Degradation and resilience in Louisiana salt marshes after the BP–*Deepwater Horizon* oil spill

Brian R. Silliman[a,1], Johan van de Koppel[b,c], Michael W. McCoy[a], Jessica Diller[a], Gabriel N. Kasozi[d], Kamala Earl[a], Peter N. Adams[d], and Andrew R. Zimmerman[d]

[a]Department of Biology, University of Florida, Gainesville, FL 32611; [b]Spatial Ecology Department, Royal Netherlands Institute for Sea Research (NIOZ), 4401NT 7, Yerseke, The Netherlands; [c]Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, 9747AG 7, Groningen, The Netherlands; and [d]Department of Geological Sciences, University of Florida, Gainesville, FL 32611

More than 2 y have passed since the BP–*Deepwater Horizon* oil spill in the Gulf of Mexico, yet we still have little understanding of its ecological impacts. Examining effects of this oil spill will generate much-needed insight into how shoreline habitats and the valuable ecological services they provide (e.g., shoreline protection) are affected by and recover from large-scale disturbance. Here we report on not only rapid salt-marsh recovery (high resilience) but also permanent marsh area loss after the BP–*Deepwater Horizon* oil spill. Field observations, experimental manipulations, and wave-propagation modeling reveal that (*i*) oil coverage was primarily concentrated on the seaward edge of marshes; (*ii*) there were thresholds of oil coverage that were associated with severity of salt-marsh damage, with heavy oiling leading to plant mortality; (*iii*) oil-driven plant death on the edges of these marshes more than doubled rates of shoreline erosion, further driving marsh platform loss that is likely to be permanent; and (*iv*) after 18 mo, marsh grasses have largely recovered into previously oiled, noneroded areas, and the elevated shoreline retreat rates observed at oiled sites have decreased to levels at reference marsh sites. This paper highlights that heavy oil coverage on the shorelines of Louisiana marshes, already experiencing elevated retreat because of intense human activities, induced a geomorphic feedback that amplified this erosion and thereby set limits to the recovery of otherwise resilient vegetation. It thus warns of the enhanced vulnerability of already degraded marshes to heavy oil coverage and provides a clear example of how multiple human-induced stressors can interact to hasten ecosystem decline.

geomorphology | multiple stressor | wetland | human impacts

Human activities severely threaten coastal ecosystems and the critical services they provide worldwide (1–4). Pollution from point-source release is often among the most intense of these anthropogenic stressors and can drive severe and rapid degradation of local habitats, such as seagrasses, mangroves, and coral reefs (e.g., refs. 5–8). Oil spills, in particular, pose a heightened threat to ecosystem health because they are unpredictable in space and time, and the resources needed to minimize impacts are often not immediately available (e.g., a containment cap for a well blowout) (9). Past oil spills in coastal habitats have led to immediate effects such as widespread animal die-offs and losses of ecosystem services (e.g., refs. 5, 7, 10–12) as well as longer-lasting effects, such as alteration of animal behaviors and persistence of oil-derived compounds in food webs (e.g., refs. 5–8, and 13–21).

In April 2010, well blowout on the seafloor below the BP-contracted *Deepwater Horizon* (BP-DWH) oil-drilling vessel, ~80 km off the Louisiana coast, led to the eventual release of an estimated 4,900,000 barrels of crude into Gulf of Mexico waters (22), some portion of which ultimately landed in nearby shoreline ecosystems (23). Various sources estimate that ~75 linear km of salt marsh in Louisiana experienced moderate to heavy oiling, the most of any state (24, 25) (Fig. S1). Gulf of Mexico coastal habitats are economically important, generating more than $10 billion per year in revenues through fisheries and

tourism (4, 24, 26). Salt marshes, as one of the most common ecosystems in this region, are critical to maintaining these valuable ecosystem services (4, 26, 27). Past studies investigating effects of oil spills on salt marshes indicate that negative impacts on plants can be overcome by vegetation regrowth into disturbed areas once the oil has been degraded (8, 28–30). This finding suggests that marshes are intrinsically resilient to (i.e., able to recover from) oil-induced perturbation, especially in warmer climates such as the Gulf of Mexico, where oil degradation and plant growth rates may be high.

Here, we report on underappreciated indirect effects caused by the interaction between shoreline oiling and geomorphic feedbacks in salt marshes that dramatically reduce salt-marsh resilience to oil disturbance. In oil spill-impacted Louisiana marshes, we examined (*i*) the magnitude of oil contamination at different distances from the shoreline; (*ii*) the effects of this oil contamination on salt-marsh flora, fauna, and shoreline position; and (*iii*) the recovery of salt-marsh ecosystems after intense and localized oil coverage. To evaluate oil impacts on the marsh ecosystem, we used a multicomponent approach of (*i*) replicated, control-impact–paired time-series studies; (*ii*) shallow-water, oceanographic wave-propagation modeling; and (*iii*) in situ field experiments.

Results and Discussion

In October 2010, about 5 mo after initial oil contact, we surveyed marsh sites throughout Barataria Bay, LA, a coastal region that experienced some of the most extensive BP-DWH oil contamination (Fig. S1). Although interior marsh regions were intact (vegetation >15 m from the marsh edge), marsh shoreline habitats (<15 m from the marsh edge) were mixtures of apparently healthy and severely degraded, oil-impacted sites (i.e., muddy areas laden with oil-covered dead and horizontally laying, decaying grass stems). At oil-impacted sites (*n* = 3; *Methods*), we found abundant oil residues (up to 82% on an aerial basis; Figs. 1*A* and 2) on the marsh substrate, in contrast to the low levels of other known plant stressors (i.e., redox potential, soil salinities, fungal-farming snails; Figs. S2 and S3) that have driven previous marsh community die-offs (31–35). No oil residue was observed at our reference sites (*n* = 3) on either marsh plants or the substrate (Fig. 1*A*). In addition, levels of total polyaromatic hydrocarbons (PAHs; a proxy for oil residue abundance) found in the surface sediments at impacted sites was >100 times higher than concentrations found in reference marshes (Fig. 1*B*).

Fig. 1. Surveys of oil cover and cordgrass across transects at impacted (●) and reference (○) sites in October 2010. (*A*) Change in the proportion of plants oiled with distance from shoreline (defined as marsh platform edge). (*B*) Sediment PAH concentrations at three impacted and three reference sites at 3 m and 15 m from the shoreline. The more than 100-fold greater difference between concentrations at reference and impacted sites was not significant at inshore regions. (*C*) Change in the proportion of aboveground plants dead with distance from the marsh edge. A significantly greater proportion of the surface was oiled at impacted than at reference sites ($P < 0.001$), but oil coverage declined rapidly with distance reaching less than 50% coverage by 8.2 m from the marsh edge. There was also a greater proportion of plants dead at impacted sites (confirming our site characterizations) ($P < 0.001$). However, concomitant with the reduction in oil coverage with distance from shoreline, the proportion of dead plants at impacted sites also decreased with distance from the marsh edge, with the proportion of plants surviving exceeding 50% beyond 8.3 m from shore. Data illustrated in *A* and *C* are means from replicated surveys ($n = 5$) at three different reference and impacted sites. (*D*) Change in proportion of rhizomes dead at 3 m and 15 m distances from the shoreline at reference and impacted sites. There was a significant interaction between site type and distance from shore ($P = 0.0003$). This result is driven by the near-shore die-off zone where rhizome mortality was 63%

higher at impacted than at reference sites. Data illustrated in *B* and *D* are means from three different reference and impacted sites ($n = 3$). Error bars are SEs.

Ecological Effects. Concomitant with elevated oil cover and sediment PAH concentrations at impacted sites, we observed significantly lower snail densities (although invertebrates were generally low at all sites; Fig. S3), piles of dead snails (Fig. 2*D*), empty mussel shells (Fig. 2*C*), and near complete loss of standing aboveground plant cover extending 5–10 m from the shoreline (Fig. 1*C*). Importantly, examination of the belowground plant material revealed that ~95% of rhizomes sampled in this near-shore portion of the impacted sites were also dead, whereas only 36% of rhizomes in the same near-shore portion of the shoreline

Fig. 2. Picture of (*A*) reference marsh (*B*) impacted marsh, (*C*), dead mussel at impacted site, (*D*) large pile of dead snails in impacted area, (*E*) clapper rail foraging on heavily oiled grasses at impacted site, and (*F*) typical covering of oil residue on the marsh surface at an impacted site.

in reference marshes were dead (Fig. 1*D*). Oil cover on marsh surfaces dropped precipitously at impacted sites at distances beyond 10 m from the shoreline, and live plant cover concomitantly increased to more than 50% (Fig. 1 *A* and *C*). Levels of PAHs decreased beyond 15 m from the shoreline and were not statistically different from those at reference marsh sites (Fig. 1*B*). Aboveground plant and rhizome concentrations also increased beyond 15 m to match those found in reference marshes (Fig. 1 *C* and *D*).

These data provide evidence of salt-marsh community die-off in the near-shore portion of the Louisiana shoreline after the BP-DWH oil spill because of high concentrations of oil at the edge of the marsh. Specifically, these findings suggest that the vegetation at the marsh edge, by reaching above the highest high-tide line in the microtidal environment of the Gulf of Mexico, blocked and confined incoming oil to the shoreline region of the marsh. This shoreline containment of the oil may have protected inland marsh but led to extensive mortality of marsh plants located from the marsh edge to 5–10 m inland and to sublethal plant impacts on plants 10–20 m from the shoreline, where plant oiling was less severe. This assertion is also supported by data from our field experiment and supplemental field surveys that assessed impacts of covering by oil (collected from the marsh surface) on the health of live marsh plants (Fig. 3, *Methods*, and *SI Methods*). Specifically, our studies revealed a nonlinear relationship between stem oil coverage and stem death and a threshold of oil coverage of ∼65%, beyond which plant death occurred—the same high-oil coverage observed on plants and the marsh surface at the seaward edge of our impacted marsh sites and across an additional four oiled sites we surveyed (Fig. 3). Moreover, tests of alternative causes for marsh die-offs, such as drought, inundation, or grazers, all failed to explain the observed pattern of ecosystem loss (*SI Methods*). These data also suggest that the mechanism of the lethal effects of oil are more

likely derived from interference with respiration and photosynthesis (reviewed in ref. 8) than from direct toxicity because plant death only occurred at high levels of oil coverage.

Biogeomorphological Feedback. Oil concentrated on the marsh edge enhanced the rate of decline of Louisiana salt marshes, which are known to be degrading at an alarming pace (e.g., refs. 35–38). Specifically, erosion on the steep edges of these already receding marsh platforms was more than twice as high at oil-impacted sites than at reference sites during the period between October 2010 (∼5 mo after oil was reported on Louisiana marshes) and October 2011 (Fig. 4*A*). After October 2011, erosion rates did not differ between impacted and reference sites (Fig. 4*A*). In nondegraded salt-marsh plant communities, belowground plant architecture is characterized by a complex network of underground roots and rhizomes generated by clonally reproducing plants (39–41). This elaborate root matrix helps to maintain shoreline structure and retard erosion by binding sediments and increasing concentrations of organic matter that act as adhesive agents (38, 42–45). Our results suggest that oil-generated death of this stabilizing root matrix at the edges of these marshes triggered a geomorphic response that led to accelerated erosion of the marsh edge, hastening the degradation of the elevated platform on which marsh vegetation depends (35, 46–50) (Fig. 4). Our study sites were all of similar physiographic character because there were no differences in the shallow-water slopes among reference and impacted sites ($P = 0.55$). We conducted numerical simulations of wind-generated wave growth and propagation with SWAN (51) to ensure that differences in observed erosion rates between impacted and reference sites were not attributable to a predisposition of the impacted sites to higher erosion rates (Fig. S4). In fact, the model results demonstrate that our reference sites receive slightly higher wave-energy fluxes than the impacted sites (Fig. S4).

Ecosystem Resilience and Degradation. Despite the deleterious effects of the oil spill on marsh vegetation and erosion rates, we found clear evidence for recovery processes. In our transect surveys at impacted sites in April 2011 (∼11 mo after oil coverage occurred on these marshes), we documented significant increases in plant cover (up to 33%, on average ∼20%; Fig. 4 *C–F*) in areas that were barren and had nearly complete die-back of roots during our initial surveys (Figs. 1*C* and 2). Because we observed no seedling establishment in impacted areas, this recovery likely occurred via plant lateral regrowth (i.e., clonal growth) originating from interior marsh areas where plants were less affected or from nearby, small remnant patches in the impacted areas (52). This clonal regrowth of marsh plants continued throughout the summer of 2011, with full recovery of the marsh plant cover occurring sometime between October 2011 and January 2012, ∼1.5 y after the oil spill (Fig. 4). As predicted from past studies (36, 42–45), plant shoreline reestablishment suppressed the observed accelerated erosion rates at impacted sites to values not significantly different from those at reference sites (Fig. 4 and Fig. S4). However, no plant recovery was observed in the marsh platforms lost to accelerated erosion, and marsh plants that were transplanted into these eroded areas in June 2011 died within 2 mo (Fig. S5 and *SI Methods*), whereas those planted in nonoiled areas of both reference and impacted sites remained alive as of January 2012. Our observations agree with past modeling studies revealing that accelerated erosion on marsh cliffs in Louisiana reduces substrate surface to subtidal elevations and thereby prohibits the recovery of salt-marsh vegetation (48, 53, 54). However, our observations are in contrast to a number of previous studies from other regions that found, under natural conditions, salt-marsh vegetation is resilient to this stress and reestablishes seaward of eroding edges (33, 48, 55). The absence of recovery of marsh vegetation seaward of the
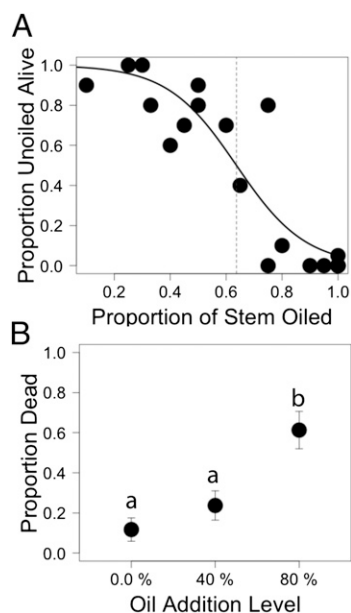

Fig. 3. Oil cover versus plant death as assessed from field observations and from manipulations. (*A*) Field observations of level of oil on individual plants and resultant plant death, indicated by blade browning. The proportion of plant stems that were green and alive is greater than the proportion dead (i.e., indicating improved health) when oil coverage dropped below 64%. (*B*) Observation of blade browning 30 d after a treatment of oil coverage of 40% or 80% of the plant's height ($n = 6$ per oil-addition treatment). Superscript letters indicate treatments that were significantly different ($P < 0.05$) based on Tukey's HSD post hoc comparison. Error bars are SEs.
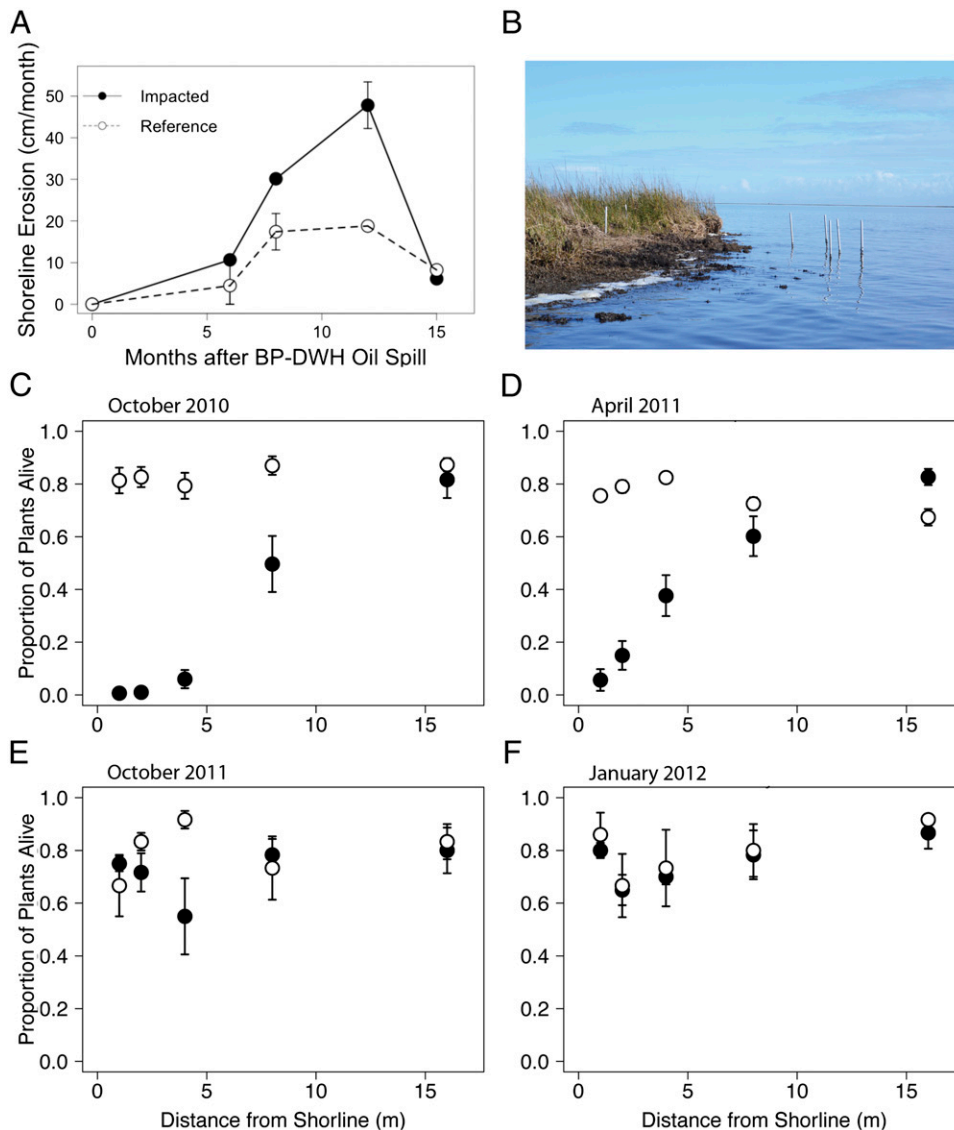
Fig. 4. (*A*) There was a significant increase in average lateral shoreline erosion rate between reference and impacted sites (*P* = 0.007) based on measurements at each site type. Error bars are SEs, and unseen error bars are smaller than symbols. (*B*) Photo of erosion monitoring poles at an impacted site. Right-most PVC poles were installed to mark the marsh platform edge, and retreat of the marsh from this initial starting point is apparent. (*C–F*) Comparison between average percentage of plants alive at four times at impacted and reference sites from 0 to 15 m from the shoreline (*n* = 3). There was a significant effect of the presence of oil, the distance from shoreline, and time (*P* < 0.0001), with much lower plant coverage near shore for impacted sites than for reference sites during October 2010 and April 2011 but with similar levels of coverage near shore during October 2011 and January 2012 at these sites. Plant coverage was similar for all sites and times at greater distances from the shoreline beyond 10 m from the marsh edge.

retreating marsh cliffs in Barataria Bay underscores that this oil spill has decreased the resilience of these marshes by triggering accelerated substrate erosion, which, in turn, reduces the overall area that can be recolonized by plants (Fig. S5).

Our results suggest that there are reasons for both optimism and concern about the impact of this oil spill on Mississippi deltaic marshes of Louisiana. On one hand, our results reveal that marsh vegetation displays remarkable resilience to oil spills by concentrating and confining the effects of oil to the marsh edge, recovering fully in noneroded areas after ~1.5 y, and suppressing, through this recolonization, further accelerated erosion rates along the shoreline. The lack of oil on the marsh surface or on grasses at distances greater than 15 m from the shoreline at any site (Fig. 1*A*) suggests that incoming oil sheens were contained and prevented from moving into interior marshes by a baffling wall of live and dying salt-marsh grasses, a process

that in itself increases the resistance of the extensive marsh ecosystem to oil spill. However, this resistance comes at a high cost for the impacted areas because marsh grass die-off and subsequent sediment exposure to waves resulted in a more than doubling of the rate of erosion of the intertidal platform, leading to permanent marsh ecosystem loss (Fig. 4). Specifically, we observed an average rate of marsh shoreline retreat of ~1.38 m·y^{-1} (Fig. 4*A*) at our reference sites, a level consistent with that reported in other studies for this area of Louisiana (0.8–1.3 m·y^{-1}) (38). This already high rate of shoreline retreat increased by more than 125% to ~3.0 m·y^{-1} at oil-impacted sites. Indeed, the extent of habitat loss could have been even more severe if a large storm or hurricane had coincided with the period of increased shoreline exposure after oil-driven die-off. In fact, the rapid shoreline retreat rates observed between April and October 2011 may be attributable to the effects of Hurricane Lee in September

2011, which made landfall immediately west of Barataria Bay, bringing high winds and surge-related flooding to the region. The highly elevated erosion rates after oil-driven marsh grass die-off observed in this study (Barataria Bay and Bay Jimmy; Fig. S1) are likely general and can be extrapolated to the other marshes in Louisiana that also experienced moderate-to-heavy oil coverage because these marshes are also typically characterized by erosive edges (33, 55–57).

More broadly, our results reveal that multiple stressors are interacting in Louisiana marshes to hasten ecosystem decline. Louisiana experiences some of the highest rates of salt-marsh loss in North America (~75 km²/y) as a result of natural subsidence and channelization of the Mississippi River, which reduces sediment supply to the coast, causing submersion of the marsh interiors and formation of erosion-prone, cliffed edges (31, 37, 54). Our observations and experimental work demonstrate that intense oil coverage of these already degraded marsh edges interacts with preexisting sediment-limitation stress to amplify permanent habitat loss along the marsh margins. The edges of healthy marshes are typically characterized by more gently sloping banks and therefore tend to be more resistant to erosion than subsiding, deltaic-plain marshes in Louisiana that are often characterized by erosive cliff edges (33, 55–57). This study highlights the enhanced vulnerability of these already degraded marshes to heavy oil coverage associated with oil spills and provides a clear example of how multiple human-induced stressors can interact to hasten the loss of a critical marine ecosystem and the services it provides.

Although the amount of increased erosion caused by loss of marsh plants from oiling is, in many ways, specific to these oil-impacted areas in Louisiana (e.g., because of the microtidal environment and long-term sediment deprivation from river channelization), the mechanisms underlying these results can likely be extended to other oil-impacted coastal salt marshes that are also characterized by erosive edges or cliffs. In fact, erosion of marshes in response to oil coverage has been observed or suggested in studies in New England, Florida, and Louisiana (58–62). Our study goes one step further to show that direct vegetation die-off is the primary result of heavy oil coverage, but that erosion caused by biogeomorphological feedback and subsequent habitat loss may ultimately determine the long-term effect of oil pollution in salt marshes. Future research should focus on how the interplay between biological and geomorphological processes affects the vulnerability of salt marshes facing multiple anthropogenic stressors.

Methods

All work was conducted in *Spartina alterniflora* (cordgrass)-dominated salt marshes in Barataria Bay, LA, one of the heaviest-impacted areas after the BP-DWH oil spill (Fig. S1). Sites were identified as either "impacted" or "reference." Impacted sites had substrate that were denuded and/or laden with dead and decaying cordgrass stems. Reference sites were dominated by standing live cordgrass plants. All impacted sites were located in the northeast corner of Barataria Bay, near Bay Jimmy, which received large amounts of oil coverage because of prevailing winds and currents after the BP-DWH oil spill (Table S1). Two reference sites were selected in the northwest corner of the bay, east of Hackberry Bay, and an additional reference site was located in Grand Isle State Park on the south side of the bay. All sites were located within 30 km of each other. All but the Grand Isle State Park site faced outward into the same portion of open Barataria Bay, thus experiencing similar tidal fluctuations and weather conditions. Because the Grand Isle site was relatively protected from wave action, this site was not included in our comparison of erosion rates between reference and impacted sites (see Table S1 for coordinates of reference and impacted sites). At both reference and impacted sites, we ran an oil-addition and a marsh plant transplant experiment, and we conducted surveys in which oil coverage, PAH concentrations, live plant (*S. alterniflora*) coverage and survival, invertebrate abundances, pH, redox and salinity, as well as erosion potential and erosion rates were quantified (for detailed sampling and analytical methods, see SI Methods).

1. Griffis RB, Kimball KW (1996) Ecosystem approaches to coastal and ocean stewardship. *Ecol Appl* 6(3):708–712.
2. Scavia D, et al. (2002) Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries Coasts* 25(2):149–164.
3. Waycott M, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106(30):12377–12381.
4. Mitsch WJ, Gosselink JG (2000) The value of wetlands: Importance of scale and landscape setting. *Ecol Econ* 35(1):25–33.
5. Cubit JD, et al. (1987) An oil spill affecting coral reefs and mangroves on the Caribbean coast of Panama. *Proceedings of the 1987 Oil Spill Conference* (American Petroleum Institute, Washington, DC), pp 401–406.
6. Duke NC, Pinzón M, Zuleika S, Prada T, Martha C (1997) Large scale damage to mangrove forests following two large oil spills in Panama. *Biotropica* 29:2–14.
7. Jackson JBC, et al. (1989) Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* 243(4887):37–44.
8. Pezeshki SR, Hester MW, Lin Q, Nyman JA (2000) The effects of oil spill and clean-up on dominant US Gulf coast marsh macrophytes: A review. *Environ Pollut* 108(2):129–139.
9. Lin Q, Mendelssohn IA (1998) The combined effects of phytoremediation and biostimulation in enhancing habitat restoration and oil degradation of petroleum contaminated wetlands. *Ecol Eng* 10(3):263–274.
10. Garrott RA, Eberhardt LL, Burn DM (1993) Mortality of sea otters in Prince William Sound following the *Exxon Valdez* oil-spill. *Mar Mamm Sci* 9(4):343–359.
11. Jewett SC, Dean TA, Smith RO, Blanchard A (1999) "*Exxon Valdez*" oil spill: Impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds. *Mar Ecol Prog Ser* 185:59–83.
12. Jackson JBC, et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293(5530):629–637.
13. Andrade ML, Covelo EF, Vega FA, Marcet P (2004) Effect of the *Prestige* oil spill on salt marsh soils on the coast of Galicia (northwestern Spain). *J Environ Qual* 33(6):2103–2110.
14. Day RH, et al. (1997) Effects of the *Exxon Valdez* oil spill on habitat use by birds in Prince William Sound, Alaska. *Ecol Appl* 7(2):593–613.
15. Monson DH, Doak DF, Ballachey BE, Johnson A, Bodkin JL (2000) Long-term impacts of the *Exxon Valdez* oil spill on sea otters, assessed through age-dependent mortality patterns. *Proc Natl Acad Sci USA* 97(12):6562–6567.
16. Murphy ML, Heintz RA, Short JW, Larsen ML, Rice SD (1999) Recovery of pink salmon spawning areas after the *Exxon Valdez* oil spill. *Trans Am Fish Soc* 128(5):909–918.
17. Ocon CS, Rodrigues Capítulo A, Paggi AC (2008) Evaluation of zoobenthic assemblages and recovery following petroleum spill in a coastal area of Río de la Plata estuarine system, South America. *Environ Pollut* 156(1):82–89.
18. Peterson CH, et al. (2003) Long-term ecosystem response to the *Exxon Valdez* oil spill. *Science* 302(5653):2082–2086.
19. Short JW, et al. (2004) Estimate of oil persisting on the beaches of Prince William Sound 12 years after the *Exxon Valdez* oil spill. *Environ Sci Technol* 38(1):19–25.
20. Trust KA, Esler D, Woodin BR, Stegeman JJ (2000) Cytochrome P450 1A induction in sea ducks inhabiting nearshore areas of Prince William Sound, Alaska. *Mar Pollut Bull* 40(5):397–403.
21. Culbertson JB, et al. (2007) Long-term biological effects of petroleum residues on fiddler crabs in salt marshes. *Mar Pollut Bull* 54(7):955–962.
22. McNutt M, et al. (2011) *Assessment of Flow Rate Estimates for the Deepwater Horizon/Macondo Well Oil Spill. Flow Rate Technical Group Report to the National Incident Command, Interagency Solutions Group.* Available at http://www.doi.gov/deepwaterhorizon/loader.cfm?csModule=security/getfile&PageID=237763. Accessed May 4, 2012.
23. Thibodeaux LJ, et al. (2011) Marine oil fate: Knowledge gaps, basic research, and development needs; A perspective based on the *Deepwater Horizon* spill. *Environ Eng Sci* 28(2):87–93.
24. Oil Spill Commission (2011) Deep Water: The Gulf Oil Disaster and the Future of Offshore Drilling. Available at http://www.gpo.gov/fdsys/pkg/GPO-OILCOMMISSION/content-detail.html. Accessed March 2011.
25. Lehner P, Deans B (2010) *In Deep Water: The Anatomy of a Disaster, the Fate of the Gulf, and Ending Our Oil Addiction* (Experiment LLC, New York).
26. Engle VD (2011) Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. *Wetlands* 31(1):179–193.
27. Barbier EB, Heal GM (2006) Valuing ecosystem services. *Economists' Voice* 3(3):2.

28. Alexander SK, Webb JW (1985) Seasonal response of *Spartina alterniflora* to oil. *Proceedings of the 1985 Oil Spill Conference (Prevention, Behavior, Control, Cleanup)* (American Petroleum Institute, Washington, DC), pp 355–357.

29. DeLaune RD, Pezeshki SR, Jugsujinda A, Lindau CW (2003) Sensitivity of US Gulf of Mexico coastal marsh vegetation to crude oil: Comparison of greenhouse and field responses. *Aquat Ecol* 37(4):351–360.

30. Lytle JS (1975) Fate and effect of crude oil on an estuarine pond. *Proceedings of the Joint Conference on Prevention and Control of Oil Pollution* (American Petroleum Institute, Washington, DC), pp 595–600.

31. Gedan KB, Silliman BR (2009) Patterns of salt marsh loss within coastal regions of North America: Presettlement to present. *Human Impacts on Salt Marshes: A Global Perspective*, eds Silliman BR, Grosholz ED, Bertness MD (Univ of California Press, Berkeley), pp 253–266.

32. Kennish MJ (2002) Environmental threats and environmental future of estuaries. *Environ Conserv* 29(1):78–107.

33. Kirwan ML, et al. (2010) Limits on the adaptability of coastal marshes to rising sea level. *Geophys Res Lett* 37(23):L23401.

34. Silliman BR, van de Koppel J, Bertness MD, Stanton LE, Mendelssohn IA (2005) Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310 (5755):1803–1806.

35. DeLaune RD, Nyman JA, Patrick WH, Jr. (1994) Peat collapse, ponding and wetland loss in a rapidly submerging coastal marsh. *J Coast Res* 10:1021–1030.

36. Hatton RS, DeLaune RD, Patrick WH, Jr. (1983) Sedimentation, accretion, and subsidence in marshes of Barataria Basin, Louisiana. *Limnol Oceanogr* 28(3):494–502.

37. Reed DJ (1989) Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne Bay, Louisiana: The role of winter storms. *Estuaries Coasts* 12(4):222–227.

38. Wilson CA, Allison MA (2008) An equilibrium profile model for retreating marsh shorelines in southeast Louisiana. *Estuar Coast Shelf Sci* 80(4):483–494.

39. Gallagher JL, Plumley FG (1979) Underground biomass profiles and productivity in Atlantic coastal marshes. *Am J Bot* 66(2):156–161.

40. Smith KK, Good RE, Good NF (1979) Production dynamics for above and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuar Coast Mar Sci* 9 (2):189–201.

41. Valiela I, Teal JM, Persson NY (1976) Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnol Oceanogr* 21(2): 245–252.

42. Knutson PL, Ford JC, Inskeep MR, Oyler J (1981) National survey of planted salt marshes (vegetative stabilization and wave stress). *Wetlands* 1(1):129–157.

43. Woodhouse WW, Jr., Seneca ED, Broome SW (1974) *Propagation of Spartina alterniflora for Substrate Stabilization and Salt Marsh Development* (U.S. Army Corps of Engineers Coastal Engineering Research Center, Fort Belvoir, VA), Tech Memo 46.

44. Woodhouse WW, Jr., Seneca ED, Broome SW (1976) North Carolina State Univ at Raleigh. *Propagation and Use of Spartina alterniflora for Shoreline Erosion Abatement* (U.S. Army Corps of Engineers Coastal Engineering Research Center, Fort Belvoir, VA), Tech Rep 76-2.

45. Stagg CL, Mendelssohn IA (2011) Controls on resilience and stability in a sediment-subsidized salt marsh. *Ecol Appl* 21(5):1731–1744.

46. Cahoon DR, et al. (2003) Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *J Ecol* 91(6):1093–1105.

47. Hughes ZJ, et al. (2009) Rapid headward erosion of marsh creeks in response to relative sea level rise. *Geophys Res Lett* 36:1–5.

48. Kirwan ML, Murray AB (2007) A coupled geomorphic and ecological model of tidal marsh evolution. *Proc Natl Acad Sci USA* 104(15):6118–6122.

49. Marani M, D'Alpaos A, Lanzoni S, Carniello L, Rinaldo A (2007) Biologically-controlled multiple equilibria of tidal landforms and the fate of the Venice lagoon. *Geophys Res Lett* 34:1–5.

50. Smith SM (2009) Multi-decadal changes in salt Marshes of Cape Cod, MA: Photographic analyses of vegetation loss, species shifts, and geomorphic change. *Northeast Nat* 16(2):183–208.

51. Booij N, Ris R, Holthuijsen L (1999) A third-generation wave model for coastal regions. 1. Model description and validation. *J Geophys Res* 104(C4):7649–7666.

52. Angelini C, Silliman BR (2012) Patch size-dependent community recovery after massive disturbance. *Ecology* 93:101–110.

53. Mendelssohn IA, Morris JT (2002) Eco-physiological controls on the productivity of *Spartina alterniflora*. *Concepts and Controversies in Tidal Marsh Ecology*, eds Weinstein NP, Kreeger DA (Kluwer Academic, Boston), pp 59–80.

54. Blum MD, Roberts HH (2009) Drowning of the Mississippi Delta due to insufficient sediment supply and global sea-level rise. *Nat Geosci* 2(7):488–491.

55. Mariotti G, Fagherazzi S (2010) A numerical model for the coupled long-term evolution of salt marshes and tidal flats. *J Geophys Res* 115:F01004.

56. Kirwan ML, Murray AB, Donnelly JP, Corbett DR (2011) Rapid wetland expansion during European settlement and its implication for marsh survival under modern sediment delivery rates. *Geology* 39(5):507–510.

57. Möller I, Spencer T (2002) Wave dissipation over macro-tidal saltmarshes: Effects of marsh edge typology and vegetation change. *J Coast Res* 36:506–521.

58. DeLaune RD, White JR (2011) Will coastal wetlands continue to sequester carbon in response to an increase in global sea level?: A case study of the rapidly subsiding Mississippi river deltaic plain. *Clim Change* 110(1-2):1–18.

59. Hampson GR, Moul ET (1978) No. 2 fuel oil spill in Bourne, Massachusetts: Immediate assessment of the effects on marine invertebrates and a 3-year study of growth and recovery of a salt marsh. *J Fish Res Board Can* 35(5):731–744.

60. Hartig EK, Gornitz V, Kolker A, Mushacke F, Fallon D (2002) Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City. *Wetlands* 22(1): 71–89.

61. McBride RA, Byrnes MR (1997) Regional variations in shore response along barrier island systems of the Mississippi River delta plain: Historical change and future prediction. *J Coast Res* 13:628–655.

62. Peacock EE, et al. (2007) The 1974 spill of the Bouchard 65 oil barge: Petroleum hydrocarbons persist in Winsor Cove salt marsh sediments. *Mar Pollut Bull* 54(2): 214–225.

ECOLOGY

Supporting Information

Silliman et al. 10.1073/pnas.1204922109

SI Methods

Oil and Plants. Plant oiling and ecological surveys were conducted at three reference and three impacted sites in October 2010 with follow-up surveys at the same locations occurring until April 2011. Five transects were surveyed at each site, and the percentage of live plant cover and the percentage of oil cover at 1, 2, 4, 8, 16, and 32 m along a line perpendicular to the marsh edge were recorded. Transects were spaced ~2 m apart. Belowground samples of ~20 cm depth and 15 cm diameter were also collected at each site at 3 m and 15 m distances from the marsh edge to quantify differences in proportion of live rhizomes. Samples were rinsed in a sieve, and rhizomes were sorted from debris. Rhizomes were then categorized as alive if white and turgid or dead if dark and flaccid by using established protocols.

Animals. We surveyed animals at our impacted and reference sites during October 2010, April 2011, and then again during January 2012. The densities of live *Littoraria irrorata*, *Geukensia demissa*, *Pagurus longicarpus*, and *Uca pugnax* burrows were collected with 50×50 cm quadrats ($n = 5$) at both 3 m and 15 m distances from the shoreline at all survey sites. However, here we only present data from 3-m samples where we documented consistent oiling, and we also exclude data for *G. demissa* because they were exceedingly rare in all samples. Indeed, animal counts were low at all sites for all species, but changes were detectable.

Polyaromatic Hydrocarbon (PAH) Concentrations. Soil samples were collected at each survey site during October 2010 at 3 m and 15 m from the marsh edge. For each sample, four cores, 5 cm in depth, were homogenized in the field, and subsamples were placed in precombusted glass jars (3 h, 450 °C) and then frozen the evening of collection. Frozen samples were maintained in a cooler until reaching the laboratory, where they were stored in a freezer set at −80 °C.

Aliquots of 0.05–2.5 g wet weight were placed in 16–30 g baked sodium sulfate before extraction. Samples were spiked with 100 μL of surrogate standard containing 120 μg/mL *n*-tetradecane d-30, 109.92 μg/mL *n*-tetracosane d-50, 40 μg/mL naphthalene d-8, and 42.48 μg/mL fluoranthene d-10. The samples were extracted three times by the accelerated solvent extractor by using a hexane and acetone mixture (50:50, vol/vol). After extraction and reduction of the sample to 1 mL in a TurboVap concentrator, extracts were back-extracted three times into a 50:50 (vol/vol) mixture of sodium chloride solution and hexane to remove the remaining water. Samples were purified and separated into alkane and PAH compound classes by using activated silica open-column chromatography. Deuterated internal standards were added to the samples before compound quantification with GC/MS via direct injection onto a 30 m × 0·32 mm i.d. DB-5, 0.25 μm, fused silica capillary column (J & W Scientific). Details of silica column, chromatograph, and use of standards for compound quantification can be found in ref. 1.

pH, Redox, and Salinity. On June 25, 2010, we collected data to test for differences in pH, redox, and soil salinity for two reference and two impacted sites. Measurements for all three parameters were taken at 3 m and 15 m. A minimum of four evenly spaced samples (~2 m apart) was quantified at each site. Redox and pH measurements were taken ~5 cm below the marsh surface with a Hanna Instruments HI98183-01 pH/ORP portable meter. Salinity measurements (parts per thousand) were taken from pore water extracted from the top 5 cm of sediment in each area with a refractometer.

Oiled Plant Survival and Oil-Addition Experiments. To determine the relationship between oil coverage and plant survival, we did a field survey and a manipulative experiment. For the field survey, we went to four oiled sites and took five random quadrat samples at each site. In each quadrat, we quantified the proportion of stems covered with oil and the proportion of the stem that remained green. For the manipulated field experiment, we selected a reference and a nearby impacted site for oil-addition manipulations. On October 18, 2010, we identified 18 live stems with similar heights, live cover, and stem width, and each was randomly assigned to one of three treatments: (*i*) control, (*ii*) 40% oil addition, or (*iii*) 80% oil addition ($n = 6$, 18 total). Weathered oil was collected from a pool found during surveys of impacted sites (Fig. 3*F*) and applied to the designated plants within 4 h. Plants assigned to oil-addition treatments were manually covered with a thick coating of weathered oil from their base to either 40% or 80% of their total height. Control plants were rubbed with a clean latex glove for the same amount of time and in a similar manner as a procedural control. On December 10, 2010, plant senescence was quantified by recording the number of leaves that remained alive at a point approximately halfway up the plant. On 80% oil-addition plants, this measurement was taken under the layer of oil by wiping away weathered oil. Although some staining of live plant tissue did occur under the oil, green color was still identifiable in live leaves and, as a conservative measure, only completely brown and brittle leaves were quantified as dead. At the end of the experiment, plants were removed and properly disposed of to prevent contamination of the area.

Transplant Experiment. In June 2011, we took 12 cores that were 10 cm diameter and 20 cm deep from the reference area of three impacted sites, standardized so that each consisted of 10 *Spartina* stems. We then replanted a third of the cores back into the reference area as a procedural control for transplant shock, a third into the impacted area, and a third in the eroded area and counted the number of stems present after 4 mo.

Shoreline Erosion. In October 2010, PVC poles were placed into the ground abutted to marsh peat edge and the open water at six monitoring points along the shoreline of each impacted site and at six points along the shoreline of each reference site. PVC markers were not placed at locations with extreme shoreline curvature. In April 2011, June 2011, October 2011, and again in January 2012, we quantified erosion at these sites by measuring the distance between the marsh edge and the PVC poles.

Shoreline slopes. To quantify erosion potential for our reference and impacted sites, we quantified shoreline slopes at each of three impacted and reference sites. We used the same three impacted sites as above; however, we identified one alternative reference site for quantifying shoreline slope, erosion rates (described above), and modeling erosion potential (below). We chose one alternate reference site for these measurements (erosion rates, slope, and modeled wave stress) because one of the reference sites that we monitored was located in a state park and protected by a bulkhead. Our alternate site was similar in characteristics and wave exposure to our other five sites (exact locations are in Table S1). At 20 randomly selected points at each site, we measured the change in substrate height that occurred from the edge of the shoreline to a distance of 3 m seaward.

Modeling methods. To test the alternative hypothesis to influence of oil on erosion rates, that variation in measured marsh erosion rates could be attributable to their position relative to wave energy, we used SWAN, a numerical model of wind-generated wave growth and propagation (2). A 3-arcsec computation grid of bathymetry, obtained from the National Oceanic and Atmospheric Administration/National Geophysical Data Center US Coastal Relief Model (http://www.ngdc.noaa.gov/mgg/coastal/crm.html), was used for the wave field calculation over the region from $-90.05°$ to $-89.75°$ longitude and $29.25°$ to $29.5°$ latitude. Wind speeds were set at 20 m/s at a reference height of 10 m above ground or water surface. Eight SWAN simulations were conducted to investigate the influence of wind direction. Wind directions were varied from $0°$ (northerly) by $45°$ intervals through $315°$ (northwesterly). Significant wave heights (the average of the highest third of waves over a time interval) were queried and reported from the model output for submerged sites chosen as the closest point along the 1-m isobaths to each of the six erosion observation sites.

Statistical Methods.

All statistics were performed in the R statistical programming environment. Model assumptions for all statistical (3) tests were evaluated visually and quantitatively with residual, quantile-quantile, and leverage plots.

To describe and compare oiling and marsh plant mortality as a function of distance from the shore at reference and impacted sites, we fit standard logistic curves. Model fits were performed via generalized nonlinear least squares, and hypothesis tests to determine whether there were differences among sites were inferred from likelihood ratio tests (LRT). To describe the relationship between proportions of plant stems covered with oil and proportion of unoiled plant stems that consisted of green tissue, we fit this logistic curve and used the delta method to obtain estimates of uncertainty around parameters estimates.

To determine whether there were differences in the amount of belowground plant material alive in these two kinds of sites, we compared the proportion of *Spartina* rhizomes alive at 3-m and 15-m locations in reference and impacted sites. Specifically, we tested for an effect of site type, distance from shore, and the interaction between these two factors on probability of rhizome mortality by using a generalized linear mixed-effects model with a binomial family error distribution. To account for the hierarchical structure, we modeled the effects of site type (reference or impacted; $n = 3$ each), transect ($n = 5$) nested within site type, and location on transect ($n = 2$–3 and 15 m) as nested random effects.

To test whether the abundances of each of three common invertebrate species differed between reference and impacted sites, we used a generalized linear mixed-effects model with a zero-inflated negative binomial distribution with site type (reference or impacted) treated as a fixed effect and transect nested within site replicate treated as random effects.

To determine whether plant and rhizome loss was associated with accelerated rates of shoreline erosion over time, we used linear mixed-effects models to compare the distances between poles placed at the shoreline (six per site) immediately after the oil spill and the location of the shoreline in successive weeks at both reference and impacted sites. Because of losses of poles from shoreline clean-up efforts and stochastic events, we had different amounts of replication among sites and over time. Therefore, we treated sites nested in time as random effects in the model.

We used a generalized additive model with site type treated as a categorical fixed effect and degrees from North as a continuous fixed effect to test whether there were differences in wave heights (based on output from the SWAN numerical wave model) at our impacted and reference sites.

To test whether there were differences in the success of transplants in the reference, impacted, and eroded intertidal regions, we used a generalized linear model with quasi-Poisson family error distribution (to account for overdispersion) to test for differences in stem densities.

Finally, to test whether there were signs of recovery of salt-marsh grasses, we compared the proportion of plants alive from the shoreline to 15 m inland for four time points spanning a period of 15 mo by using linear mixed-effects models with site nested in time treated as a random effect.

To determine whether there were differences in the concentration of PAHs at reference and impacted sites, we compared sediment loads from 3-m and 15-m locations in reference and impacted sites. Using these data, we tested for an effect of site type, distance from shoreline, and the interaction between these two factors with a linear mixed-effects model on log-transformed concentrations. To account for the hierarchical structure of these data (i.e., locations are nested within replicate reference and impacted site), we modeled replicates of each site type (reference or impacted; $n = 3$ each) as a random effect.

To determine how oil cover affected the survival probability of cordgrass, we compared plant survival at 0.0%, 40%, or 80% oil coverage by using a generalized linear model with a quasibinomial error distribution. We used the quasibinomial error distribution to account for overdispersion in these data (dispersion parameter for the quasibinomial was 1.12).

1. Mitra S, Bianchi TS (2003) A preliminary assessment of polycyclic aromatic hydrocarbon distributions in the lower Mississippi River and Gulf of Mexico. *Mar Chem* 82(3-4):273–288.
2. Booij N, Ris R, Holthuijsen L (1999) A third-generation wave model for coastal regions. 1. Model description and validation. *J Geophys Res* 104(C4):7649–7666.
3. R Development Core Team (2011) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria).
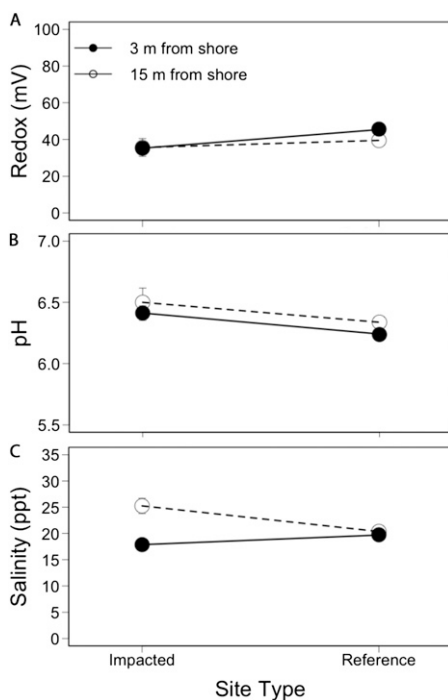
Fig. S1. Map of oil coverage along Louisiana coastline (*A*) and Barataria Bay (*B*) as of May 2011. Warmer colors represent more intense oil coverage. Map was accessed at http://www.noaa.gov/deepwaterhorizon/maps/ on May 8, 2011.

Fig. S2. Results from comparisons of abiotic characteristics often associated with die-offs. (*A*) There were no differences in the levels of redox at impacted and reference sites (LRT, $P = 0.12$) or at different distances from the shore (LRT, $P = 0.65$). (*B*) There were also no detectable differences in soil pH between site types (LRT, $P = 0.14$) or distances (LRT, $P = 0.49$). (*C*) There was a significant interaction effect between site type and distance from shoreline on measures of soil salinity (LRT, $P = 0.002$), with impacted sites 15 m from the shoreline having higher salinities than any other sites. This elevated salinity is unlikely related to observed die-off because die-off occurred predominantly in plants located <10 m from the shoreline (Fig. 1*C*).
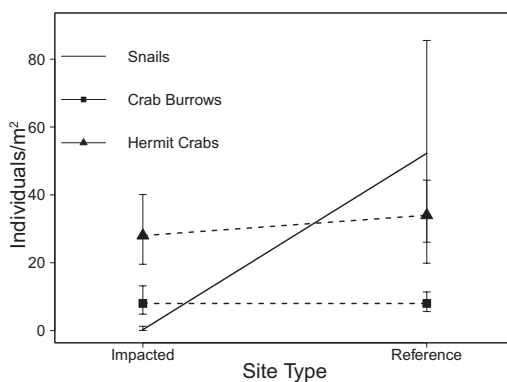

Fig. S3. Densities of the three common macroinvertebrate animals from surveys in reference and impacted sites in October 2010 at 3 m from the shoreline. There were significantly fewer snails at impacted sites (LRT, $P = 0.005$); however, there were no differences in the numbers of hermit crabs or crab burrows (used as a proxy for fiddler crab density). Data were analyzed with a generalized linear model with zero-inflated negative binomial error distribution. Data were collected from surveys at three reference and three impacted sites ($n = 5$) ($n = 15$ total). Means and SE bars are extracted from model fits.
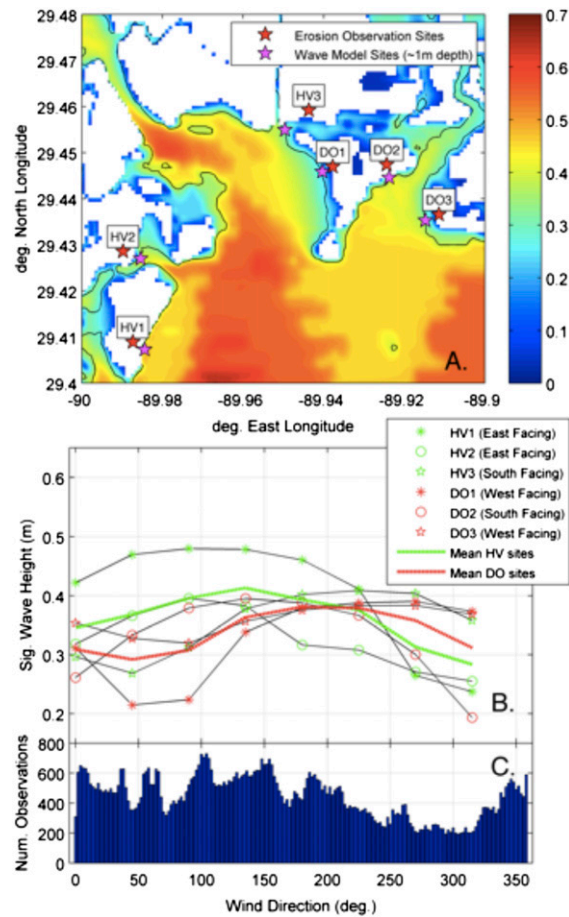
Fig. S4. Results of SWAN numerical modeling of wave height distributions within northern Barataria Bay region. (*A*) Color map showing spatial distribution of modeled significant wave height (color bar scale in units of meters) for a 20 m/s easterly wind field. Locations of erosion observation sites and adjacent wave model query sites are shown and labeled. Black line shows the approximate location of the 1-m bathymetric contour. (*B*) Line plot of modeled significant wave heights at each erosion observation site as a function of wind direction for a wind speed of 20 m/s from the east (90°). Red data markers represent sites that experienced significant vegetation die-off, and green data markers represents sites where vegetation was healthy. Also shown are the mean wave heights for all impacted and reference vegetation sites over the range of wind directions. (*C*) Histogram of observed wind directions observed at the National Oceanic and Atmospheric Administration/National Geophysical Data Center station GISL1, located along the southern boundary of Barataria Bay, for the 14-mo interval from October 2010 through November 2011. Data for the intervals April 3 to May 4 and August 7 to September 17, 2011, were unavailable. Waves appear to be influenced by orientation, fetch, and bathymetry, with larger waves occupying at east-facing shoreline sites. Wind fields oriented from northerly, easterly, and southerly directions result in larger wave heights at reference sites than at impacted sites. Because the majority of wind observations are from northerly, easterly, and southerly directions, it would be expected that the larger waves assailing east-facing sites should drive more rapid marsh shoreline retreat rates than witnessed at west-facing sites; this is not the case, however. In fact, wave heights were significantly higher on average at reference sites (df = 1, F= 5.32, P = 0.026) than at oiled sites, which casts doubt on the possibility that the higher marsh erosion rates documented at oiled sites were predisposed to rapid erosion as a consequence of their position in the landscape.
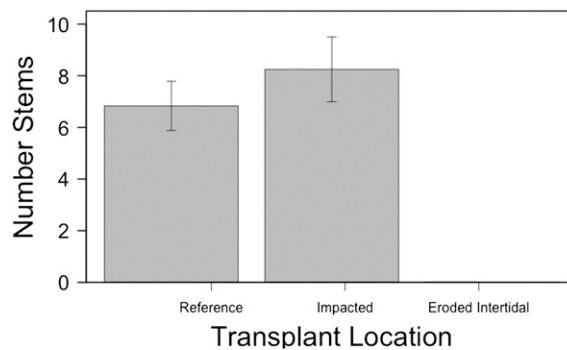

Fig. S5. Results from *Spartina alterniflora* transplant experiment in which healthy *Spartina* stems were planted in reference, impacted, and eroded intertidal regions of impacted sites. There was no difference in survival among the reference and impacted areas at these sites, but plants at these sites performed significantly better than plants in the eroded intertidal did (F = 57.26, P < 0.0001), with no stems persisting in the eroded intertidal zone.

Table S1. Coordinates of reference and impacted sites

Sites	Latitude	Longitude
Reference	29°24′535″N	89°59′239″W
	29°25′717″N	89°59′388″W
	29°13′402″N	90°00′443″W
	29°27′553″N	89°56′619″W
Impacted	29°26′819″N	89°56′264″W
	29°26′847″N	89°55′460″W
	29°26′196″N	89°54′681″W