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The impact of Hurricane Ivan on the primary productivity and metabolism of marsh tidal creeks in the NorthCentral Gulf of Mexico

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Abstract Past research has examined hurricane impacts on marine communities such as seagrass beds, coral reefs, and mangroves, but studies on how hurricanes affect marsh tidal creeks are lacking despite the important ecological roles that marsh tidal creeks have in coastal ecosystems. Here we report on the impact of Hurricane Ivan, which made landfall on September 16, 2004, on the primary productivity and metabolism of six marsh tidal creeks in the NorthCentral Gulf of Mexico. The hurricane did not seem to have any large, lasting impact on nutrient concentrations, primary productivity, metabolism, and chlorophyll *a* concentration in the water-column of the marsh tidal creeks. In contrast, the hurricane seemed to largely decrease gross primary productivity, net productivity, and chlorophyll *a* concentration in the sediment of the marsh tidal creeks. The results observed for Hurricane Ivan were coincident with those observed for four other major storms that made landfall close to the study area during 2005, Tropical Storm Arlene and Hurricanes Cindy, Dennis, and Katrina. However, the apparent negative impact of major storms on the sediment of the marsh tidal creeks did not seem to be long-lived and appeared to be dissipated within a few weeks or months after landfall. This suggests that marsh tidal creeks mostly covered with bare sediment are less disturbed by hurricanes than other types of marine communities populated with bottom-attached and/or more rigid organisms, such as seagrass meadows, coral reefs, and mangroves, where hurricane impacts can be larger and last longer.

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Introduction

Tidal creeks play an important role in many coastal ecosystems. Due to their shallow depth and often convoluted morphology, which offer protection from wave action, tidal creeks provide habitat and refuge from predators for many invertebrate and vertebrate organisms (Stout 1984; Able and Fahay 1998).

Numerous organisms also find food in tidal creeks, which normally feature a complex trophic web fueled by the multitude of primary producers that grow in the creeks and inputs of organic matter from the surrounding marsh (Alongi 1998). Tidal creeks also mediate the exchange of carbon and nutrients between land and the coastal ocean (Valiela et al. 2000a; Tobias et al. 2003a) and contribute significantly to the metabolism of coastal ecosystems (Heip et al. 1995; Gazeau et al. 2004).

Large-scale disturbances, such as cyclones and hurricanes, have the potential to significantly impact marsh tidal creeks. Yet, while numerous studies have addressed the impact of hurricanes on marine communities such as mangroves (Smith et al. 1994; Armentano et al. 1995; Doyle et al. 1995; McCoy et al. 1996), artificial (Turpin and Bortone 2002) and natural coral reefs (Woodley et al. 1981; Lugo et al. 2000), and seagrass beds (Glynn et al. 1964; Wanless et al. 1988; Poiner et al. 1989; Rodriguez et al. 1994; Tilmant et al. 1994; van Tussenbroek 1994; Preen et al. 1995; Michot et al. 2002; Fourqurean and Rutten 2004), studies addressing the impact of hurricanes on marsh tidal creeks are lacking. Indeed, a recent special issue of ''Estuaries and Coasts'' on hurricane impacts on coastal ecosystems (Greening, Doering and, Corbett, eds., 2006, Volume 29, Number 6A) compiled examples of hurricane impacts on seagrass beds, mangroves, coastal wetlands, coral reefs and the water circulation, water quality, phytoplankton and fish assemblages of bays, coastal lagoons and estuaries, but no examples of impacts on marsh tidal creeks were provided.

In June 2004, we began monitoring six tidal creeks located near the mouth of Mobile Bay, Alabama (Fig. 1), to obtain baseline information required for an oyster restoration experiment that started in March 2005. The creeks are moderate in size, ranging from 147.0 to 2,116.7 m^2, shallow, with mean depth (±SE) ranging from 0.27 (±0.02) to 0.54 (±0.02) m, and entirely contoured by black needlerush (*Juncus romerianus*) marsh. The bottom of all creeks is completely covered with sandy and muddy sediment. The tide in the area examined is mostly diurnal, with a mean amplitude (±SE) of 0.38 ± 0.02 m recorded at a level logger located at the Dauphin Island Sea Lab, which is <1 nautical miles from creeks one to four and <3 nautical miles from creeks five and six (Fig. 1). Thus, in view of their shallowness, the water-column in the creeks studied is renewed through tidal forcing within a few days at most (Monbet 1992; Valiela et al. 2000b).

On September 16, 2004, Hurricane Ivan made landfall approximately 35 nautical miles to the east of the creeks and caused devastation throughout coastal Alabama. At landfall the storm was generating winds in excess of 150 km h^{-1} and a surge greater than 2 m in the area of study (as measured on Dauphin Island, AL, <5 nautical miles from the study sites). Due to the relatively fast speed of the eye at landfall (i.e., 21–26 km h^{-1}), the amount of rainfall in the area of study, however, was not as large (i.e., 184.3 mm over 48 h, measured in Mobile, AL, <35 nautical miles from the study sites) as with other hurricanes. The passage of Hurricane Ivan close to the creeks created an excellent opportunity to assess the impacts of the hurricane on the creeks examined. Here we focus on the impacts of the hurricane on microalgal biomass, primary productivity, and metabolism of the creeks. In particular, we hypothesized that, due to sediment disturbance, Hurricane Ivan had a longer-lasting impact on the sediment than on the highly flushed, fast turning-over water-column of the marsh tidal creeks examined.

Materials and methods

Sampling design

This study is contained within the frame of a larger study intended to evaluate the effects of restored oyster reefs on the ecology of marsh tidal creeks. As such, the sampling design of this study is inevitably linked to the sampling design of the oyster restoration study. A rectangular experimental area that represented 10% of the creek open water surface was delineated within the lower (downstream) half of each of the creeks. The experimental area in creeks 2, 3, and 5 was seeded with oysters at a density of 150 oysters per square meter in March 2005, whereas creeks 1, 4, and 6 were left unseeded (i.e., control creeks in the oyster restoration study). Five permanent stations were located adjacent to the experimental area along the longitudinal axis of the creek in an effort to assess the effects of restored oyster reefs on the surrounding environment. Namely, stations 1 and 2 were situated 2 and 0.5 m downstream from the

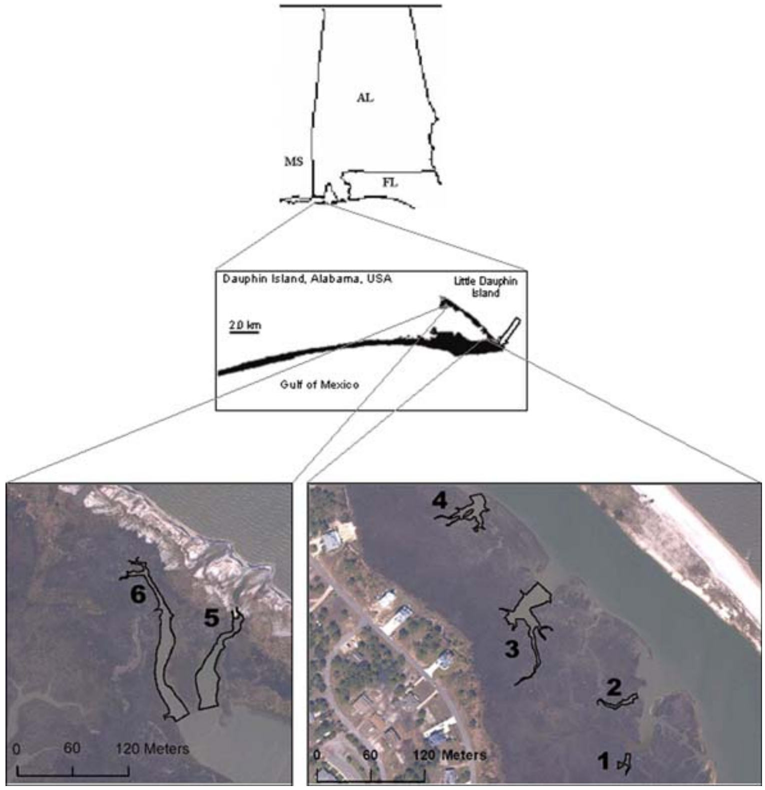

Fig. 1 Study area and creeks examined. The arrow indicates the position of the level logger at the Dauphin Island Sea Lab

downstream edge (i.e., closer to the mouth of the creek) of the experimental area, and stations 3, 4, and 5 were situated 0.5, 2, and 4 m upstream from the upstream edge.

Sampling started in June 2004 and proceeded monthly throughout summer 2006 with the exception of a few months where unfavorable meteorological conditions prevented sampling. Here we report data through March 2006. The last sampling date before the landfall of Hurricane Ivan (i.e., September 16 2004) was August 25, 2004 and the first sampling date after landfall was September 27 2004. We were not able to go back to the creeks for 11 days after landfall due to the damage and power outages that followed the passage of the hurricane. In this article, we report data for all creeks from June 2004 to February 2005, but only for creeks 1, 4, and 6 (i.e., control creeks with no oysters added) after February 2005 because the experimental area in the other three creeks was seeded with oysters a few days before the March 2005 sampling date. Thus, had we included the creeks seeded with oysters in the analysis, the effect of the newly implanted oysters could have masked the impact of the hurricane in those creeks.

Variables measured

Water-column nutrients

Concentrations of dissolved inorganic nitrogen (DIN; NO_3, NO_2, NH_4, in μM), phosphate (PO_4, in μM), dissolved organic nitrogen (DON, in μM), particulate organic nitrogen (PON, in mg l^{-1}), dissolved organic carbon (DOC, in ppm), and particulate organic carbon (POC, in mg l^{-1}) were examined from a sample collected in the mid water-column, which was put on ice and brought back to the laboratory for processing within <4 h from collection. In the laboratory, 400 ml was filtered through a Pall® 47 mm glass fiber filter (A/E) (same sample used for POM analysis, data not reported here). About 10 ml of filtrate was retrieved for DOC analysis. Dissolved organic carbon samples were stored in muffled 25 ml vials with a screw-tight lid and frozen at -80°C until analysis using a Shimadzu

TOC-500 and standard procedures (Pennock and Cowan 2001). About 60 ml of filtrate was used for the analyses of DIN, DON, and PO_4. Those samples were also frozen at −80°C until analysis using a Skalar Autoanalyzer and standard procedures (Pennock and Cowan 2001). Finally, from the same water sample, another 100 ml was filtered onto a Whatman® 25 mm premuffled glass microfiber filter (GF/F) for analysis of PON and POC in a CarloErba CNS using standard procedures (Pennock and Cowan 2001).

Chlorophyll a

Chlorophyll *a* (chla) concentration in the water-column (μg l^{-1}) was examined as an indicator of microalgal biomass (see Pinckney et al. 1994). In the laboratory, 100 ml from the same mid water-column sample collected for nutrient analysis was filtered onto a Pall® 47 mm glass fiber filter (A/E) and the filter frozen at −80°C until further analysis. To quantify sediment chla concentration (μg cm^{-2}), the top 1 cm of sediment was collected using a hollow tube with a radius of approximately 2.5 cm and samples were frozen at −80°C until analysis. Chlorophyll *a* was extracted from filters and sediment samples using respectively 10 and 25 ml of a 2:3 mixture of dimethyl sulfoxide (DMSO):90% acetone (Shoaf and Lium 1976), and chla content was determined fluorometrically (Turner Designs® TD-700) using the non-acidification method (Welschmeyer 1994).

Primary productivity and metabolism

Primary productivity and metabolism were measured using clear/dark incubations (i.e., the oxygen evolution method). Water was collected with a bucket from the mid-water-column and siphoned into 300 ml BOD clear and dark bottles. Care was taken when filling the buckets and bottles to avoid bubbling. Immediately after filling the bottles, water dissolved oxygen concentration (mg l^{-1} and % saturation) in the bottles was measured using a WTW® oxy 157*i* oxygen meter and stirrox g field probe. At each station one pair of bottles (one clear and one dark) was deployed at the water surface with buoys and a second pair was anchored to the bottom with PVC poles.

Additionally, a pair of benthic chambers, one clear and one dark, was deployed at each station along with the two pairs of bottles. Each chamber had a base diameter of 18.4 cm, a total volume of approximately 3 l, and was inserted approximately 2 cm into the sediment. We assumed that the initial water oxygen concentration in the chambers corresponded to the initial concentration for the bottom bottles in the same station (i.e., initial concentration in clear chamber equaled initial concentration in bottom clear bottle and initial concentration in dark chamber equaled initial concentration in bottom dark bottle), since the chambers were deployed as the initial concentrations in the bottles were being measured and they were also filled up with mid water-column water.

Bottles and chambers were incubated from 3 to 5 h around solar noon and final water oxygen concentrations read at the end of the incubation period. All incubations were done on mostly sunny days. The water in the chambers was not stirred up during incubation but that was inconsequential for the large changes in oxygen concentration due to photosynthetic production or respiration that are normally observed for sediment incubations in subtropical marsh creeks (see Stutes et al. 2006 for further elaboration). To measure final oxygen concentration in the chambers, water was extracted by inserting a syringe through a hole drilled at the top of the chamber, which had remained capped during incubation, and transferred to a 60-ml BOD bottle. From the measurements of initial and final oxygen concentrations, we derived water-column net productivity using the clear bottles and respiration using the dark bottles (WNP and WR, in mg C l^{-1} h^{-1}), and sediment net productivity using the clear chambers and respiration using the dark chambers (SNP and SR, in mg C m^{-2} h^{-1}) for each station. Surface and bottom bottles were averaged for the derivation of water-column net productivity and respiration at each station. In addition, to remove the contribution by the water enclosed in the benthic chambers and include only sediment processes, changes in oxygen concentration measured in bottom clear and dark bottles were subtracted from the overall (i.e., sediment and enclosed water) changes recorded in corresponding (i.e., placed at the same station) clear and dark chambers. The equations are:

$$\mathrm{WNP} = C_{\mathrm{NP}}(F_{\mathrm{CB}} - I_{\mathrm{CB}})/t \quad (1)$$

$$\mathrm{WR} = C_{\mathrm{R}}(F_{\mathrm{DB}} - I_{\mathrm{DB}})/t \quad (2)$$

$$\mathrm{SNP} = V\ C_{\mathrm{NP}}((F_{\mathrm{CC}} - I_{\mathrm{CC}}) - (F_{\mathrm{CB}} - I_{\mathrm{CB}}))/(t\ A) \quad (3)$$

$$\mathrm{SR} = V\ C_{\mathrm{R}}((F_{\mathrm{DC}} - I_{\mathrm{DC}}) - (F_{\mathrm{DB}} - I_{\mathrm{DB}}))/(t\ A) \quad (4)$$

where F_{CB}, F_{DB}, F_{CC}, and F_{DC} are the final oxygen concentrations in clear bottles, dark bottles, clear chambers and dark chambers (mg O_2 l^{-1}), I_{CB}, I_{DB}, I_{CC}, and I_{DC} are the initial oxygen concentrations in clear bottles, dark bottles, clear chambers and dark chambers (mg O_2 l^{-1}), t is incubation time (h), C_{NP} (0.313 mg C mg O_2^{-1}) and C_R (0.375 mg C mg O_2^{-1}) represent the conversion factors from oxygen to carbon assuming photosynthetic and respiratory quotients of 1.2 and 1 (Strickland and Parsons 1972), V is the volume of water enclosed in the chamber (l), and A is the area of the incubation chamber (m^2). Finally, we derived water-column and sediment gross primary productivity for each station as the sum between net productivity and the absolute value of respiration.

Statistical analyses

To obtain an integrated view of how the variables examined varied with time, across creeks, and whether the variability with time depended on the creek considered (i.e., significant interaction between time and creek), we used a two-way repeated measures analysis of variance since we repeatedly sampled the same stations. Creek was the among-subject factor and time was the within-subject factor. If the variable differed significantly with time, we then compared the sampling dates of August and September 2004 using a paired t-test to determine whether the variable differed between the last sampling date before hurricane landfall and the first sampling date after hurricane landfall. Finally, if the variable was different between those two sampling dates, we compared the sampling date of August 2004 with all the other pre-hurricane summer sampling dates using paired t-tests to put the differences observed 11 days after the passage of the hurricane in perspective with the natural variability observed during the summer months prior to hurricane landfall. If the variable examined did not differ significantly across creeks, and time and creek did not interact significantly, all creeks were pooled for the paired t-tests but, if differences among creeks and/or the interaction term were significant, the tests were done separately for each creek. Therefore, this procedure allowed us to analyze the changes observed with the passage of Hurricane Ivan in the context of the natural temporal variability observed in the creeks during the summer months prior to hurricane landfall, and whether those changes were common or varied among creeks.

The two-way repeated measures analysis of variance was conducted from August 2004 to February 2005 for water-column chla since only station 4 was sampled for this variable in June and July 2004 and, thus, we could not analyze differences among creeks in water-column chla for June and July 2004. For the same reason, the analysis was conducted from July 2004 to February 2005 for water-column primary productivity and metabolism (i.e., only station 4 was sampled for these variables in June 2004). For sediment chla, primary productivity and metabolism the analysis was conducted from June 2004 to February 2005. Water-column nutrients were measured only at station 4 throughout February 2005 and, thus, for nutrient variables, we could not examine differences among creeks and only tested for temporal differences using a single repeated measures analysis of variance.

We did not extend our analyses beyond February 2005 because only three creeks were left unseeded after that date and, thus, extending the analyses beyond February 2005 with only three creeks would have represented an unbalanced design and substantial loss of statistical power (Quinn and Keough 2002). At any rate, the post-seeding data for the three unseeded creeks, extending 18 months after landfall, provides a longer timeline to better examine the dynamics of the three unseeded creeks after the landfall of Hurricane Ivan. In addition, four other major storms impacted the study area to varying degrees during the summer of 2005 (Tropical Storm Arlene made landfall approximately 52 nautical miles east of the study site on June 11, Hurricane Cindy made landfall approximately 104 nautical miles west of the study site on July 5, Hurricane Dennis made landfall approximately 58 nautical miles east of the study site on July 10, and Hurricane Katrina made landfall approximately 78 nautical miles west of the study site on August 29), providing us with an opportunity to compare the changes observed with the passage of Hurricane Ivan with the changes observed with these four other major storms.

Normality, which was met in all analyses, was evaluated using the Shapiro–Wilk statistic (Zar 1999). In addition, prior to conducting the analyses, Mauchly's tests of sphericity were performed, and when the assumption of sphericity was not met, Greenhouse Geisser corrected tests were used. All statistical analyses were performed using SPSS 12.0 (SPSS, Inc. 2003) and statistical significance was accepted at $P < 0.01$ to enhance the robustness of our results.

Results

Water-column nutrients, primary productivity, metabolism, and chlorophyll a

Out of all the nutrient variables measured, only DIN ($F_{5,25} = 16.5$, $P < 0.01$) and PO_4 ($F_{5,25} = 6.6$, $P < 0.01$) varied significantly through time (Fig. 2), but we did not find any significant differences between the most immediate pre- (August 2004) and post-hurricane (September 2004) sampling dates (both paired *t*-tests were non-significant).

Water-column gross primary productivity varied significantly among sampling dates ($F_{3.1,74.2} = 84.1$, $P < 0.01$, Fig. 3) and among creeks ($F_{5,24} = 20.0$, $P < 0.01$). The nature and extent of temporal variability in water-column gross primary productivity depended on the creek considered, as revealed by the significant interaction between time and creek ($F_{15.5,74.2} = 19.9$, $P < 0.01$). Therefore, the paired *t*-tests between the last sampling date before hurricane landfall and the first sampling date after landfall were done separately for each creek. Significant differences between those two dates were found only for creeks 3, 4, and 5 and, in those cases, the differences were of similar magnitude to the inherent temporal variability among summer months prior to landfall as revealed by Fig. 3 and by the magnitude and

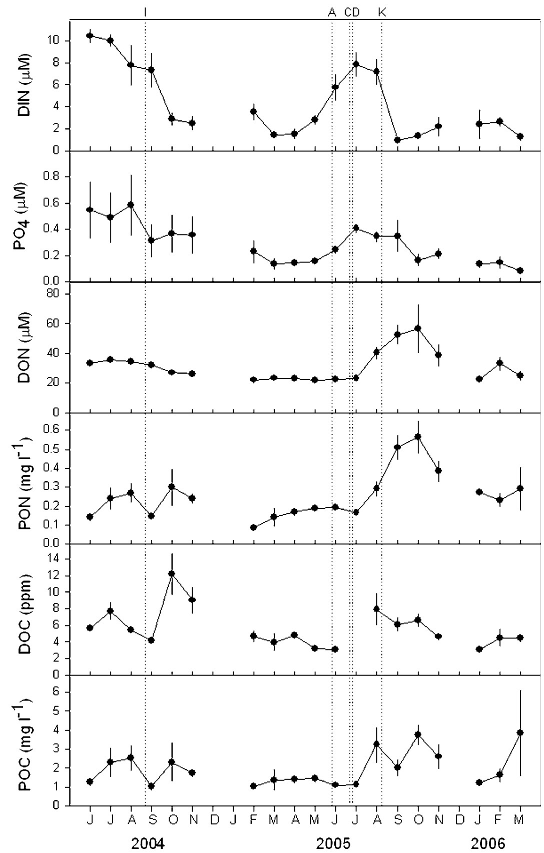

Fig. 2 Concentrations of dissolved inorganic nitrogen (DIN), phosphate (PO_4), dissolved organic nitrogen (DON), particulate organic nitrogen (PON), dissolved organic carbon (DOC), and particulate organic carbon (POC) in the water-column of the creeks examined. Symbols represent the average of the values measured at station 4 for all creeks on each given date and bars the standard error. Only creeks 1, 4, and 6 (unseeded creeks) are included from March 2005 on. Dotted lines correspond to the timing of the major storms (I: Hurricane Ivan; A: Tropical Storm Arlene; C: Hurricane Cindy; D: Hurricane Dennis; K: Hurricane Katrina)

significance of the *t*-statistics of the paired *t*-tests between August and July 2004.

Similar results were found with the 2005 data for the three creeks not seeded with oysters. Tropical Storm Cindy made landfall 2 days before our sampling date in June 2005, Hurrricanes Cindy and Dennis 8 and 3 days before our sampling date in July 2005, and Hurricane Katrina 22 days before our sampling date in September 2005. Yet, in general the changes observed between the most immediate pre- and post-storm sampling dates were not larger than

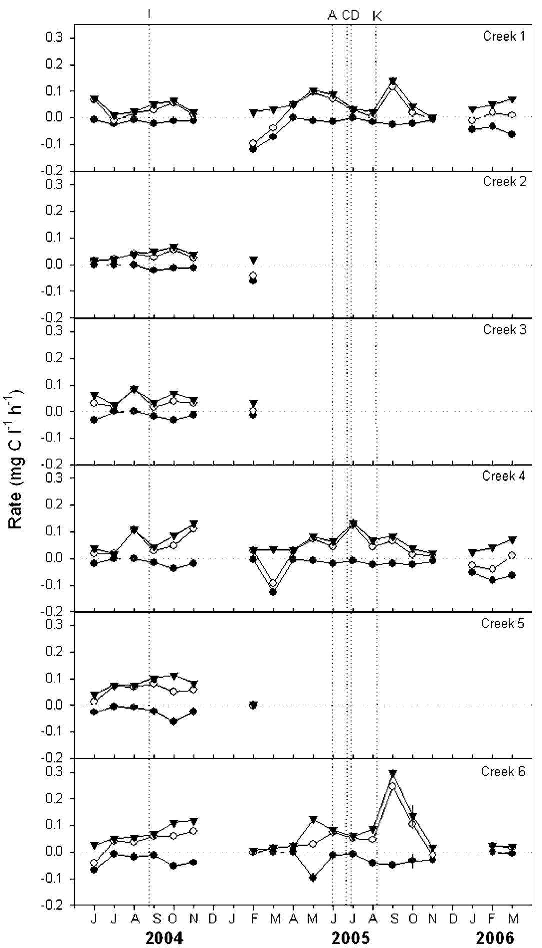

Fig. 3 Rates of water-column gross primary productivity (inverted solid triangles), net productivity (open circles), and respiration (solid circles) in the creeks examined. Symbols represent the average of the values measured for all stations in the creek on each given date and bars the standard error. The variables are depicted separately for each creek because time and creek interacted significantly in the repeated measures analysis of variance. Dotted lines correspond to the timing of the major storms (I: Hurricane Ivan; A: Tropical Storm Arlene; C: Hurricane Cindy; D: Hurricane Dennis; K: Hurricane Katrina)

the variability observed among sampling dates prior to the passage of the storms (Fig. 3).

The results obtained for water-column net productivity were similar to those observed for gross primary productivity (Fig. 3). Water-column net productivity varied significantly with time ($F_{5,120}$ = 135.7, $P < 0.01$), among creeks ($F_{5,24}$ = 43.5, $P < 0.01$), and there was a significant interaction between time and creek ($F_{25,120}$ = 24.6, $P < 0.01$). When paired *t*-tests were done between August and September 2004 for each creek separately, only creeks 3 and 4 displayed significant differences and, again, those differences were of similar magnitude to the inherent temporal variability among summer months prior to hurricane landfall. Similar results were found for 2005, where the changes observed between the most immediate pre- and post-storm sampling dates were not larger than the variability observed among sampling dates prior to the passage of the storms.

Water-column respiration differed among sampling dates ($F_{2.1,50.8}$ = 33.7, $P < 0.01$, Fig. 3), among creeks ($F_{5,24}$ = 5.8, $P < 0.01$), and the interaction between time and creek was significant ($F_{10.6,50.8}$ = 16.7, $P < 0.01$). Only creeks 1, 2, and 3 showed a significant difference when August and September 2004 were compared with a paired *t*-test and, as found for gross and net productivity, those differences were of similar magnitude to the differences found among summer months prior to hurricane landfall. Similarly, the changes observed with the passage of major storms in 2005 were not larger than the differences observed among sampling dates prior to the passage of the storms.

Water-column chlorophyll *a* concentration varied significantly with time ($F_{1.8,42.4}$ = 9.4, $P < 0.01$, Fig. 4) but, unlike water-column primary productivity and metabolism, it did not differ among creeks ($F_{5,23}$ = 2.0, P = 0.12) nor was the interaction between time and creek significant ($F_{9.2,42.4}$ = 1.5, P = 0.17). Hence, all creeks were pooled for the comparison between August and September 2004, which did not differ significantly. Little change, except between August and September 2005, was found in water-column Chlorophyll *a* concentration between the most immediate pre- and post-storm sampling dates during 2005.

Sediment primary productivity, metabolism, and chlorophyll a

Sediment gross primary productivity varied significantly among sampling dates ($F_{6,36}$ = 5.1, $P < 0.01$, Fig. 5), but not among creeks ($F_{5,6}$ = 1.0, P = 0.49). In addition, time and creek did not interact significantly ($F_{30,36}$ = 1.3, P = 0.20). Thus, all creeks were pooled for the comparison between August and September 2004, which showed a large decrease in

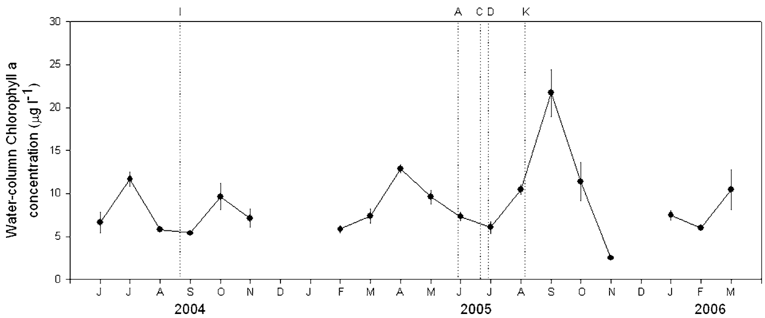

Fig. 4 Water-column chlorophyll *a* concentration in the creeks examined. Symbols represent the average of the values measured for all stations in all creeks on each given date and bars the standard error. The variable is depicted for all creeks pooled together because it did not vary significantly among creeks and time and creek did not interact significantly in the repeated measures analysis of variance. Only creeks 1, 4, and 6 (unseeded creeks) are included from March 2005 on. Dotted lines correspond to the timing of the major storms (I: Hurricane Ivan; A: Tropical Storm Arlene; C: Hurricane Cindy; D: Hurricane Dennis; K: Hurricane Katrina)

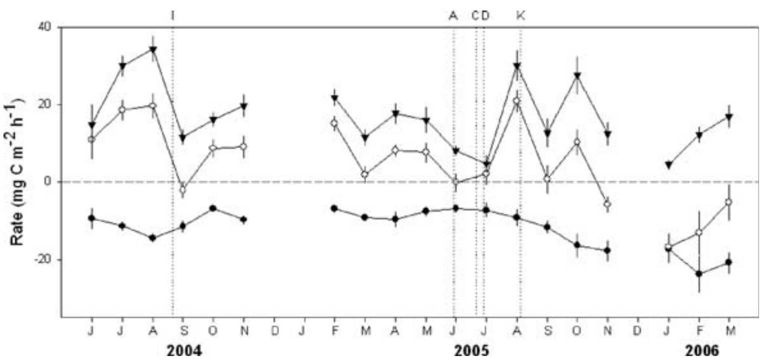

Fig. 5 Rates of sediment gross primary productivity (inverted solid triangles), net productivity (open circles), and respiration (solid circles) in the creeks examined. Symbols represent the average of the values measured for all stations in all creeks on each given date and bars the standard error. The variables are depicted for all creeks pooled together because they did not vary significantly among creeks and time and creek did not interact significantly in the repeated measures analysis of variance. Only creeks 1, 4, and 6 (unseeded creeks) are included from March 2005 on. Dotted lines correspond to the timing of the major storms (I: Hurricane Ivan; A: Tropical Storm Arlene; C: Hurricane Cindy; D: Hurricane Dennis; K: Hurricane Katrina)

gross primary productivity (paired *t*-test, $P < 0.01$). Such a decrease contrasted with the lack of significant differences among summer months prior to hurricane landfall (all paired *t*-tests between August and the other pre-hurricane summer months, $P > 0.01$).

Interestingly, similar decreases were observed in the unseeded creeks with the passage of four major storms near the study site in 2005. Depressed values of sediment gross primary productivity were measured on the June (2 days after landfall of Tropical Storm Arlene) and July (8 and 3 days after landfalls of Hurricanes Cindy and Dennis) sampling dates relative to the values observed during the previous Spring 2005 months (Fig. 5). Similarly, Hurricane Katrina made landfall 4 days after our August sampling date and 22 days before our September sampling date, and a substantial drop in sediment gross primary productivity was observed between those two sampling dates (Fig. 5).

The results found for sediment net productivity were almost identical to those found for gross primary productivity. Net productivity varied with time ($F_{6,36} = 6.0$, $P < 0.01$, Fig. 5), but not among creeks ($F_{5,6} = 4.1$, $P = 0.06$), and the interaction between time and creek was not significant

($F_{30,36}$ = 1.4, P = 0.17). A substantial drop in net productivity occurred from August to September 2004, which contrasted with the lack of significant differences between the summer months prior to hurricane landfall. Substantial drops in sediment net productivity were also observed with the passage of major storms in 2005 (Fig. 5).

Sediment respiration did not differ significantly among sampling dates ($F_{6,36}$ = 2.2, P = 0.07, Fig. 5) or among creeks ($F_{5,6}$ = 1.3, P = 0.36). This lack of significant differences with time, and in particular between the August and September 2004 sampling dates, contrasts with the results found for gross and net productivity. Similarly, no apparent changes in sediment respiration were observed with the passage of major storms in 2005 (Fig. 5).

Sediment Chlorophyll *a* concentration differed with time ($F_{1.9,11.4}$ = 51.0, P < 0.01, Fig. 6), but not among creeks ($F_{5,6}$ = 0.3, P = 0.90). Time and creek did not interact significantly ($F_{9.5,11.4}$ = 1.3, P = 0.35). Similarly to the results observed for gross and net productivity, Chlorophyll *a* concentration dropped considerably from August to September 2004, but did not differ among the summer months prior to hurricane landfall. Large decreases in sediment Chlorophyll *a* concentration were also observed with the passage of major storms in 2005.

Discussion

Our results suggest that the effects of Hurricane Ivan on the water-column and sediment of the marsh tidal creeks examined are disparate, in accordance with our initial hypotheses. In general, Hurricane Ivan did not appear to have a large, lasting impact on the water-column variables measured. None of the nutrient variables measured differed significantly between the two most immediate pre- and post-hurricane sampling dates. Only a subset of the creeks examined showed significant differences in water-column primary productivity and metabolism between the last sampling date before hurricane landfall and the first sampling date after landfall, but those differences were similar to the differences found among summer months prior to landfall. Water-column Chlorophyll *a* concentration did not differ between the two most immediate pre- and post-hurricane sampling dates. Therefore, Hurricane Ivan did not seem to have an impact on the water-column variables examined that lasted longer than 11 days after landfall and that was larger than their inherent temporal variability. The four major storms that made landfall close to the study site in 2005 did not seem to have a large, lasting impact either. In general, the changes observed in the water-column with the passage of the 2005 storms were not larger than the differences found among sampling dates prior to the passage of the storms, even though we sampled just a few days after the passage of three of the storms.

The apparent lack of a large, lasting impact by major storms on the water-column of the creeks examined probably arises from the fast turnover experienced by that water-column. With a mean diurnal tidal amplitude (±SE) of 0.38 ± 0.02 m and a mean water-column depth (±SE) ranging from 0.27

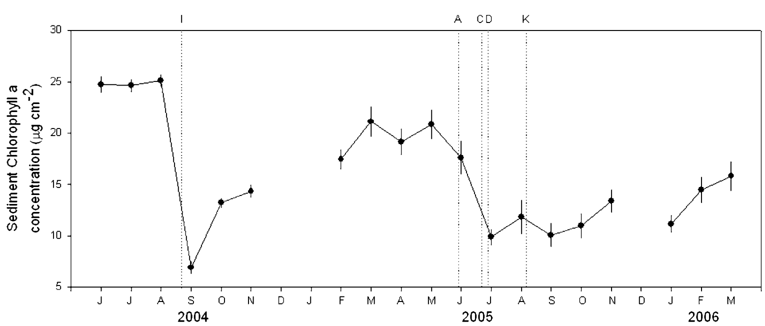

Fig. 6 Sediment chlorophyll *a* concentration in the creeks examined. Symbols represent the average of the values measured for all stations in all creeks on each given date and bars the standard error. The variable is depicted for all creeks pooled together because it did not vary significantly among creeks and time and creek did not interact significantly in the repeated measures analysis of variance. Only creeks 1, 4, and 6 (unseeded creeks) are included from March 2005 on. Dotted lines correspond to the timing of the major storms (I: Hurricane Ivan; A: Tropical Storm Arlene; C: Hurricane Cindy; D: Hurricane Dennis; K: Hurricane Katrina)

(±0.02) to 0.54 (±0.02) m among creeks, the water-column in all the creeks studied would have most likely turned over at least a few times before we could go back to the creeks (i.e., 11 days after Hurricane Ivan, 2 days after Tropical Storm Arlene, 8 and 3 days after Hurricanes Cindy and Dennis, and 22 days after Hurricane Katrina). In turn, this fast water-column turnover would have attenuated to a large extent any possible effects of the storms on the water-column variables examined (Monbet 1992; Valiela et al. 2000b). As a result, we either did not find any significant differences between the most immediate pre- and post-storm sampling dates or, if we did, those differences were not larger than the differences found among sampling dates prior to the passage of the storms. While these major storms could have had some substantial impacts on the water-column variables examined, those impacts would have been extremely short-lived since they were no longer apparent a few days after landfall, in accordance with reports of storm effects on water-column variables elsewhere (Woodley et al. 1981; Valiela et al. 1998; Lugo et al. 2000).

In contrast to the results observed for the water-column, our results suggest that major storms can substantially depress sediment microalgal biomass, gross primary productivity and net productivity in the creeks studied for at least some days after landfall (11 days for Hurricane Ivan, 2 days for Tropical Storm Arlene, 3 to 8 days for Hurricanes Cindy and Dennis, and 22 days for Hurricane Katrina). With the passage of Hurricane Ivan, we observed large decreases in these three variables in relation to the values measured during the summer months prior to hurricane landfall. This was also the case for the major storms that made landfall close to our study sites in 2005. With the passage of Tropical Storm Arlene and Hurricanes Cindy and Dennis, we observed depressed values in relation to the values measured during Spring 2005 prior to the landfall of the storms. With the passage of Hurricane Katrina, we also observed a large decrease from the last sampling date before hurricane landfall to the first sampling date after hurricane landfall.

It is noteworthy that, four out of the six large drops observed in sediment gross primary productivity in our time series, three out of the five large drops in sediment net productivity, and four out of the five large drops in sediment Chlorophyll *a*, coincide with the passage of major storms. This supports a true deleterious impact of major storms on sediment gross primary productivity, net productivity, and Chlorophyll *a* concentration in the marsh tidal creeks studied, even more so because all drops coincident with the passage of major storms occur during the summer season where, due to seasonal forcing, these variables tend to show higher values than for the rest of the year.

The causes for the apparent decrease in sediment gross primary productivity, net productivity and Chlorophyll *a* concentration with the passage of major storms remain unclear. We did not measure any significant decreases in PAR intensity (in μmol per square meter per second) and salinity with the passage of the five major storms examined here (data not shown). We did observe, however, a relatively thick layer of fine sediment in some of the creeks in our first visit after the passage of the storms, most notably after the passage of Hurricane Ivan, that we had not seen before landfall. This observation suggests the conjecture that this layer of fine sediment generated by the storm could have buried and induced substantial mortality of benthic microalgae, thereby decreasing gross primary productivity, net productivity and Chlorophyll *a* concentration in the sediment of the marsh tidal creeks studied. This conjecture may arguably receive some support from the result that sediment respiration did not change with the passage of the storms; micro- and macro-faunal organisms could have survived burial by crawling up to the surface of the new sediment layer (Thistle 1981; Goldfinch and Carman 2000; Guarini et al. 2000), and the decrease in sediment respiration due to buried, dead microalgae could have been compensated by increased faunal respiration due to the release of exudates by the decaying microalgae and the input of organic matter with the new sediment (Heip et al. 1995; del Giorgio and Cole 1998), such that sediment respiration values would remain little altered despite substantial burial and mortality of benthic microalgae.

Previous reports of hurricane effects on other marine habitats have also found a longer-lasting impact on benthic than on water-column communities. For instance, in 1991 Hurricane Bob caused extensive losses of leaf biomass in eelgrass (*Zostera marina*) meadows in estuaries of Waquoit Bay

(Massachussetts, USA), which did not recover until the following growing season (Valiela et al. 1998). The hurricane also produced, through elevated ammonium concentrations in the water-column, massive phytoplankton blooms, but the blooms only lasted 3 days. Similarly, in 1980 Hurricane Allen inflicted major damage to some coral reefs in the northern shore of Jamaica, particularly to branching corals and for which intense mortality continued 5 months after hurricane landfall (Woodley et al. 1981). In contrast, just 10 days after the passage of Hurricane Allen, total planktonic abundance at nighttime was similar to the abundance recorded for pre-hurricane samples, although more predatory polychaetes were found at daytime in post- than in pre-hurricane samples. Fish abundance in hurricane-damaged coral reefs also seemed to return to pre-hurricane levels much faster than did living coral abundance (Woodley et al. 1981; Lugo et al. 2000). Depending on their orientation, size and speed, hurricanes may sometimes have little impact on coastal systems (Tilmant et al. 1994) but, when they exert a substantial impact, longer-lasting effects on benthic communities in comparison with water-column communities may be a common occurrence.

The apparent decrease in sediment microalgal productivity and biomass following the passage of major storms could have a number of consequences for marsh tidal creeks, given the important roles sediment microalgae play in those creeks. First, because sediment microalgae often contribute significantly to the total primary productivity of marsh tidal creeks (Sullivan and Moncreiff 1988; Moncreiff et al. 1992), major storms could depress the total primary productivity of marsh tidal creeks. For instance, assuming that total gross primary productivity in each of the creeks examined corresponds to the sum of integrated water-column (i.e., after conversion to mg C m^{-2} h^{-1} using the depth measured in the given creek on the specific sampling date) and sediment gross primary productivity, the mean total gross primary productivity for all the creeks following the passage of Hurricane Ivan on the sampling dates of September, October, and November 2004 was 83.1, 75.1, and ca. 100% of the mean total gross primary productivity on the last sampling date before hurricane landfall (i.e., 53.0 mg C m^{-2} h^{-1}). Similarly, assuming that total net productivity corresponds to the sum of integrated water-column and sediment net productivity, the mean total net productivity for all the creeks on the sampling dates of September, October, and November 2004 was 71.5, 64.6, and 99.3% of the mean total net productivity on the last sampling date before the landfall of Hurricane Ivan (i.e., 35.4 mg C m^{-2} h^{-1}).

Second, reduced sediment microalgal productivity could represent lower food availability for the many organisms that preferentially feed upon these microalgae (Sullivan and Moncreiff 1990; De Jonge and Beusekom 1992; Carman and Fry 2002; Pinckney et al. 2003). On this basis, major storms, other than depressing total primary productivity in marsh tidal creeks, could also reduce the productivity of meio-, micro-, and macro-fauna that feed upon sediment microalgae. In turn, decreased herbivorous productivity could have cascading negative effects on the productivity of higher trophic levels that feed upon the herbivores. Finally, reduced sediment microalgal biomass would also likely impact sediment biogeochemistry through, for instance, reduced oxygen production and mucilage excretion (Baillie 1986; MacIntyre et al. 1996; Tobias et al. 2003b), nutrient exchange between sediment and water-column (Sundback et al. 1991; Rizzo et al. 1992), and sediment cohesiveness (Underwood et al. 1995; Wolfstein and Stal 2002).

Nevertheless, the apparent negative impacts of major storms on the gross primary productivity, net productivity, and Chlorophyll *a* concentration in the sediment of the marsh tidal creeks examined, while apparently lasting longer than impacts on the water-column, do not seem to be long-lived. On the August 2005 sampling date, which took place 51 and 46 days after the landfalls of Hurricane Cindy and Dennis, values of sediment gross primary productivity and net productivity were much higher than any of the values recorded during Spring 2005 prior to the passage of the hurricanes. The same was true for the October 2005 sampling date, which took place 50 days after the landfall of Hurricane Katrina. Sediment Chlorophyll *a* concentration seemed to be recovering, although to a much smaller extent than gross primary and net productivity, by the August and October 2005 sampling dates. Sediment gross primary productivity, net productivity, and Chlorophyll *a* concentration appeared to be recovering by the October and November 2004 sampling dates, which took place 32 and 46 days after the landfall of Hurricane Ivan, although they did not reach values as high as recorded during Summer 2004 prior to the landfall of the hurricane possibly due to unfavorable seasonal forcing (i.e., decreasing photoperiod and temperature).

Conclusion

Hurricane Ivan, and also four other major storms during 2005, seemed to have disparate effects on the water-column and sediment of marsh tidal creeks in the NorthCentral Gulf of Mexico. The storms did not seem to have a large, lasting effect on the primary productivity, metabolism, and Chlorophyll *a* concentration in the water-column of the marsh tidal creeks examined. These variables often did not differ significantly between the most immediate pre- and post-storm sampling dates, and when they did, those differences were not larger than the natural temporal variability found before landfall. In contrast, the storms did appear to largely decrease gross primary productivity, net productivity, and Chlorophyll *a* concentration in the sediment of the creeks for time periods ranging from a few days to a few weeks. Large decreases were always found with the passage of major storms that contrasted with the much smaller natural temporal variability found before landfall. In fact, most of the large decreases observed in the 22-month-long time series of these variables corresponded with the passage of major storms. At any rate, this apparent negative impact by major storms on the sediment of marsh tidal creeks did not seem to be long-lived and appeared to be dissipated within weeks or months after the passage of the storms. This suggests that marsh tidal creeks dominated by bare sediment are less disturbed by major storms than other marine systems populated with bottom-attached or more rigid organisms, such as seagrass meadows, mangroves, and coral reefs, where hurricane impacts may be larger and last longer.

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