LOW IMPACT OF HURRICANE KATRINA ON SEAGRASS COMMUNITY STRUCTURE AND FUNCTIONING IN THE NORTHERN GULF OF MEXICO

Andrea Anton, Just Cebrian, Carlos M. Duarte, Kenneth L. Heck Jr., and Joshua Goff

ABSTRACT

Hurricanes are large-scale disturbances with the potential to exert extensive damage in coastal ecosystems. On August 29, 2005 Hurricane Katrina catastrophically impacted a large area of the Gulf of Mexico spreading from coastal Alabama to Louisiana. For five months before hurricane landfall we were assessing the structure and functioning of a mixed seagrass bed located in an area greatly affected by the hurricane. The storm provided an opportunity to assess the effect of a large-scale disturbance on the structure and functioning of that seagrass bed. A comparison of surveys before and after the hurricane showed no decreases in seagrass density, associated fauna, or the microalgal abundance in the water column and sediment. We found no major impact on gross primary productivity, respiration, or net productivity of the water column or the sediment, suggesting that the hurricane had little impact on the metabolism of the seagrass bed studied. Overall, natural temporal changes recorded before the storm were larger than any post-hurricane changes. These findings indicate that this seagrass meadow was naturally highly dynamic and very resistant to Hurricane Katrina.

Seagrass meadows provide key ecological services to the marine environment (Hemminga and Duarte, 2000; Orth et al., 2006). They achieve high structural complexity, which provides habitat and refuge for a great diversity of adult and juvenile organisms (Orth et al., 1984; Heck and Crowder, 1991; Heck et al., 2003). Seagrass meadows are also highly productive systems (Duarte and Chiscano, 1999) that support large food webs and accumulate extensive pools of above- and below-ground biomass (Romero et al., 1994; Duarte and Cebrian, 1996), but inhabit an environment that often experiences disturbances that may disrupt these functions (Preen et al., 1995).

The damage of hurricanes to seagrass meadows as well as other coastal habitats is quite variable and depends on the hurricane itself and the location (Smith et al., 1994; Courtemanche et al., 1999; Paerl et al., 2001; Coles and Brown, 2007; Cebrian et al., 2008). For instance, a cyclone and associated rainfall caused the loss of approximately 1000 km² of seagrass in Hervey Bay, Australia (Preen et al., 1995). On the other hand, other reports have shown overall small impacts of hurricanes on seagrass beds and associated macrophytes (e.g., Fourquean and Rutten, 2004; Tilmant et al., 1994) and major Hurricanes Ivan in 2004 and Katrina in 2005 did not have a large impact on the distribution of seagrasses along the Alabama coast (Byron and Heck, 2006). Moreover, the impact of hurricanes can be very patchy, causing substantial damage in a number of scattered locations but leaving others unaltered. For instance, Steward et al. (2006) reported that roughly 4% of their study sites in Florida Bay suffered significant physical damage (e.g., complete seagrass eradication) after four major storms in 2004.
The majority of studies assessing hurricane impacts on seagrass beds have focused on structural (distribution of abundance and biomass at different trophic levels) and dynamic properties of the dominant seagrass species such as plant abundance, density, biomass, and growth (Marba et al., 1994; Fourqurean and Rutten, 2004; Cruz-Palacios and van Tussenbroek, 2005; Byron and Heck, 2006; Ridler et al., 2006). However, to our knowledge, no studies have yet assessed the impacts of hurricanes on the abundance of the diverse producers and consumers that inhabit seagrass beds (e.g., community structure) and the consequences for the overall metabolic functioning (e.g., community respiration and net and gross production) of the seagrass ecosystem.

In April 2005, we initiated a survey of community structure and function in a seagrass bed in the northern Gulf of Mexico. The survey assessed abundance of producers (seagrass, epiphytes, benthic microalgae, and phytoplankton) and fauna (epifauna, infauna, and fish), as well as benthic and water-column productivity and respiration in the bed. Hurricane Katrina, which was one of the most destructive storms in the history of the United States with winds over 264 km hr\(^{-1}\) and a maximum surge of 7.8–8.5 m in the western coast of Mississippi (Hsu et al., 2005), made landfall approximately 100 km west of our study site on August 29, 2005. The bed studied for 5 mo before landfall was well in range of the hurricane force conditions (Knabb et al., 2005). Indeed, the hurricane produced catastrophic property damage and destroyed most of the houses shoreward of the study site.

Our goal was to assess the impact of Hurricane Katrina on seagrass ecosystem structure and functioning. We did so by continuing our measurements for a year after the passage of the storm and by comparing the pre- and post-storm dynamics of the bed.

**Methods**

**Study Site.**—The study was conducted in Sandy Bay (30°22´28˝N, 88°15´22˝W, Bayou La Batre, Alabama, USA), a shallow embayment surrounded mostly by marsh and maritime forest, and characterized by muddy sediments, moderate freshwater input, and large oscillations in turbidity. The embayment contains a mixed seagrass bed composed of *Halodule wrightii* Aschers. and *Ruppia maritima* (Linnaeus, 1753). Dunton (1990) found such mixed meadows to be highly dynamic, with *R. maritima* growing in cool temperatures and senescing after flowering, and *H. wrightii* growing year-round to reach maximum above-ground biomass by the end of the summer.

**Study Design.**—Three permanent 30 m\(^2\) (5 × 6 m) rectangular plots were set up in the patchy mixed seagrass bed. All plots were parallel to the shore, at the same depth, and the distance between consecutive plots was 7 m. The study was carried out from April 20 2005 to September 15 2006. Measurements of seagrasses, metabolism, infauna, and environmental parameters were taken approximately every month before hurricane landfall (i.e., from April to August 2005), every 2 wks until December 2005 after landfall (in August 29 2005), and four times in 2006 (i.e., April, June, August, and September). Dissolved inorganic nutrients, particulate organic matter (POM), chlorophyll \(a\) (Chl \(a\)), and fish abundance were measured only during 2005. We took our first measurements after the passage of Hurricane Katrina 2 wks after landfall, except for the environmental variables, which were measured for the first time 1 mo after landfall.

**Dissolved Inorganic Nutrients, POM, and Environmental Variables.**—Water samples were collected in each plot at mid-distance between the top of the seagrass canopy and water surface. Concentrations of dissolved inorganic nitrate, nitrite, ammonium, and
phosphorus were determined following standard wet chemical techniques (Strickland and Parsons, 1972) adapted to the Skalar San+ Autoanalyzer. A known volume of water (400 ml) was filtered through a 47 mm Whatman GF/F filter to determine particulate organic matter (POM) concentration. Filters were dried for 3 d (60 °C) and burned (450 °C) to obtain the weight of POM, and concentration determined by dividing the volume filtered.

Environmental measurements included water depth, salinity, dissolved oxygen, temperature, and photosynthetically active radiation (PAR). Salinity, dissolved oxygen, and temperature measurements were taken at mid water-column with a model 85 YSI probe. PAR at the top of the seagrass canopy was measured with a LICOR 1000 data logger connected to a 4p spherical cell. All environmental measurements were taken around midday in each of the plots.

Primary Producers.—Leaf density and biomass for both seagrass species (H. wrightii and R. maritima) were quantified using a 15 cm-diameter core. Seagrasses were sorted by species, leaves were counted, and above- and below-ground biomass were separated, dried, and weighed. One core was taken in each plot within the destructive area of the plot and its location marked and not sampled again.

Chl $a$ concentration was used as a proxy for the abundance of phytoplankton in the water-column and benthic microalgae in the sediment. To measure Chl $a$ concentration in the water-column, 100 ml of the water collected for the nutrient analysis was filtered through a 47 mm Whatman GF/F filter. Sediment Chl $a$ concentration was quantified by sampling the top centimeter of sediment with a 3 cm-diameter core. One core was taken per plot in the destructive area of the plot. Chlorophyll $a$ was extracted from water and sediment samples using 10 and 25 ml, respectively, of a 2:3 mixture of dimethyl sulfoxide (DMSO):90% acetone (Shoaf and Lium, 1976) and Chl $a$ content determined by fluorometry following the non-acidification method (Welschmeyer, 1994).

Faunal Measurements.—The abundance of infaunal and epifaunal macroinvertebrates (> 500 mm) were obtained from the same core samples used for seagrasses. Macroinvertebrates were classified into five major groups (amphipods, isopods, gastropods, bivalves, and polychaetes) and their abundance determined. The abundance of demersal fauna (fish and crustaceans) was assessed using a Beam Plankton Trawl (BPT, mesh size of 1 mm). BPT samples were collected within a 10 m$^2$ specific area in the plots. One BPT sample was obtained in each plot.

Metabolism.—Water-column and benthic gross primary productivity, respiration, and net productivity were estimated by measuring oxygen evolution in clear and dark bottles and chambers. Water from each plot was placed into one 300 ml BOD clear and one dark bottle. Water oxygen concentration (mg L$^{-1}$) was measured using a HQ 10 Hach Portable LDO oxygen meter. The pair of bottles was anchored with PVC poles at the canopy level in the plot. Two bell-shaped benthic chambers (one clear and one dark) with a height of 16 cm and diameter of 17 cm were inserted 3 cm into the sediment in each plot. The initial oxygen concentration in the chambers was equated to the mean initial concentration in the bottles of the corresponding plot. Bottles and chambers were incubated for 3–4 hrs around midday and final oxygen concentrations were recorded at the end of the incubation period. All incubations were done in the non-destructive area of the plot. Water was extracted from the chambers by inserting a syringe through a hole in the top of the chamber that had remained capped during incubation and transferred to a 60 ml BOD bottle for reading. From the measurements of initial and final oxygen concentrations, water-column ($WNP$) and benthic net productivity ($BNP$) and respiration ($WR$, $BR$) were assessed in mg C m$^{-2}$ hr$^{-1}$. We estimated the benthic rates by removing the contribution by the overlying water enclosed in the benthic chambers. Water-column rates were integrated with depth. The equations used were:
\[
WNP = (F_{CB} - I_{CB})1000 \, D \, C_{NP} \, t^{-1} \tag{1}
\]
\[
WR = (F_{DB} - I_{DB})1000 \, D \, C_{R} \, t^{-1} \tag{2}
\]
\[
BNP = [(F_{CC} - I_{CC}) - (F_{CB} - I_{CB})] \, V \, C_{NP} \, t^{-1} \, A^{-1} \tag{3}
\]
\[
BR = [(F_{DC} - I_{DC}) - (F_{DB} - I_{DB})] \, V \, C_{R} \, t^{-1} \, A^{-1} \tag{4}
\]

where \(I_{CB}, I_{DB}, I_{CC}, I_{DC}\) are initial oxygen concentration in clear and dark bottles and chambers (mg \(O_2\) L\(^{-1}\)), respectively; \(F_{CB}, F_{DB}, F_{CC}, F_{DC}\) are the final oxygen concentrations in clear and dark bottles and chambers (mg \(O_2\) L\(^{-1}\)), respectively; \(D\) is depth (m), \(t\) is incubation time (hrs), \(C_{NP}\) (0.313 mg C mg \(O_2\) \(^{-1}\)), and \(C_{R}\) (0.375 mg C mg \(O_2\) \(^{-1}\)) are the conversion factors from oxygen to carbon assuming photosynthetic and respiratory quotients of 1.2 and 1 (Strickland and Parsons, 1972), \(V\) is volume (L) and \(A\) is area (m\(^2\)) of the chamber.

We derived water-column and benthic gross primary productivity (\(WGPP\) and \(BGPP\)) as the sum between the respective values of net productivity and the absolute value of respiration:

\[
WGPP = WNP + \frac{1}{WR} \tag{5}
\]
\[
BGPP = BNP + \frac{1}{BR} \tag{6}
\]

Finally, we obtained system-integrated gross primary productivity, respiration, and net productivity (\(SGPP\), \(SR\), and \(SNP\)) by adding up the values obtained for the water-column and the benthos:

\[
SGPP = WGPP + BGPP \tag{7}
\]
\[
SR = WR + BR \tag{8}
\]
\[
SNP = WNP + BNP \tag{9}
\]

**Statistical Analysis.**—We used one-way repeated measures analysis of variance (ANOVA) since the same plots were sampled repeatedly during our survey. Our analysis examined the natural temporal variability in the bed studied and whether the impact of the hurricane was greater than natural variability. To do that, we included all pre- and post-hurricane sampling dates in the repeated measures ANOVA. If an overall significant effect of time was found (\(P < 0.05\) for the main effect of time, the within-subject factor), we ran a post-hoc Tukey test to account for short-term (comparing the last sampling date before landfall with the first sampling date after landfall) and long-term impact (comparing first sampling date after landfall in September 2005 with September 2006). If those two dates did not differ significantly, we concluded no major short- and/or long-term effect of the hurricane. If those two dates did differ significantly but the extent of that difference (as indicated by the magnitude of the test statistic) was similar to the extent of the natural temporal variability, we also concluded no major effect of the hurricane. We only concluded a major effect of the hurricane when the magnitude was greater than the natural temporal variability. Long-term analysis was carried out for environmental variables (salinity, temperature, light at the bottom, and dissolved oxygen), seagrass density and biomass, epifauna and infauna (amphipods, isopods, gastropods, bivalves, and polychaetes), and metabolism. When data transformation did not meet the assumptions of ANOVA, we ran a Friedman repeated measures ANOVA on ranks and post-hoc comparisons using a Q-test.

**Results**

**Dissolved Inorganic Nutrients, POM, and Environmental Parameters.**—Dissolved inorganic nutrients (nitrite, nitrate, and ammonium) varied significantly with time (Table 1). However, no significant differences were found between the last
Table 1. Statistical analysis of seasonality (repeated measures ANOVA), and both short- (post-hoc Tukey test analysis comparing pre- and immediate post-hurricane values) and long-term effects (post-hoc Tukey test analysis between September 2005 and September 2006) of Hurricane Katrina. Bold values are significant at P < 0.05.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Seasonality</th>
<th>Short-term</th>
<th>Long-term</th>
<th>Variable</th>
<th>Seasonality</th>
<th>Short-term</th>
<th>Long-term</th>
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<td>&gt; 0.05</td>
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<tr>
<td><em>Halodule</em> biomass</td>
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<td>&gt; 0.05</td>
<td>&gt; 0.05</td>
<td>Seagrass biomass</td>
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<td>&gt; 0.05</td>
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<tr>
<td><em>Ruppia</em> density</td>
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<td>&gt; 0.05</td>
<td>Phytoplankton</td>
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<td>&gt; 0.05</td>
<td>Microphytobenthos</td>
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<td>&gt; 0.05</td>
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<td>---</td>
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<td>&gt; 0.05</td>
<td>System respiration</td>
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<td>&gt; 0.05</td>
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<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>Benthic net produc.</td>
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<td>&gt; 0.05</td>
<td>&gt; 0.05</td>
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<td>Benthic respiration</td>
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<td>Water respiration</td>
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sampling date before hurricane landfall and the first sampling date after hurricane landfall. The only exception was phosphate, where lower values were found on the first sampling date after landfall in comparison with the last sampling date before landfall, but that decrease was similar in magnitude to the temporal oscillations found before landfall (Table 1). Similarly, POM (Table 1) varied significantly with time but not between the two immediate dates around hurricane landfall.

Environmental variables (i.e., temperature, light at the bottom, and salinity) showed strong seasonal variability during the study period (Table 1). We found significant differences between the last sampling date before hurricane landfall and the first sampling date after landfall (except for dissolved oxygen), but the magnitude of those differences was similar to, and in some cases smaller than, the magnitude of the temporal differences found before landfall. We found no long-term impact of the storm on the environmental variables one year after the hurricane landfall.

**Primary Producers.**—We recorded large but not statistically significant decreases in *H. wrightii* leaf density (50%) and biomass (48% and 70% for above- and belowground, respectively) 2 wks after the passage of the storm (Table 1, Figs. 1A, 2A). The abundance of *R. maritima* was very low at the time of hurricane landfall due to seasonal decline, but we also recorded similar non-significant decreases in leaf den-

![Figure 1](image.png)

Figure 1. Specific and total seagrass density. (A) Seagrass density (# leaves m\(^{-2}\)). (B) Total seagrass density (# leaves m\(^{-2}\)) of both *Halodule wrightii* and *Ruppia maritima*. Error bars are SE. Dashed line is water temperature (°C). The dotted vertical line marks the landing of Hurricane Katrina on August 29, 2005.
Figure 2. Biomass (gDW m$^{-2}$) of the seagrasses (A) Halodule wrightii and (B) Ruppia maritima. (C) Total seagrass biomass of both species. Error bars are SE. The dotted line marks the landing of Hurricane Katrina on August 29, 2005.

sity and biomass for that species two weeks after the passage of the storm (Table 1, Figs. 1A, 2B). Consequently, total seagrass density and biomass did not significantly decrease from the last sampling date before landfall to the first sampling date after landfall (Table 1, Figs. 1B, 2C). We also found non significant effect of the hurricane on seagrass density and biomass one year after landfall.
The lack of a significant impact by Hurricane Katrina contrasts with the large decrease in total seagrass density observed during the summer prior to hurricane landfall (e.g., decrease of > 60% from April to May). This decrease was associated with high temperatures (Pearson correlation coefficient between total seagrass density and temperature, $r = -0.54$, $P < 0.05$, Fig. 1B). The optimal temperature for *H. wrightii* growth is unknown, but for a similar species, *Halodule uninervis* [(Forsskål) Ascherson, 1882], it is between 23–26 °C (Lee et al., 2007). The bed studied seems to display a bimodal growth pattern, with biomass peaks in spring and fall and depressed values during the summer probably due to temperature stress. Such a bimodal seasonal pattern has also been found for other beds in the Gulf of Mexico (Dunton, 1990) and elsewhere (Duarte, 1989). We did not find any significant differences in water-column and benthic Chl $a$ concentration between the last sampling date before hurricane landfall and the first sampling date after landfall (Table 1, Fig. 3A,B).

**Fauna Measurements.**—There were no significant changes in the abundance of infaunal and epifaunal (amphipods, isopods, gastropods, bivalves, and polychaetes) invertebrates for both short- and long-term following the passage of Hurricane Katrina (Table 1, Figs. 4, 5). Similar results were observed for fish and crustaceans, where the differences in abundance between the last sampling date before landfall and the first sampling date after landfall were non-significant (Table 1, Fig. 5).

**Metabolism.**—In most cases, we did not find a significant metabolic difference between the last sampling date before landfall and the first sampling date after landfall (Table 1, Fig. 6). When a significant decrease occurred (i.e., system-integrated and water-column gross primary productivity and water-column net production; Table 1, Fig. 6 B,I), the magnitude of that decrease was similar to the magnitude of the natural temporal oscillations found during the summer before landfall. Also, we found no significant long-term effect of the hurricane on the metabolism of the seagrass meadow (with the exception of system-integrated and water-column net productivity and water-column gross primary productivity; Table 1, Fig. 6 B,I). Again, the magnitude of those decreases was similar to the magnitude of the natural temporal oscillations.

**Discussion**

Seagrass beds are periodically battered by hurricanes. Previous studies have shown the impact of hurricanes on seagrass abundance, biomass, and productivity can differ in extent, depending on the hurricane itself, the time of the year, and the place (Marba et al., 1994; Fourqurean and Rutten, 2004; Cruz-Palacios and van Tussenbroek, 2005; Byron and Heck, 2006; Ridler et al., 2006). We know little, however, about how hurricanes influence the community of producers and consumers that inhabit seagrass beds, and the consequences of those impacts for community-integrated processes such as bed metabolism. This study is an initial attempt towards that end. We show that Hurricane Katrina did not have a major impact on the community structure (abundance of producers and consumers) and the metabolic functioning of the bed studied (primary and net production and respiration) within one year of landfall. This conclusion is based on the results observed in the three 30 m$^2$ rectangular plots repeatedly monitored in the bed studied. Perhaps larger impacts occurred in other locations of the bed, as it has been observed in other studies where hurricane impacts were found to be location-specific (Fourqurean and Rutten, 2004;
However, we think this is not likely since we frequently waded throughout the bed during the duration of the study and, both for the pre- and post-hurricane periods, we never noticed any large differences in the visual appearance of the seagrass within the plots and at other locations of the bed.

In August 2005, Hurricane Katrina caused major material damage throughout the northern Gulf of Mexico, including the area around the seagrass bed studied. Yet, we observed no short- or long-term impact of the storm in the density and biomass of *H. wrightii* and *R. maritima*. We noticed neither accumulation nor erosion of the sediment after passage of the hurricane (pers. obs.). We also did not notice any changes in the water quality (e.g., turbidity, and nutrients) within 1 yr after landfall.

We did not find a strong effect of the hurricane on the fauna that inhabit the bed studied. Infaunal and epifauna macroinvertebrates displayed high abundance in the spring (e.g., amphipods, isopods, and bivalves) and/or in the fall (e.g., gastropods and bivalves), and fish showed high abundance in late summer/early fall, which coincided with elevated seagrass density and biomass. Through the provision of shelter and

Figure 3. Densities of (A) Microphytobenthos (mg cm$^{-2}$) and (B) Phytoplankton (mg L$^{-1}$) from May to December 2005. Error bars are SE. The dotted line marks the landing of Hurricane Katrina on August 29, 2005.
food, seagrass density and biomass strongly influence the abundance of resident organisms (Orth et al., 1984) and post-hurricane studies have shown fast recovery rates for fauna as their habitat recovers rapidly (Greenwood et al., 2006; Langtimm et al., 2006; Paperno et al., 2006). The lack of strong impacts of the hurricane on the abundance of seagrass-associated organisms was probably mediated by the lack of strong impacts on seagrass density and biomass.

We found no short-term effect of the hurricane on the concentration of Chl $a$ in the sediment. Cebrian et al. (2008) found negative impacts by Hurricane Ivan in 2004 and by four major storms in 2005 on Chl $a$ concentration in the sediment of six
marsh tidal creeks in the northern Gulf of Mexico. They attributed the reduced Chl α concentrations observed after the passage of the storms to increased burial and benthic microalgal mortality. In our study, we did not observe any noticeable burial 15 d after the passage of the hurricane. The canopy of seagrass leaves and belowground web of roots and rhizomes could have helped stabilize the sediment, reducing resuspension and the loss of benthic microalgae during the hurricane (Hemminga and Duarte, 2000).

The hurricane did not have a major impact on the metabolism of the bed studied. This may be due in part to the lack of a major impact on the abundance of three major types of primary producers (seagrasses, benthic microalgae, and phytoplankton),
Figure 6. Rates of (A, B, C) gross primary production (GPP), (D, E, F) respiration (R), and (G, H, I) net production (NP) in the benthos, the water-column, and integrated system (mgC m\(^{-2}\) hr\(^{-1}\)). Error bars are SE. The dotted line marks the landing of Hurricane Katrina on August 29, 2005.
since producer biomass is often an important driver of system metabolism (Murray and Wetzel, 1987; Moncreiff et al., 1992; Stutes et al., 2007). The lack of major impacts on the nutrient concentrations and physical characteristics (i.e., salinity, temperature, dissolved oxygen, and light at the bottom) of the water-column may have also contributed to the lack of a major impact on the metabolism of the bed (e.g., Garcia et al., 2005; Stutes et al., 2006).

The lack of significant impacts on resident fauna and metabolism of the bed was likely a result of no effect on the abundance of seagrasses, benthic microalgae, and phytoplankton. Our results document that seagrass meadows in the northern Gulf of Mexico composed of *H. wrightii* and *R. maritima* experience large natural temporal variability and may be very resistant to large disturbances such as hurricanes.

**Acknowledgments**

We are thankful to K. Sheehan, N.-E. Miller, L. Linn, D. del Valle, and the DISL tech support for their help in the field and at the lab. Thanks to Mr. Bosarge and the Crockett family for allowing us to cross their properties at Sandy Bay. Thanks to N. Gerald, M. O’Connor, I. Vu, M. Simpson, and three anonymous reviewers who improved earlier versions of the manuscript. This publication was supported by NOAA Grants NA86RG0039 and NA16RG2258, the Mississippi-Alabama Sea Grant Consortium and the Alabama Center for Estuarine Studies (Grants # 5-21838 and 5-21871).

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**Date Submitted:** 25 February, 2009.

**Date Accepted:** 8 May, 2009.

**Available Online:** 16 June, 2009.