THE IMPACT OF HURRICANE GEORGES ON SOFT-BOTTOM, BACK REEF COMMUNITIES: SITE- AND SPECIES-SPECIFIC EFFECTS IN SOUTH FLORIDA SEAGRASS BEDS

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ABSTRACT

Seagrass beds are the dominant benthic marine communities in the back reef environment of the Florida Keys. At a network of 30 permanent monitoring stations in this back reef environment, the seagrass *Thalassia testudinum* Banks & Soland. ex Koenig was the most common marine macrophyte, but the seagrasses *Syringodium filiforme* Kuetz., and *Halodule wrightii* Aschers., as well as many taxa of macroalgae, were also commonly encountered. The calcareous green macroalgae, especially *Halimeda* spp. and *Penicillus* spp., were the most common macroalgae. The passage of Hurricane Georges on September 25, 1998 caused an immediate loss of 3% of the density of *T. testudinum*, compared to 19% of the *S. filiforme* and 24% of the calcareous green algae. The seagrass beds at three of the stations were completely obliterated by the storm. Stations that had little to moderate sediment deposition recovered from the storm within 1 yr, while the station buried by 50 cm of sediment and the two stations that experienced substantial erosion had recovered very little during the 3 yrs after the storm. Early colonizers to these severely disturbed sites were calcareous green algae. Hurricanes may increase benthic macrophyte diversity by creating disturbed patches with the landscape, but moderate storm disturbance may actually reduce macrophyte diversity by removing the early successional species from mixed-species seagrass beds.

Hurricanes and cyclones are important structuring forces in nearshore marine communities. High winds, large waves, torrential rains, and storm surge impact submarine communities like seagrass beds and coral reefs, emergent plant communities like salt marshes and mangroves, and upland ecosystems. Tropical cyclones are an often-cited cause of damage to seagrass beds. For example, 70% of the seagrass cover in the Gulf of Carpinteria, Australia, was uprooted by the 12 m waves generated by the 220 km h^{-1} winds of Cyclone Sandy (Poiner et al., 1989), and over 1000 km^2 of seagrass beds were lost due to wave action, flooding and turbidity caused by a cyclone in Hervey Bay, Australia (Preen et al., 1995).

In the Gulf of Mexico/Caribbean region, smaller-scale hurricane impacts to seagrass beds are commonly reported (e.g., Glynn et al., 1964; Wanless et al., 1988; Rodríguez et al., 1994; van Tussenbroek, 1994), but it is interesting to note that some of the most severe storms in south Florida during the past half-century have had relatively little impact on seagrass beds. Hurricane Donna, a category 4 hurricane which passed directly over the Florida Keys in 1960, had negligible impact on seagrass biomass and mud bank topography of Florida Bay (Ball et al., 1967), and despite depositing 2 m deep wracklines of seagrass blades along the shore, had little impact on seagrass distribution in Biscayne Bay (Thomas et al., 1961). Hurricane Andrew, another category 4 storm in 1992, had a devastating impact on the mangrove forests and terrestrial ecosystems of south Florida (Smith et al., 1994; Armentano et al., 1995; Doyle et al., 1995; McCoy et al., 1996), but caused little damage to seagrass beds immediately seaward of the mangroves (Tilmant et al., 1994). It is apparent that factors other than maximum wind speed of a hurricane are important determinants of the degree to which a hurricane will affect seagrass beds.

Some have proposed a positive impact of mechanical storm damage on seagrass beds over the long term. Moderate disturbance may help maintain species diversity in ecosystems (Connell and Slatyer, 1977; Paine and Levin, 1981). Ecological succession in seagrass beds of the tropical Atlantic tends towards a seagrass bed dominated by *Thalassia testudinum* Banks & Soland. ex Koenig (Den Hartog, 1971; Zieman, 1982). Storm-generated bare patches in dense *T. testudinum* meadows are colonized by early successional macrophytes, like calcareous green algae and the seagrasses *Halodule wrightii* Kuetz. and *Syringodium filiforme* Aschers., thereby enhancing the diversity of these disturbed beds (Patriquin, 1975). In south Florida, mixed-species seagrass beds support higher densities of fish and invertebrates than *T. testudinum* -dominated seagrass beds (Thayer and Chester, 1989). In addition to this role in maintaining diversity, it has even been proposed that periodic removal of sediment, organic matter, and biomass by hurricanes can be necessary for the long-term homeostasis of some seagrass beds (Zieman et al., 1989).

The time required for seagrass beds to recover from a disturbance is a function of the size of the disturbance. Recolonization of even a small gap (<1 m^2) in a seagrass bed can take up to a decade, since most seagrass colonization occurs through vegetative growth into the gap instead of through seedling recruitment (Zieman, 1976; Rollon et al., 1998). Dynamic erosional features <10 m wide in *T. testudinum* beds caused by storm events are colonized by calcareous algae, *H. wrightii*, and *S. filiforme* years before *T. testudinum* can become reestablished (Patriquin, 1975). Larger disturbances, whether caused by tropical cyclones, mass die-off (Robblee et al., 1991; Seddon et al., 2000), catastrophic grazing (Maciá and Lirman, 1999; Rose et al., 1999; Peterson et al., 2002), or any other factor, may persist for many decades. Studying the dynamics of recovery from such a large-scale disturbance is made difficult by this time scale, but understanding the rate and mechanisms of recovery of seagrass beds from such disturbances is important not just for the scientific aspects of the exercise, but also for aiding in guiding restoration and management of damaged seagrass ecosystems.

Studying the effects of hurricanes is also problematic because of the unpredictability of their occurrence. Since 1920, 24 hurricanes have passed over the Florida Keys National Marine Sanctuary, but those hurricanes have not been equally distributed over those 81 yrs (data from the U.S National Oceanographic and Atmospheric Administration's National Hurricane Center, <www.nhc.noaa.gov>). The 1940s and 1960s were particularly active times for hurricanes in the region, with six hurricanes in each decade. In contrast, there was only one hurricane (Floyd, a small, category 1 storm in 1987) during the period 1970–1991, and since 1992 there have been three hurricanes. One reliable way to ensure that the effects of hurricanes on the living resources of an area can be measured is to establish a spatially comprehensive, long-term monitoring program. Such a program will increase the chances of a storm influencing at least some areas of known character during the course of the program. Further, a long-lived program is necessary to assess the long-term impacts of the hurricane disturbance. Such a monitoring program was established in 1995 as part of the Water Quality Protection Plan for the Florida Keys National Marine Sanctuary (FKNMS). In this paper, we examine the data from 6 yrs of this monitoring program to describe the relative abundance of seagrasses and macroalgae in south Florida and to assess the immediate impacts and first 3 yrs of recovery of benthic soft-bottom marine communities from the passage of a hurricane. This publication is part of a series of papers resulting from a scientific workshop held at

the Caribbean Marine Research Center (December 2001) to evaluate the importance of back reef systems for supporting biodiversity and productivity of marine ecosystems.

Methods

Site Description.—The FKNMS encompasses about 9000 km^2 of near-shore, subtropical marine communities (Fig. 1). Over most of this area, the water is very shallow (<20 m); the Florida Keys barrier coral reef on the Atlantic Ocean side of the Florida Keys parallels the islands 7–10 km offshore. Between the barrier reef and the islands, and on the Gulf of Mexico side of the islands, lie extensive seagrass beds. There are some relatively small areas where active patch reefs and the lack of sediment preclude the presence of seagrass beds, but seagrass communities dominate over 80% of the bottom between the barrier reef and the islands (Fourqurean et al., 2001, 2002). Although these communities are called seagrass beds, it is important to note that they contain a wide variety of benthic plants and animals in addition to the seagrasses themselves; in fact, macroalgal primary production may rival seagrass primary production over much of the backreef environment of the Florida Keys (Davis and Fourqurean, 2001).

Hurricanes in the Study Area, 1995–2001.—Fortunately for the residents of south Florida, few hurricanes have passed over the study area since 1995, and these (Georges in 1998, Irene in 1999) were relatively mild over the Florida Keys. Hurricane Georges was the most intense storm during this period; it was a category 2 when it passed over Key West on September 25, 1998 (see storm track on Fig. 1, inset). The hurricane force winds were restricted to a relatively narrow band in the lower and middle Florida Keys. Maximum sustained winds of 90 knots (145 km h^{-1}) were recorded in Key West, 81 knots (130 km h^{-1}) offshore of Marathon, but only 46 knots (75 km h^{-1}) offshore in the upper Keys. Irene was a small category 1 hurricane when it passed over the upper Keys in 1999, maximum sustained winds were not recorded over 57 knots (92 km h^{-1}). These relatively small hurricanes did have very substantial, but localized, effects on the natural resources and economic interests Florida Keys.

Station Selection.—In order to assess the dynamics of the soft-bottom benthic communities in the back-reef environment in south Florida, data were gathered from the network of 30 permanent seagrass monitoring stations in the FKNMS (Fig. 1, see Fourqurean et al., 2001; Fourqurean and Rutten, 2003 for a description of the monitoring program). These stations were originally located using a stratified-random approach, with two random locations being chosen within three strata (inshore, offshore, and intermediate) in each of five defined segments of the Sanctuary (Klein and Orlando, 1994). At each seagrass monitoring station, a permanent 50 m long transect was established at the beginning of the study period by driving steel rods into the substratum at both ends of the transect. Data on the species composition and abundance of the benthic macrophyte community was collected from these stations four times per year, beginning in December 1995. By serendipity, a survey was completed the week prior to the passage of Hurricane Georges on September 25, 1998. In response to this storm, all 30 stations were resurveyed the week after the storm passed. Thereafter, surveys continued four times per year until the end of 2001. During these resurveys, recent sediment deposition and/or erosion were noted. For cases of minor deposition, the depth of recent sediments above the previous sediment horizon and covering the seagrass blades was measured. Bare areas in the seagrass beds created by the storm were excavated, and the depth to the rhizome layer of the previously extant seagrass community was recorded if there had been deposition. In the event of erosion, the amount of erosion was estimated by examining the remaining seagrass short shoots for signs of previous sediment depth (often, this is indicated by the location of chlorophyll in outer leaves in a short shoot); if the previous seagrass community was completely missing and not buried, a rough estimate of the extent of erosion was made by examining the depth of the rhizomes of nearby but unaffected seagrass beds.

Braun Blanquet Monitoring.—We assessed the species composition and relative abundance of benthic macrophytes at the permanent monitoring stations using Braun-Blanquet cover-abundance surveys (Fourqurean et al., 2001, 2002). In order to codify the data collection, a list of taxa was established to define the monitoring targets (Table 1). In some instances, the taxa consist
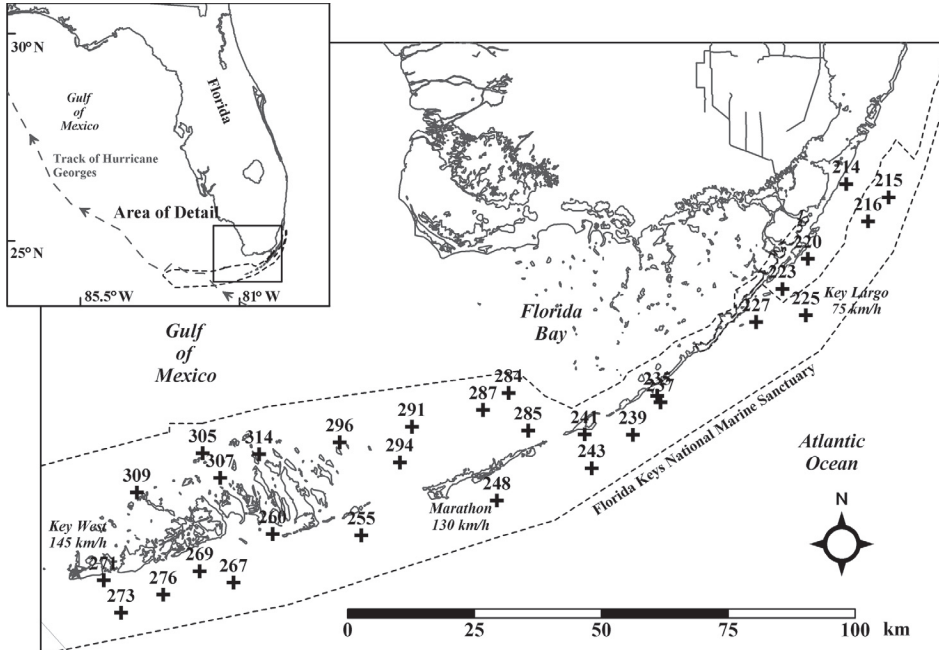
Figure 1. Map of study area, showing geographic location, position of monitoring stations, track of Hurricane Georges relative to study area, and maximum sustained winds experienced during the passage of Hurricane Georges on September 25, 1998 in Key West, Marathon, and Key Largo.

of single species (e.g., the seagrasses *T. testudinum*, *S. filiforme*, etc.), while other taxa were more broadly defined to simplify the in situ data collection. All conspicuous macrophytes fell into one of the categories in Table 2. Ten quadrats (0.25 m^2) were placed along each 50 m transect at predetermined random distances from one of the marker rods. A new set of random sampling positions were chosen before each visit to a station. Each quadrat was examined using SCUBA. For each quadrat, the taxa occurring in the quadrat were listed, and a score based on the cover of each taxon in that quadrat was assigned (Table 2).

From the observations of cover in each quadrat at a station, three statistics were computed for each taxon: frequency, abundance, and density. Frequency was calculated as

$$F_i = N_i / n$$

<div align="right">Eq. 1</div>

where F_i = the frequency of taxon i, n = the total number of quadrats sampled at a station, and N_i is the number of quadrats at a station in which taxon i was present; such that $0 \leq F_i \leq 1$.

Abundance was calculated as

$$A_i = \sum_{j=1}^{n} S_{ij} / N_i$$

<div align="right">Eq. 2</div>

where A_i = the abundance of taxon i, j = quadrat number from 1 to n, the total number of quadrats sampled at a station; S_{ij} = the Braun-Blanquet score for taxon i in quadrat j; and N_i is the number of quadrats at a station in which taxon i was present. For any taxon, A can range between 0 and 5, the maximum Braun-Blanquet score.

Density was calculated as

Table 1. Taxa list used to describe macrophyte species composition of soft-bottom back reef areas in south Florida.

Code	Taxa	Example species
Seagrasses:		
T	*Thalassia testudinum*	
S	*Syringodium filiforme*	
H	*Halodule wrightii*	
Hd	*Halophila decipiens*	
He	*Halophila engelmanni*	
Macroalgae:		
CGH	Calcareous green *Halimeda* spp.	*Halimeda incrassata*
CGU	Calcareous green *Udotea* spp.	*Udotea flabellum*
CGP	Calcareous green *Penicillus* spp.	*Penicillus capitatus*
CGR	Calcareous green *Rhipocephalus* spp.	*Rhipocephalus phoenix*
CGA	Calcareous green *Acetabularia* spp.	*Acetabularia crenulata*
CGO	Calcareous green other	*Cymopolia barbata*
CGT	Calcareous green total, all species	
CA	*Caulerpa* spp.	*Caulerpa prolifera*
GO	Green other	*Anadyomene stellata*
DR	Drift red	*Laurencia intricata*
CR	Coralline red	*Jania adhaerens*
RO	Red other	*Heterosiphonia gibbesii*
SAR	Sargassum spp.	*Sargassum natans*
BO	Brown other	*Dictyota cervivornis*
O	Other, unidentified	

$$D_i = \sum_{j=1}^{n} S_{ij} / n$$

Eq. 3

where D_i = density of taxon i; j = quadrat number from 1 to n, the total number of quadrats sampled at a station, and S_{ij} = the Braun-Blanquet score for taxon i in quadrat j. For any species, D can range between 0 and 5, the maximum Braun-Blanquet score (note that $D_i = F_i \times A_i$, and $D_i \leq A_i$). At a station, however, the sum of all taxa D values can be greater than 5, becausse of the relatively broad cover ranges for each Braun-Blanquet value and the fact that seagrass canopies are three dimensional. It should also be noted that a taxon may be observed at a station by the sample collector, but unless the taxon falls within one of the randomly-placed observation quadrats, the taxon receives a $D = 0$.

Changes in benthic macrophyte abundance caused by the storm were quantified by calculatiing the fractional change (Δ) in the Braun-Blanquet A, F and D scores for a taxon at each site:

$$\Delta X_i = \frac{X_i after - X_i before}{X_i before}$$

Eq. 4

where X represents one of the three Braun Blanquet metrics (A, F, or D) for taxon i either immediately *before* or *after* the passage of Georges. To facilitate the visualization of the spatial pattern in storm-induced change, contour plots of ΔD for the three most common taxa (*T. testudinum*, *S. filiforme*, and Calcareous Green Algae) were generated using a kriging algorithm (point kriging using a linear variogram and no nugget).

Table 2. Braun-Blanquet abundance scale used to assess seagrass density. Cover is defined as the fraction of the bottom that is obscured by the species when viewed by a diver from directly above.

Cover class	Description
0	Absent
0.1	Solitary individual or ramet, less than 5% cover
0.5	Few individuals or ramets, less than 5% cover
1	Many individuals or ramets, less than 5% cover
2	5–25% cover
3	25–50% cover
4	50–75% cover
5	75–100% cover

Results

Thalassia testudinum was the most common macrophyte encountered on the Braun-Blanquet surveys, it was found on 96% of the 690 transects samples from the 30 stations over the period December 1995–December 2001 (Table 3). On those surveys, it was found with a mean F of 0.77, but a median F of 1.00, since it was found in every quadrat of more than half of all transects (Fig. 2). It was often found with high A, and it had the highest mean A (2.02) of any of the monitored taxa. Of the other seagrass species, *S. filiforme* was the next most common taxa, occurring on 64% of all transects. *Syringodium filiforme* was rarely encountered with high A; mean A was 1.33 while the median A was only 1.00. *Halodule wrightii* was found on only 14% of transects, with a mean A of 0.14. *Halophila* spp. were rarely encountered. *Thalassia testudinum* and *S. filiforme* tended to occur as continuous, the most common F class for each was 90–100% cover (Fig. 2). In contrast, *H. wrightii* was most often distributed in small patches; it was most often observed with a frequency of 0–10% when it was present on transects.

Calcareous green algae were by far the most common macroalgae encountered on the Braun-Blanquet surveys, with at least one taxon being recorded on 92% of the surveys (Fig. 2). *Halimeda* spp. and *Penicillus* spp. were the most common calcareous green algae; both occurred on ca. 80% of all transects. Both "Other Red Algae" and *Caulerpa* spp. were relatively common, occurring on 48 and 24% of all transects, respectively. Macroalgae rarely had A scores over 2, indicating they rarely covered more than 25% of a quadrat, but occasionally *Halimeda* spp., *Penicillus* spp., or red algae were found to cover the majority of a quadrat (Table 3).

The Braun-Blanquet surveys produced data of sufficient precision to identify intra-annual patterns in the relative abundance of the target taxa (Fig. 3). Station 223 was a dense *T. testudinum* bed, with an understory of other macrophyte taxa. *Thalassia testudinum* was always found in every quadrat at this station (F = 1). The most common taxa in the understory at this station were *S. filiforme* and calcareous green algae (CGT), but the frequency of encountering these understory plants followed a pronounced seasonal pattern, with summertime peaks in F for both taxa. Peaks for CGT were ca. 0.6, and peaks for *S. filiforme* were around 0.2. Abundance of *T. testudinum* peaked around A = 4.2 each summer, while the common understory taxa had peaks in abundance ≤ 1. Note that there was no measurable alteration of the seasonal patterns in frequency, abundance, or density associated with the passage of Georges at this station.

In contrast to station 223 (Fig. 3), at many stations there was a marked decrease in

Table 3. Summary statistics of the Braun-Blanquet survey data for the surveyed taxa. The minimum score for frequency, abundance, and density for all taxa was 0. Occurrence is the proportion of all transects (n = 691) on which the taxa was present.

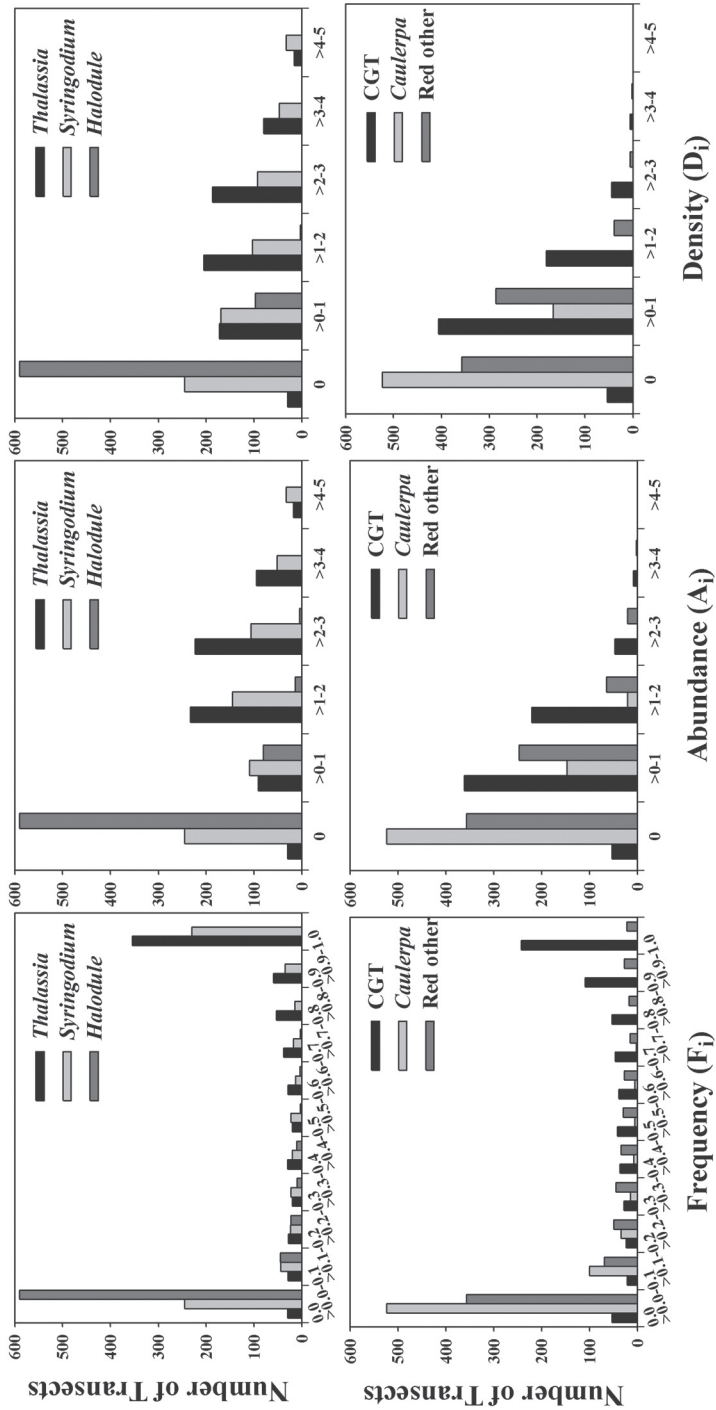|	Occurrence	Frequency (F)			Abundance (A)			Density (D)		
		Mean	Median	Max	Mean	Median	Max	Mean	Median	Max
Thalassia testudinum	0.96	0.77	1.00	1.00	2.02	1.88	5.00	1.74	1.80	5.00
Syringodium filiforme	0.64	0.48	0.80	1.00	1.33	1.00	5.00	1.14	0.75	5.00
Halodule wrightii	0.14	0.03	0.00	0.80	0.14	0.00	3.00	0.03	0.00	1.40
Halophila engelmanni	0.01	0.00	0.00	0.20	0.00	0.00	2.00	0.00	0.00	0.20
Halophila decipiens	0.00	0.00	0.00	0.10	0.00	0.00	0.10	0.00	0.00	0.01
Calcareous green algae:										
Halimeda spp.	0.81	0.51	0.00	1.00	0.65	0.00	5.00	0.44	0.00	2.35
Udotea spp.	0.62	0.26	0.00	1.00	0.25	0.00	1.78	0.13	0.00	1.60
Penicillus spp.	0.78	0.43	0.00	1.00	0.46	0.00	3.00	0.31	0.00	2.70
Ripocephalus spp.	0.41	0.10	0.00	1.00	0.13	0.00	2.00	0.03	0.00	0.67
Acetabularia spp.	0.18	0.08	0.00	1.00	0.08	0.00	1.65	0.04	0.00	1.65
Calcareous green other	0.08	0.02	0.00	0.90	0.07	0.00	4.50	0.02	0.00	2.05
Calcareous green total	0.92	0.70	0.80	1.00	0.97	0.66	4.50	0.83	0.51	3.70
Caulerpa spp.	0.24	0.04	0.00	0.70	0.16	0.00	2.00	0.03	0.00	1.20
Green other	0.34	0.11	0.00	1.00	0.18	0.00	2.44	0.07	0.00	2.20
Drift red	0.19	0.06	0.00	1.00	0.20	0.00	4.00	0.08	0.00	3.50
Coralline red	0.13	0.04	0.00	1.00	0.12	0.00	3.00	0.04	0.00	1.75
Red other	0.48	0.21	0.00	1.00	0.41	0.00	3.50	0.22	0.00	3.50
Sargassum spp.	0.02	0.00	0.00	0.20	0.01	0.00	1.00	0.00	0.00	0.15
Brown other	0.26	0.08	0.00	1.00	0.17	0.00	3.71	0.07	0.00	2.60

Figure 2. Histograms of observed Braun Blanquet frequency (F), abundance (A) and density (D) for the six most common macrophyte taxa. Data were collected four times a year during the period December 1995–December 2001 from the 30 monitoring stations (Fig. 1). The total number of transects was 69l. Top row: Seagrass species. Bottom row: macroalgal taxa.
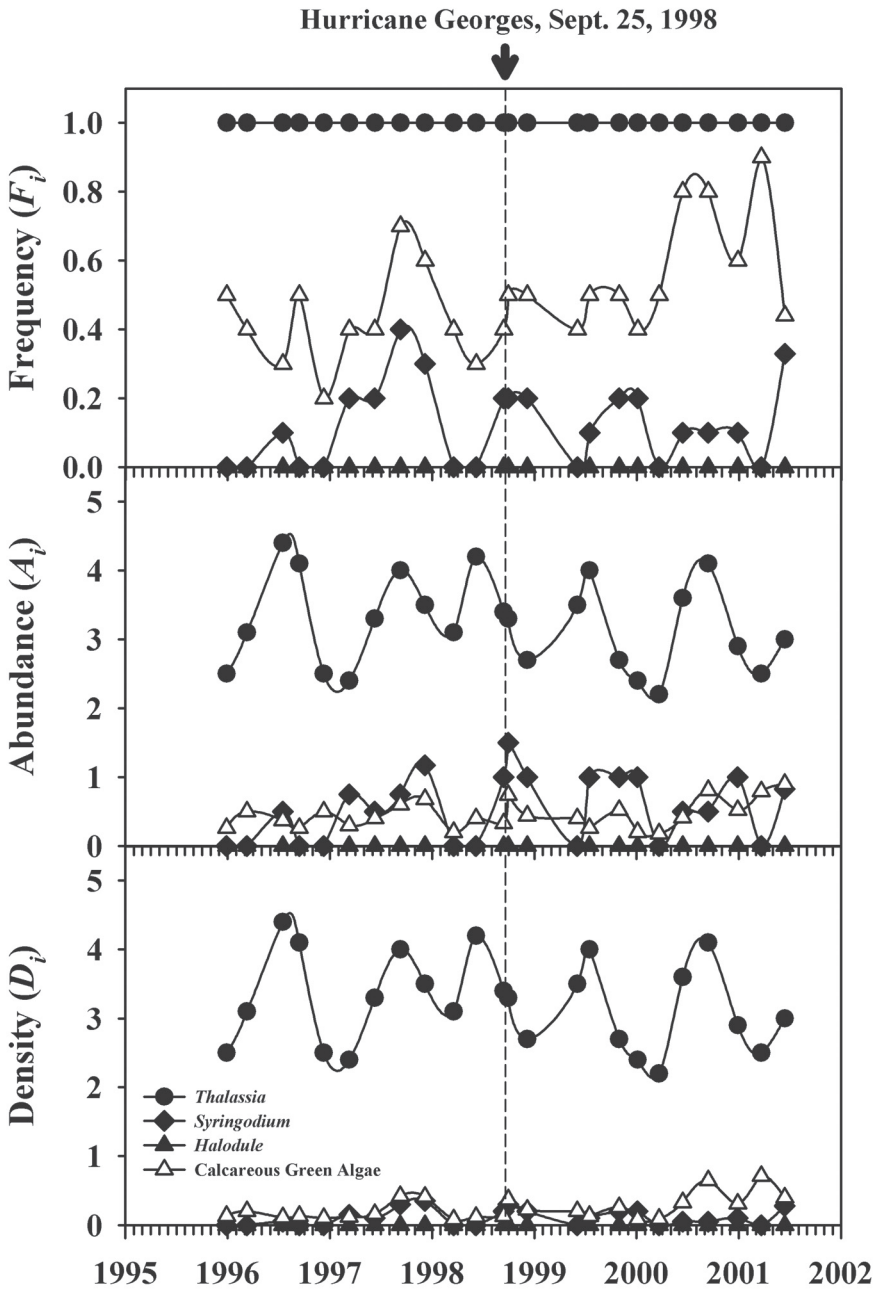
Figure 3. Example time series of Braun-Blanquet monitoring data from station 223, which was not affected by the passage of Hurricane Georges on September 25, 1998 (dashed vertical line). This station was located at 25º 03.613′ N, 80º 25.382′ W, and was 3.5 m deep.

Table 4. Mean change in Braun-Blanquet frequency (ΔF), abundance (ΔA), and density (ΔD) of the four most common taxa of benthic macrophytes at the 30 monitoring stations as a result of Hurricane Georges. Change at a station was computed as [(score after storm − score before storm) /score before storm]. Values are means ± 1 SE for the 30 stations.

Taxon	Frequency (ΔF)	Abundance (ΔA)	Density (ΔD)
Thalassia testudium	0.00 ± 0.11	−0.09 ± 0.08	−0.03 ± 0.09
Syringodium filiforme	−0.11 ± 0.11	−0.19 ± 0.08	−0.19 ± 0.08
Halodule wrightii	−0.10 ± 0.11	−0.08 ± 0.11	−0.11 ± 0.12
Calcareous green algae	−0.17 ± 0.09	−0.24 ± 0.10	−0.24 ± 0.12

the frequency, abundance, and/or density of benthic macrophytes between the surveys conducted immediately before and after the passage of Georges. Averaging across all 30 stations, the average immediate change in F for *T. testudinum* was near zero, because of small-scale patchiness in its distribution and the fact that independent observations of F were made before and after the storm. However, there was a decrease in *T. testudinum* A by an average of 9 ± 8% (± 1 standard error) and a decrease in D by 3 ± 9% (Table 4). Because D = F × A, the apparent variability in F for *T. testudinum* obscured any net change in D across all stations. The storm had a similar impact on *H. wrightii*, which decreased by ca. 10% for F, A, and D. *Syringodium filiforme* was affected to a greater degree, with a 11 ± 0.07% loss in F, 19 ± 8% loss in A, and 19 ± 8% loss in D. Calcareous green algae as a group showed the greatest immediate net loss because of the storm: F decreased by 17 ± 9%, A by 24 ± 10%, and D decreased by 24 ± 12% on average. We did not compute the average changes of other less common taxa, because the random chance of encountering these other taxa on our surveys made estimates of net change unreliable.

There was a spatial pattern in the degree of loss caused by the storm for most taxa; in general losses were greater in the western parts of our study area, and in the east-
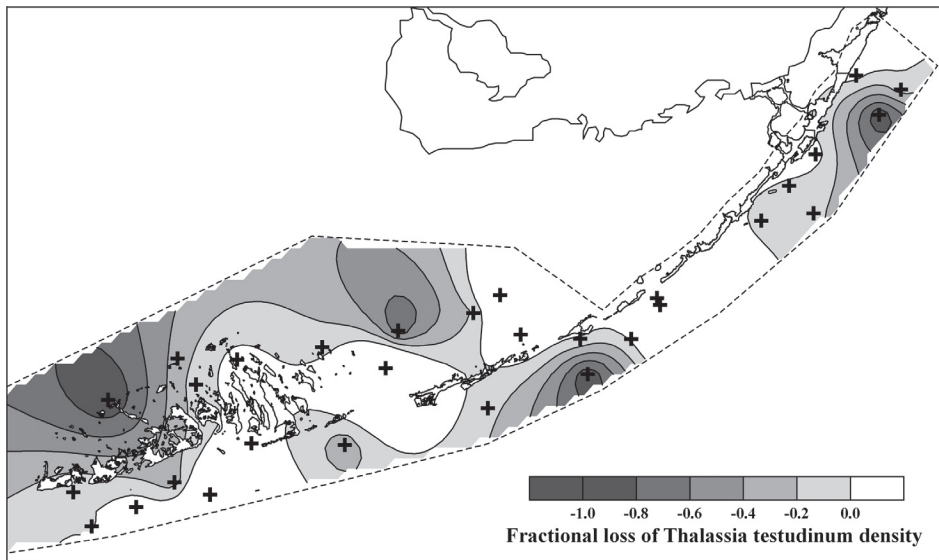

Figure 4. Spatial pattern in the short-term loss in density (ΔD) of the seagrass *Thalassia testudinum* across the study area, based on surveys made the week before and the week after the passage of Hurricane Georges on September 25, 1998. Loss was calculated as [$\Delta D = (D_{after} - D_{before})/D_{before}$]. Contours generated by interpolating between values from the 30 permanent monitoring stations, indicated by crosses.
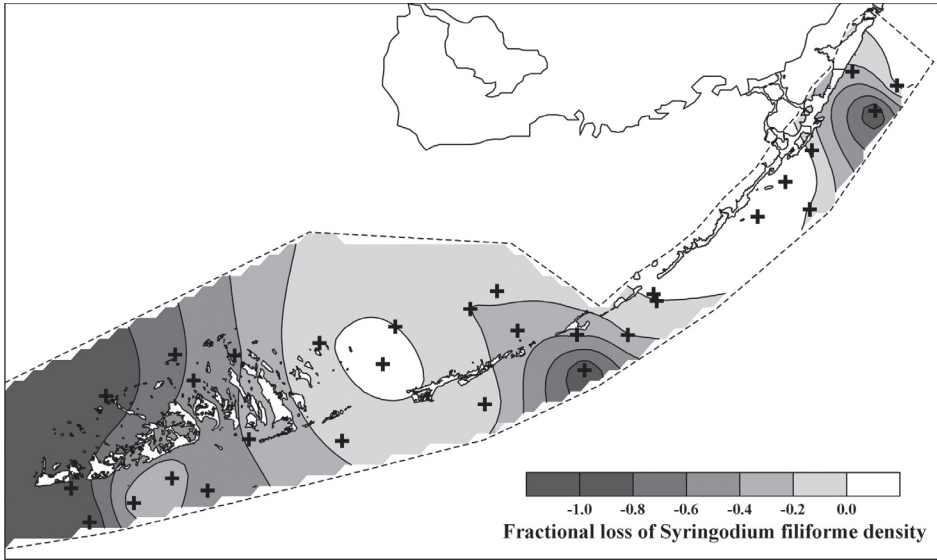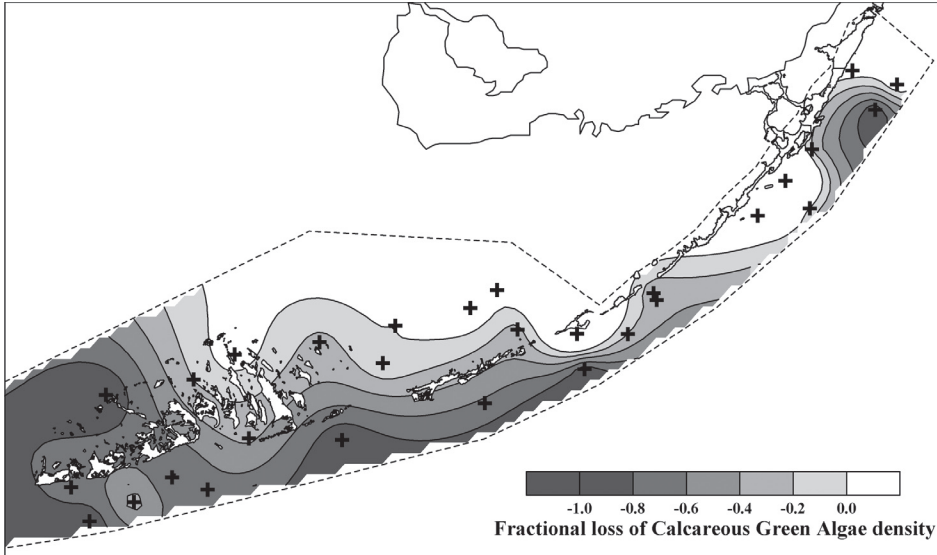
Figure 5. Spatial pattern in the short-term loss in density of the seagrass *Syringodium filiforme* (ΔD) across the study area, based on surveys made the week before and the week after the passage of Hurricane Georges on September 25, 1998. Loss was calculated as [$\Delta D = (D_{after} - D_{before})/D_{before}$]. Contours generated by interpolating between values from the 30 permanent monitoring stations, indicated by crosses.

Figure 6. Spatial pattern in the short-term loss in density (ΔD) of calcareous green algae (CGA) across the study area, based on surveys made the week before and the week after the passage of Hurricane Georges on September 25, 1998. Loss was calculated as [$\Delta D = (D_{after} - D_{before})/D_{before}$]. Contours generated by interpolating between values from the 30 permanent monitoring stations, indicated by crosses.
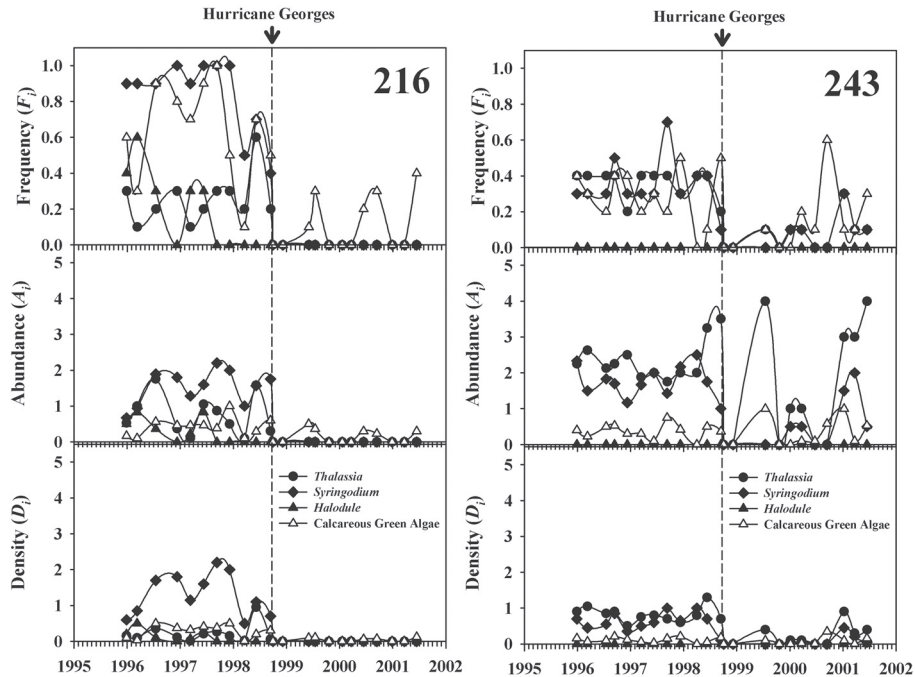
Figure 7. Time series of the frequency, abundance and density of *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, and calcareous green algae (CGA) at stations 216 and 243, which experienced significant erosion during the passage of Hurricane Georges on September 25, 1998 (dashed vertical line). Station 216 was located at 25° 10.772′ N, 80° 15.322′ W, and was 10.6 m deep. Station 243 was located at 24° 44.588′ N, 80° 47.779′ W, and was 9.2 m deep.

ern parts of our study area only offshore stations experienced large losses. There was complete loss of *T. testudinum* from three stations (stations 216 and 243 on the Atlantic Ocean side of the Florida Keys, and station 309 on the Gulf of Mexico side of the Keys; Fig. 4). These large losses in D occurred mostly on the periphery of our study area, and there tended to be little change in the benthic communities close to shore. Note also that there were other stations along the periphery that exhibited no change during the storm, even in the westernmost parts of our study area that were exposed to the strongest winds. The same general spatial pattern was evident in the loss of *S. filiforme* during the storm (Fig. 5), but the magnitude of the losses tended to be higher than for *T. testudinum*. Losses of CGT were both greater in magnitude and more widespread than the losses of the seagrass species (Fig. 6).

There were three causes of loss in macrophyte density observed on our post-storm surveys: thinning of the canopy by removal of standing leaves of seagrass or thalli of macroalgae, burial of the entire benthic community, or erosion of many centimeters of sediment and consequently the removal of the community. Thinning was responsible for the moderate losses of seagrass and macroalgae density, but burial and erosion were responsible for the severe losses. Erosion was the factor that removed the seagrass beds at the two offshore stations (216 and 243). The effect of the storm at these two stations was dramatic and long-lived (Fig. 7). Station 216 was a deep (10.6 m) seagrass bed with low-density, continuous cover of *S. filiforme* with occasional shoots of *T. testudinum*; calcareous green algae were seasonally common but not very abundant before the storm.
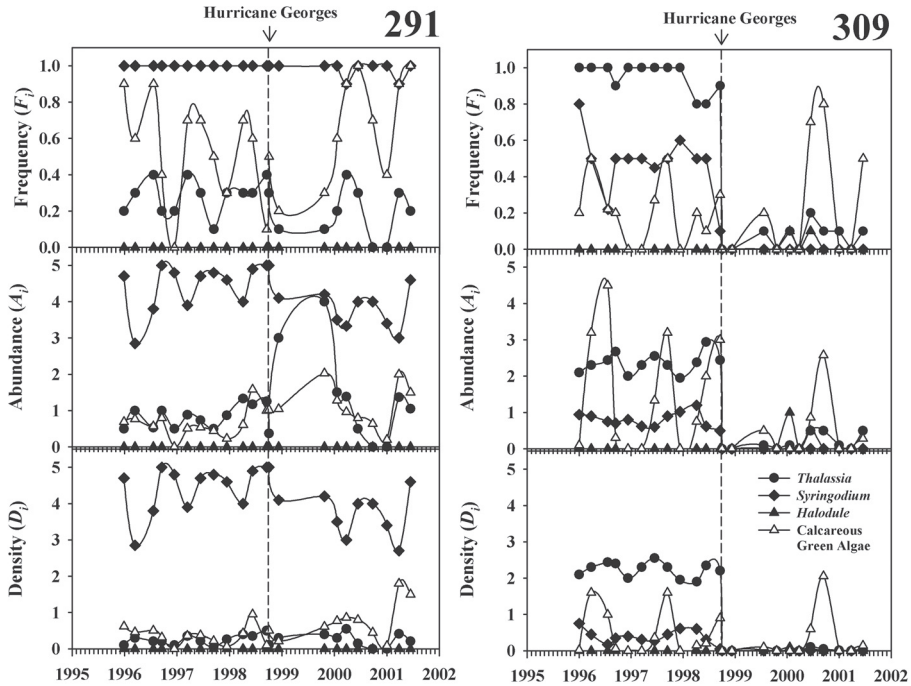
Figure 8. Time series of the frequency, abundance and density of *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, and calcareous green algae (CGA) at stations 291 and 309, which experienced significant sediment deposition during the passage of Hurricane Georges on September 25, 1998 (dashed vertical line). Station 291 was located at 24º 49.008′ N, 81º 08.828′ W, and was 2.7 m deep. Station 309 was located at 24º 41.907′ N, 81º 40.967′ W, and is 4.5 m deep.

Immediately after the storm, the station was an unvegetated sand plain, with no macrophytes of any kind. Since the storm, calcareous green algae have become reestablished, but other taxa have not recolonized the area. Station 243 was also deep (9.2 m), with a denser but patchy seagrass bed with an even mixture of the seagrasses *T. testudinum* and *S. filiforme*. Calcareous green algae were seasonally common, but not abundant. The storm eroded many of the patches of seagrass away, and reduced the size of many others, so that the probability of randomly sampling a patch was very low immediately following the storm. Since the storm, calcareous green algae have reestablished, and the remnant seagrass patches have regained their previous abundance and the patches are growing in size.

In contrast to the erosional losses on the Atlantic Ocean side of the study area, large losses on the Gulf of Mexico side were caused by burial (Fig. 8). Sediment was deposited by the storm at many of the monitoring stations, with accumulations immediately after the storm ranging from <1–50 cm at station 309 (pers. obs.). The longer-term effects of the storm were dependent on the amount of sediment deposited. At most stations, subsequent sediment redistribution following the storm deposition allowed for a complete recovery of the seagrass beds within 1 yr of the storm (see time series from sample station 291; Fig. 8). However, at station 309, the recovery from the storm resembled the trajectory of the eroded station 243 (Figs. 7,8). Seasonal blooms of calcareous green algae became reestablished in the year following the hurricane, remnant patches of *T.*

testudinum were slowly expanding and their abundance was increasing; but A was still well below pre-hurricane levels 3 yrs after the storm.

Discussion

The passage of the relatively small category 2 Hurricane Georges over the western end of the FKNMS on September 5, 1998, decreased the density of marine macrophytes in the soft-bottom back reef environments, but the magnitude of the decrease varied by species. On average, density of *T. testudinum*, the most common seagrass in the study area, decreased by only 3%, compared to 11% losses for *H. wrightii*, 19% losses for *S. filiforme*, and 24% losses of calcareous green algae. Localized losses were much more severe; at three of 30 monitoring stations, seagrass beds were completely obliterated by the hurricane. The hurricane caused losses of benthic macrophytes by three mechanisms: mechanical thinning, sediment deposition, and erosion of the underlying sediments. There were not large increases in turbid freshwater discharge from land associated with this hurricane, as were responsible for much of the loss of seagrasses in Hervey Bay, Australia (Preen et al., 1995). Losses caused by thinning were largely regained quickly after the storm. Losses caused by sediment deposition varied in magnitude. Stations with just a few cm of sediment deposition recovered very rapidly, but one station that experienced 50 cm of deposition was still largely devoid of seagrasses 3 yrs after the storm. Recovery was slowest at stations where the seagrass beds were removed by erosion.

The apparent differences in the susceptibility of different macrophytes to storm damage is probably a result of the architecture of the macrophytes. *Thalassia testudinum*, the species that was least affected by the storm, has a large investment of biomass in rhizomes and roots that are typically buried 10–40 cm deep, compared to the higher shoot: root ratios and shallower rooting depths of *S. filiforme* and *H. wrightii*. Calcareous green algae are anchored to the sediment by relatively shallow rhizoid bulbs. Among the seagrasses, there is apparently also a difference in the breaking strength of attached leaves, with *S. filiforme* leaves being much more susceptible to breakage than *T. testudinum*. After even moderate storms in Florida Bay, it is common to see large rafts of *S. filiforme* leaves floating on the surface over mixed *T. testudinum* – *S. filiforme* beds (J.W.F., pers. obs.). These differences in architecture that lead to a gradient in susceptibility to storm damage are likely a result of the different life-history strategies of the different species (Bazzaz, 1979). *Thalassia testudinum*, the late-succesional species, has a slower growth rate, greater longevity, reproduces almost exclusively by vegetative propagation, and has the high investment in belowground structures typical of a late-successional plant. These life-history characteristics also appear to provide *T. testudinum* with greater resistance to hurricane-induced thinning and erosion than the early-successional seagrasses or calcareous green algae. These conjectures about rooting strength and breaking strength remain to be tested with biophysical measurements, however.

The relative resilience of seagrasses to burial was not surprising, since seagrasses often inhabit areas with mobile sediment. Seagrasses can respond to burial by increasing the amount of internode elongation on the vertical shoots of buried plants to compensate for the burial (Patriquin, 1973; Marbà and Duarte, 1994). The elongation rate of buried shoots increases in response to reduced light reaching the meristems (Terrados, 1997), but there is a limit to the ability of seagrasses to overcome burial, with survival of shoots decreasing as burial depth increases (Marbà and Duarte, 1994). In fact, sediment redistribution during Hurricane Gilbert in the Mexican Caribbean left a clear signal in the

pattern of internode elongation rates of rhizomes of *T. testudinum* that was measurable 4 yrs after the storm (Marbà et al., 1994). Not all species have an equivalent ability to deal with burial. In an experiment conducted in a mixed-species seagrass bed in the Philippines, congeners of the species found in our study differed in their ability to survive burial, such that the early-successional *Halodule uninervis* Boiss. and *Syringodium isoetifolium* (Aschers.) Dandy survived better than *Thalassia hemprichii* Aschers. (Duarte et al., 1997). It is possible then, that frequent burial by storms could alter species composition of seagrass beds in our study area by favoring *H. wrightii* and *S. filiforme* over *T. testudinum*.

At the three stations where the seagrass beds were eradicated by the storm (Stations 216, 243, and 309), the first macrophytes to become reestablished after the storm were the calcareous green algae. Compared to the seagrasses, these plants have a very high investment in sexual reproduction and higher dispersal ability (Clifton, 1997); hence they exhibit the life-history characteristics expected of early colonizers in a successionary sequence (Bazzaz, 1979). Although our monitoring data have yet to detect invasion of these disturbed stations by seagrasses, we expect that they will be colonized by the comparatively rapidly colonizing species *H. wrightii* and *S. filiforme* before *T. testudinum* can reinvade the disturbed areas (Fonseca et al., 1987).

The densities of calcareous green algae reached only the pre-hurricane levels during the 3 yrs subsequent to the hurricane disturbance. One would expect that the disturbed stations would support larger densities of calcareous green algae, since seagrasses compete for resources with the algae (Davis and Fourqurean, 2001). But, as noted by Williams (1990), competitive exclusion of calcareous algae by seagrasses rarely occurs, calling into question the importance of competition between seagrasses and macroalgae as a mechanism underlying the often-observed successional pattern in Caribbean seagrass beds (Den Hartog, 1971; Zieman, 1982). It has been suggested that calcareous green algae facilitate the colonization of disturbed areas by seagrasses (Zieman, 1982), but this contention has not been experimentally addressed.

The mechanism often invoked to explain the increase in diversity at intermediate levels of disturbance is that the disturbance removes the late-successional species that are superior competitors, thereby allowing early-successional species with greater dispersal ability to occupy space once occupied by the former competitor (e.g., Connell and Slatyer, 1977; Tilman, 1994). The greater susceptibility of early-successional species to storm damage compared to late successional species may act counter to this mechanism, since low-to-moderate levels of disturbance can actually decrease the density of the early-successional species in a late-successional community. In this case in particular, the removal of *S. filiforme*, *H. wrightii*, and calcareous green algae may be beneficial to *T. testudinum*, since both the seagrass species (Williams 1987, 1990; Fourqurean et al., 1995) and calcareous green algae (Davis and Fourqurean, 2001) compete with *T. testudinum* for resources.

The spatial pattern in the degree of storm impact was likely due to five main factors: distance from the center of the hurricane, fetch, water depth, offshore bathymetry, and the direction of the winds associated with the storm. In general, there was greater loss in macrophyte density in the western parts of our study area, commensurate with peak winds associated with the storm. Greater losses also tended to occur offshore compared to onshore. This is likely a result of offshore bathymetry and fetch. As the storm approached the study area from the SE, the southeasterly winds associated with the northern side of a cyclone in the northern hemisphere blew over hundreds of kilometers

of deep (<100 m) ocean; the resulting oceanic swells transmitted a lot of energy to the bottom as soon as they reached shallow water at the outer reef face of the Florida Keys barrier reef (roughly coincident with the SE boundary of the FKNMS). Much of this reef face is characterized by a very shallow (ca. 5 m) coral reef; this reef line absorbed the brunt of the ocean swells. The wave energy was largely dissipated by the 10 km of shallow water between the coral reef and the Florida Keys. Our two stations 216 and 243, however, are situated in gaps in the shallow coral reefs, hence the greater degree of macrophyte loss at these stations than nearby offshore stations. For example, station 216 sits between stations 215 and 225, which are ca. 300 m directly behind Carysfort and Molasses Reefs, respectively. These two stations in the lee of the reefs exhibited much less loss than the exposed station 216. The offshore stations in the western part of our study (stations 273, 276, and 267) were similarly sheltered from the large oceanic swells. Storm wave energy absorbed by the coral reef and the back reef environment has been an important geomorphological force during the geologic history of the area. The back reef sand shoals that today are covered with seagrass beds may have originated as storm deposits resulting from past hurricanes (Ball et al., 1967).

It is likely that the spatial pattern and the magnitude of changes caused by the passage of Hurricane Georges are peculiar to this storm. The relative exposure of locations in the FKNMS to the force of a hurricane depends on many complex and interacting factors, including location, fetch, wind speed and duration, storm history and water depth. As such, it is likely that other hurricanes will generate a different pattern of impact. The existence of the seagrass-monitoring program for the FKNMS has provided a unique opportunity to study the effects of small hurricanes in the seagrass beds of the Gulf of Mexico and Caribbean. Detailed, pre-disturbance data on the species composition and abundance of multiple stations affected by one storm are rare. If this program continues over the long term, it is likely that it will provide data on the impacts of major hurricanes on seagrass beds. The time series data also allow us to be sure of the causes of the changes in the seagrass beds at these stations. This is important because the changes wrought by the storm at the most highly impacted stations (increase in the abundance of early successional species compared to late successional species) are similar to the changes predicted by models of eutrophication of seagrass beds (see Duarte, 1995; Fourqurean and Rutten, 2003). In a region as populated as the Florida Keys, recognizing early signs of eutrophication are of great importance. Hence, time-series monitoring data from fixed stations are very important to help interpret the causes of change in marine macrophyte communities.

Environmental Defense. Views expressed herein are those of the authors and do not necessarily reflect the views of CMRC, or any of the supporting agencies. This is contribution no. **x** from the Southeast Environmental Research Center at FIU.

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