, M., 2018. Ecological Resilience Indicators for Five Northern Gulf of Mexico Ecosystems. NatureServe, Arlington, VA. 381 pages.
Gordon, D.M., Grey, K.A., Chase, S.C., Simpson, C.J., 1994. Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading. Aquat. Bot. 47, 265–275. https://doi.org/10.1016/0304-3770(94)90057-4.
Green, E.P., Short, F.T., 2003. World Atlas of Seagrasses. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA.
Grice, A.M., Loneragan, N.R., Dennison, W.C., 1996. Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. J. Exp. Mar. Biol. Ecol. 195, 91–110. https://doi.org/10.1016/0022-0981(95)00096-8.
Hall, M.O., Durako, M.J., Fourqurean, J.W., Zieman, J.C., 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. Estuaries 22, 445–459. https://doi.org/10.2307/1353210.
Hall, M.O., Furman, B.T., Merello, M., Durako, M.J., 2016. Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: Initial observations. Mar. Ecol. Prog. Ser. 560, 243–249. https://doi.org/10.3354/meps11923.

Hall, M.O., Bell, S.S., Furman, B.T., Durako, M.J., 2021. Natural recovery of a marine foundation species emerges decades after landscape-scale mortality. Sci. Rep. 11, 1–10. https://doi.org/10.1038/s41598-021-86160-y.

Handley, L., Lockwood, C., 2020. Seagrass Status and Trends Update for the Northern Gulf of Mexico: 2002-2017. Gulf of Mexico Alliance, Ocean Springs, MS. 53 pages.

Handley, L., Altsman, D., DeMay, R., 2007. Seagrass status and trends in the northern Gulf of Mexico—1940–2002: U.S. Geological Survey Scientific Investigations Report 2006–5287 and U.S. Environmental Protection Agency 855–R–04–003. 267 pages.

Harwell, M.A., Myers, V., Young, T., Bartuska, A., Gassman, N., Gentile, J.H., Harwell, C. C., Appelbaum, S., Barko, J., Causey, B., Johnson, C., McLean, A., Smola, R., Templet, P., Tosini, S., 1999. A framework for an ecosystem integrity report card. BioScience 49, 543–556. https://doi.org/10.2307/1313475.

Harwell, M.A., Gentile, J.H., McKinney, L.D., Tunnell, J.W., Dennison, W.C., Kelsey, R. H., Stanzel, K.M., Stunz, G.W., Withers, K., Tunnell, J., 2019. Conceptual Framework for Assessing Ecosystem Health. Integr. Environ. Assess. Manag. 15, 544–564. https://doi.org/10.1002/ieam.4152.

Heink, U., Kowarik, I., 2010. What are indicators? On the definition of indicators in ecology and environmental planning. Ecol. Indic. 10, 584–593. https://doi.org/10.1016/j.ecolind.2009.09.009.

Hendriks, I.E., Olsen, Y.S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T.S., Howard, J., Duarte, C.M., 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. Biogeosciences 11, 333–346. https://doi.org/10.5194/bg-11-333-2014.

Herrick, J.E., Duniway, M.C., Pyke, D.A., Bestelmeyer, B.T., Wills, S.A., Brown, J.R., Karl, J.W., Havstad, K.M., 2012. A holistic strategy for adaptive land management. J. Soil Water Conserv. 67, 105–113. https://doi.org/10.2489/jswc.67.4.105A.

Holling, C.S., 1973. Resilience and stability of ecological systems. Source Annu. Rev. Ecol. Syst. 4, 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245.

Hughes, A.R., Stachowicz, J.J., 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc. Natl. Acad. Sci. u. s. a. 101, 8998–9002. https://doi.org/10.1073/pnas.0402642101.

Johnson, C.R., Koch, M.S., Pedersen, O., Madden, C.J., 2018. Hypersalinity as a trigger of seagrass (Thalassia testudinum) die-off events in Florida Bay: Evidence based on shoot meristem O2 and H2S dynamics. J. Exp. Mar. Bio. Ecol. 504, 47–52. https://doi.org/10.1016/j.jembe.2018.03.007.

Kendrick, G.A., Nowicki, R., Olsen, Y.S., Strydom, S., Fraser, M.W., Sinclair, E.A., Statton, J., Hovey, R.K., Thomson, J.A., Burkholder, D., McMahon, K.M., Kilminster, K., Hetzel, Y., Fourqurean, J.W., Heithaus, M.R., Orth, R.J., 2019. A systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community. Front. Mar. Sci. 6, 455. https://doi.org/10.3389/fmars.2019.00455.

Kenworthy, W.J., Durako, M.J., Fatemy, S.M.R., Valavi, H., Thayer, G.W., 1993. Ecology of seagrasses in northeastern Saudi Arabia one year after the Gulf-War oil spill. Mar. Pollut. Bull. 27, 213–222. https://doi.org/10.1016/0025-326X(93)90027-H.

Koch, M.S., Schopmeyer, S.A., Nielsen, O.I., Kyhn-Hansen, C., Madden, C.J., 2007. Conceptual model of seagrass die-off in Florida Bay: Links to biogeochemical processes. J. Exp. Mar. Bio. Ecol. 350, 73–88. https://doi.org/10.1016/j.jembe.2007.05.031.

Koch, M.S., Johnson, C.R., Travis, L., Pedersen, O., Madden, C.J., 2022. Hypersalinity effects on O_2 flux across the diffusive boundary layer of leaves in the tropical seagrass *Thalassia testudinum*. J. Exp. Mar. Bio. Ecol. 555, 151780 https://doi.org/10.1016/j.jembe.2022.151780.

Kurtz, J.C., Jackson, L.E., Fisher, W.S., 2001. Strategies for evaluating indicators based on guidelines from the Environmental Protection Agency's Office of Research and Development. Ecol. Indic. 1, 49–60. https://doi.org/10.1016/S1470-160X(01)00004-8.

Lavery, P.S., McMahon, K., Mulligan, M., Tennyson, A., 2009. Interactive effects of timing, intensity and duration of experimental shading on *Amphibolis griffithii*. Mar. Ecol. Prog. Ser. 394, 21–33. https://doi.org/10.3354/meps08242.

Lee, K., Dunton, K.H., 2000. Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass. Mar. Ecol. Prog. Ser. 196, 39–48. https://doi.org/10.3354/meps196039.

Liu, Y., Li, J., Fasullo, J., Galloway, D.L., 2020. Land subsidence contributions to relative sea level rise at tide gauge Galveston Pier 21. Texas. Sci. Rep. 10, 17905. https://doi.org/10.1038/s41598-020-74696-4.

Logan, M., Hu, Z., Brinkman, R., Sun, S., Sun, X., Schaffelke, B., 2020. Ecosystem health report cards: An overview of frameworks and analytical methodologies. Ecol. Indic. 113, 105834 https://doi.org/10.1016/j.ecolind.2019.105834.

Madden, C.J., Rudnick, D.T., McDonald, A.A., Cunniff, K.M., Fourqurean, J.W., 2009. Ecological indicators for assessing and communicating seagrass status and trends in Florida Bay. Ecol. Indic. 9S, S68–S82. https://doi.org/10.1016/j.ecolind.2009.02.004.

Marbà, N., Duarte, C.M., 2010. Mediterranean warming triggers seagrass (Posidonia oceanica) shoot mortality. Glob. Chang. Biol. 16, 2366–2375. https://doi.org/10.1111/j.1365-2486.2009.02130.x.

Marbà, N., Krause-Jensen, D., Alcoverro, T., Birk, S., Pedersen, A., Neto, J.M., Orfanidis, S., Garmendia, J.M., Muxika, I., Borja, Á., Dencheva, K., Duarte, C.M., 2013. Diversity of European seagrass indicators: Patterns within and across regions. Hydrobiologia 704, 265–278. https://doi.org/10.1007/s10750-012-1403-7.

Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G.A., Mazarrasa, I., Bastyan, G.R., Garcia-Orellana, J., Duarte, C.M., 2015. Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. J. Ecol. 103, 296–302. https://doi.org/10.1111/1365-2745.12370.

Marín-Guirao, L., Bernardeau-Esteller, J., Belando, M.D., García-Muñoz, R., Ramos-Segura, A., Alcoverro, T., Minguito-Frutos, M., Ruiz, J.M., 2022. Photo-acclimatory thresholds anticipate sudden shifts in seagrass ecosystem state under reduced light conditions. Mar. Environ. Res. 177 https://doi.org/10.1016/j.marenvres.2022.105636.

Martínez-Crego, B., Vergés, A., Alcoverro, T., Romero, J., 2008. Selection of multiple seagrass indicators for environmental biomonitoring. Mar. Ecol. Prog. Ser. 361, 93–109. https://doi.org/10.3354/meps07358.

McClelland, J.W., Valiela, I., Michener, R.H., 1997. Nitrogen-stable isotope signatures in estuarine food webs: A record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. 42, 930–937. https://doi.org/10.4319/lo.1997.42.5.0930.

McDonald, A.M., Prado, P., Heck, K.L., Fourqurean, J.W., Frankovich, T.A., Dunton, K. H., Cebrian, J., 2016. Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale. Aquat. Bot. 134, 87–96. https://doi.org/10.1016/j.aquabot.2016.07.007.

McMahon, K., Collier, C., Lavery, P.S., 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecol. Indic. 30, 7–15. https://doi.org/10.1016/j.ecolind.2013.01.030.

Mendelssohn, I.A., Byrnes, M.R., Kneib, R.T., Vittor, B.A., 2017. Coastal Habitats of the Gulf of Mexico. In: Ward, C. (Ed.), Habitats and Biota of the Gulf of Mexico: before the Deepwater Horizon Oil Spill. Springer, New York, pp. 359–640. https://doi.org/10.1007/978-1-4939-3447-8_6.

Neckles, H.A., Kopp, B.S., Peterson, B.J., Pooler, P.S., 2012. Integrating Scales of Seagrass Monitoring to Meet Conservation Needs. Estuaries and Coasts 35, 23–46. https://doi.org/10.1007/s12237-011-9410-x.

Neckles, H.A., 1994. Indicator Development: Seagrass Monitoring and Research in the Gulf of Mexico. U.S. Environmental Protection Agency. Office of Research and Development. Environmental Research Laboratory, Gulf Breeze, FL. EPA/620/R-94/029.

Nowicki, R.J., Thomson, J.A., Burkholder, D.A., Fourqurean, J.W., Heithaus, M.R., 2017. Predicting seagrass recovery times and their implications following an extreme climate event. Mar. Ecol. Prog. Ser. 567, 79–93. https://doi.org/10.3354/meps12029.

O'Brien, K.R., Waycott, M., Maxwell, P., Kendrick, G.A., Udy, J.W., Ferguson, A.J.P., Kilminster, K., Scanes, P., McKenzie, L.J., McMahon, K., Adams, M.P., Samper-Villarreal, J., Collier, C., Lyons, M., Mumby, P.J., Radke, L., Christianen, M.J.A., Dennison, W.C., 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Mar. Pollut. Bull. 134, 166–176. https://doi.org/10.1016/j.marpolbul.2017.09.006.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K. L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.

Orth, R.J., Dennison, W.C., Lefcheck, J.S., Gurbisz, C., Hannam, M., Keisman, J., Landry, J.B., Moore, K.A., Murphy, R.R., Patrick, C.J., Testa, J., Weller, D.E., Wilcox, D.J., 2017. Submersed aquatic vegetation in Chesapeake Bay: Sentinel species in a changing world. BioScience 67, 698–712. https://doi.org/10.1093/biosci/bix058.

Patrick, C.J., Yeager, L., Armitage, A.R., Carvallo, F., Congdon, V.M., Dunton, K.H., Fisher, M., Hardison, A.K., Hogan, J.D., Hosen, J., Hu, X., Kiel Reese, B., Kinard, S., Kominoski, J.S., Lin, X., Liu, Z., Montagna, P.A., Pennings, S.C., Walker, L., Weaver, C.A., Wetz, M., 2020. A System Level Analysis of Coastal Ecosystem Responses to Hurricane Impacts. Estuaries and Coasts 43. https://doi.org/10.1007/s12237-019-00690-3.

Patrick, C.J., Kominoski, J.S., McDowell, W.H., Branoff, B., Lagomasino, D., Leon, M., Hensel, E., Hensel, M.J.S., Strickland, B.A., Aide, T.M., Armitage, A., Campos-Cerqueira, M., Congdon, V.M., Crowl, T.A., Devlin, D.J., Douglas, S., Erisman, B.E., Feagin, R.A., Geist, S.J., Hall, N.S., Hardison, A.K., Heithaus, M.R., Hogan, J.A., Hogan, J.D., Kinard, S., Kiszka, J.J., Lin, T.C., Lu, K., Madden, C.J., Montagna, P.A., O'Connell, C.S., Proffitt, C.E., Reese, B.K., Reustle, J.W., Robinson, K.L., Rush, S.A., Santos, R.O., Schnetzer, A., Smee, D.L., Smith, R.S., Starr, G., Stauffer, B.A., Walker, L.M., Weaver, C.A., Wetz, M.S., Whitman, E.R., Wilson, S.S., Xue, J., Zou, X., 2022. A general pattern of trade-offs between ecosystem resistance and resilience to tropical cyclones. Sci. Adv. 8, 1–11. https://doi.org/10.1126/sciadv.abl9155.

Petraitis, P.S., Methratta, E.T., Rhile, E.C., Vidargas, N.A., Dudgeon, S.R., 2009. Experimental confirmation of multiple community states in a marine ecosystem. Oecologia 161, 139–148. https://doi.org/10.1007/s00442-009-1350-9.

Powell, G.V.N., Kenworthy, W.J., Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bull. Mar. Sci. 44, 324–340.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ralph, P.J., Durako, M.J., Enríquez, S., Collier, C.J., Doblin, M.A., 2007. Impact of light limitation on seagrasses. J. Exp. Mar. Bio. Ecol. 350, 176–193. https://doi.org/10.1016/j.jembe.2007.06.017.

Reyna, N.E., Hardison, A.K., Liu, Z., 2017. Influence of major storm events on the quantity and composition of particulate organic matter and the phytoplankton community in a subtropical Estuary. Texas. Front. Mar. Sci. 4 https://doi.org/10.3389/fmars.2017.00043.

Robblee, M.B., Barber, T.R., Carlson Jr, P.R., Durako, M.J., Fourqurean, J.W., Muehlstein, L.K., Porter, D., Yarbro, L.A., Zieman, R.T., Zieman, J.C., 1991. Mass mortality of the tropical seagrass Thalassia testudinum in Florida Bay (USA). Mar. Ecol. Prog. Ser. 71, 297–299. https://doi.org/10.3354/meps071297.

Roca, G., Alcoverro, T., Krause-Jensen, D., Balsby, T.J.S., Van Katwijk, M.M., Marbà, N., Santos, R., Arthur, R., Mascaró, O., Fernández-Torquemada, Y., Pérez, M., Duarte, C. M., Romero, J., 2016. Response of seagrass indicators to shifts in environmental stressors: A global review and management synthesis. Ecol. Indic. 63, 310–323. https://doi.org/10.1016/j.ecolind.2015.12.007.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. Nature 461, 53–59. https://doi.org/10.1038/nature08227.

Seager, R., Goddard, L., Nakamura, J., Henderson, N., Lee, D.E., 2014. Dynamical causes of the 2010/11 Texas-northern Mexico drought. J. Hydrometeorol. 15, 39–68. https://doi.org/10.1175/JHM-D-13-024.1.

Sen Gupta, A., Thomsen, M., Benthuysen, J.A., Hobday, A.J., Oliver, E., Alexander, L.V., Burrows, M.T., Donat, M.G., Feng, M., Holbrook, N.J., Perkins-Kirkpatrick, S., Moore, P.J., Rodrigues, R.R., Scannell, H.A., Taschetto, A.S., Ummenhofer, C.C., Wernberg, T., Smale, D.A., 2020. Drivers and impacts of the most extreme marine heatwaves events. Sci. Rep. 10, 1–15. https://doi.org/10.1038/s41598-020-75445-3.

Solis, R.S., Powell, G.L., 1999. Hydrography, mixing characteristics, and residence times of Gulf of Mexico estuaries. In: Bianchi, T.S., Pennock, J.R., Twilley, R.Y. (Eds.), Biogeochemistry of Gulf of Mexico Estuaries. John Wiley & Sons Inc, New York, pp. 29–62.

Solórzano, L., Sharp, J.H., 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr. 25, 754–758.

Texas Seagrass Monitoring Program. Texas Statewide Seagrass Monitoring Program A Seagrass Monitoring Program for Texas Coastal Waters, The University of Texas at Austin Marine Science Institute. http://www.texasseagrass.org/(accessed 1 August 2020).

Unsworth, R.K.F., Collier, C.J., Waycott, M., Mckenzie, L.J., Cullen-Unsworth, L.C., 2015. A framework for the resilience of seagrass ecosystems. Mar. Pollut. Bull. 100, 34–46. https://doi.org/10.1016/j.marpolbul.2015.08.016.

Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., Jones, B.L., Nordlund, L.M., 2018. Global challenges for seagrass conservation. Ambio 48, 801–815. https://doi.org/10.1007/s13280-018-1115-y.

van de Leemput, I.A., Dakos, V., Scheffer, M., van Nes, E.H., 2018. Slow Recovery from Local Disturbances as an Indicator for Loss of Ecosystem Resilience. Ecosystems 21, 141–152. https://doi.org/10.1007/s10021-017-0154-8.

van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. Vegetatio 39, 97–114. https://doi.org/10.1007/978-94-009-9194-1_17.

van der Maarel, E., 2007. Transformation of cover-abundance values for appropriate numerical treatment – Alternatives to the proposals by Podani. J. Veg. Sci. 18, 767–770. https://doi.org/10.1658/1100-9233(2007)18[767:tocvfa]2.0.co;2.

van Katwijk, M.M., van der Welle, M.E.W., Lucassen, E.C.H.E.T., Vonk, J.A., Christianen, M.J.A., Kiswara, W., Inayat al Hakim, I., Arifin, A., Bouma, T.J., Roelofs, J.G.M., Lamers, L.P.M., 2011. Early warning indicators for river nutrient and sediment loads in tropical seagrass beds: A benchmark from a near-pristine archipelago in Indonesia. Mar. Pollut. Bull. 62, 1512–1520. https://doi.org/10.1016/j.marpolbul.2011.04.007.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Williams, M., Longstaff, B., Buchanan, C., Llansó, R., Dennison, W., 2009. Development and evaluation of a spatially-explicit index of Chesapeake Bay health. Mar. Pollut. Bull. 59, 14–25. https://doi.org/10.1016/j.marpolbul.2008.11.018.

Wilson, S.S., Dunton, K.H., 2018. Hypersalinity During Regional Drought Drives Mass Mortality of the Seagrass *Syringodium filiforme* in a Subtropical Lagoon. Estuaries and Coasts 41, 855–865. https://doi.org/10.1007/s12237-017-0319-x.

Wilson, S.S., Furman, B.T., Hall, M.O., Fourqurean, J.W., 2020. Assessment of Hurricane Irma Impacts on South Florida Seagrass Communities Using Long-Term Monitoring Programs. Estuaries and Coasts 43, 1119–1132. https://doi.org/10.1007/s12237-019-00623-0.

Yang, X., Zhang, P., Li, W., Hu, C., Zhang, X., He, P., 2018. Evaluation of four seagrass species as early warning indicators for nitrogen overloading: Implications for eutrophic evaluation and ecosystem management. Sci. Total Environ. 635, 1132–1143. https://doi.org/10.1016/j.scitotenv.2018.04.227.

Yarbro L.A., Carlson Jr, P.R., 2011. Seagrass integrated mapping and monitoring for the State of Florida. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL. 202 pages.

Zieman, J.C., Fourqurean, J.W., Iverson, R.L., 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. Bull. Mar. Sci. 44, 292–311.

Zieman, J.C., Fourqurean, J.W., Frankovich, T.A., 1999. Seagrass Die-off in Florida Bay: Long-term Trends and Growth of Turtle Grass, *Thalassia testudinum* in Abundance. Estuaries 22, 460–470. https://doi.org/10.2307/1353211.