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POSSIBLE SUSTAINED EFFECTS OF HURRICANES OPAL AND ERIN ON THE MACROBENTHOS OF NEARSHORE HABITATS WITHIN THE GULF ISLANDS NATIONAL SEASHORE

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ABSTRACT Possible sustained effects of hurricanes Opal and Erin on the macrobenthos of nearshore habitats of the Florida district of Gulf Islands National Seashore were assessed. Pre-hurricane macrobenthic data originating mainly from a large-scale faunal inventory conducted during 1993 were compared with post-hurricane data collected one year after the 1995 disturbances. Nearshore habitats examined included both exposed and protected sand beaches, as well as grassbed and lagoon sites. Within one year after the hurricanes, few faunal effects could be discerned at exposed beach sites, whereas possible faunal effects were apparent in protected nearshore habitats. Abundances of 4 major epifaunal crustacean taxa were notably lower one year after the hurricane disturbances. Assemblages of relatively stable nearshore habitats appeared to be more diverse but less resilient than assemblages of unstable nearshore habitats, possibly reflecting the extent of disturbance normally experienced by assemblages within those habitats.

INTRODUCTION

Although catastrophic disturbances such as hurricanes exert potentially large impacts on nearshore biotic communities, relatively few studies document the effects of severe storms on macrobenthos. Several notable exceptions include studies by Tabb and Jones (1962), Boesch et al. (1976), and Posey et al. (1996). These studies document several detrimental storm-related impacts on benthic organisms, due to reduced salinity, depletion of dissolved oxygen, and direct physical disturbance of the substrate. Additional ecosystem effects of Hurricane Bob on Cape Cod included changes in nutrient dynamics, ecosystem metabolism, and hydrography (Valiela et al. 1996). Moreover, hurricane induced impacts on macrobenthos may be further exacerbated by anthropogenic practices (Mallin et al. 1999).

Depending on the environmental context, the nature and severity of hurricanes can have very different consequences for the benthic community. Posey et al. (1996) noted moderate selective effects of storm-induced sediment disturbance on an offshore benthic community at 13 m depth, wherein abundances of surface-dwelling species declined while deep burrowing species remained unchanged. Boesch et al. (1976) found many species declined from drastic storm-induced decreases in salinity and dissolved oxygen in some areas, followed by irruptive increases in several opportunistic species within one year. The deep and relatively stable mud-bottom community in the lower York estuary had still not recovered after 2.5 years, suggesting relatively low resilience for diverse equilibrium communities.

During late summer and autumn 1995, two consecutive hurricanes, Erin and Opal, severely impacted the western coast of the Florida panhandle. One year later, as part of a resource damage assessment by the National Park Service, a macrobenthic study of the nearshore habitats of the Florida district of Gulf Islands National Seashore (GUIS) was conducted. A large baseline data set was available for comparison from several previous macrobenthic assessments that were conducted within GUIS, including an early survey of sand beaches in 1986/1987 (Rakocinski et al. 1991) and a comprehensive baseline inventory of nearshore habitats in 1993 (Rakocinski et al. 1995, 1998a).

The objective of this study was to compare baseline macrobenthic data with post-hurricane data obtained one year after the storm impacts to ascertain possible sustained effects on the nearshore resources of the Florida district of GUIS. To accomplish this objective, we considered: 1) pre- and post-hurricane variation in species richness, diversity, and total abundance; 2) assemblage-level variation in 23 selected sand-beach taxa previously used to develop a historical baseline; 3) abundance patterns expressed by dominant sand-beach taxa; and 4) differences in faunal metrics and abundances of dominant taxa from grassbed and lagoon habitats.

METHODS

Hurricane Impacts

During late summer and autumn 1995, two consecutive hurricanes, Erin and Opal, severely impacted the western panhandle coast of Florida. The Category 1 Erin made landfall first along Santa Rosa Island on 3

Figure 1. Map of the Florida district of the Gulf Islands National Seashore showing study sites used for the 1993 faunal inventory and for the 1996 post-hurricane survey. Western sites fall right at the border between the Florida panhandle and Alabama. See Table 1 for site codes.

August 1995, where it displaced the upper foreshore berm gulfward over a wide area and displaced considerable sediment towards the island interior (Stone 1996). Some beach erosion also occurred and substantial sediment was displaced from the beach to the dune system.

A much harsher Hurricane Opal devastated the same coastal region exactly 2 months later on 4 October 1995, when it made landfall just east of Pensacola, Florida (Stone et al. 1996). Opal was the most severe storm of the century to affect this area. It neared Category 5 strength with sustained wind speeds of over 65 m s^{-1} , 12 hours before landing. Estimated storm surge levels reached 5 m, overwashing most of Santa Rosa Island. Opal caused major erosion and sediment displacement within the GUIS portion of Santa Rosa Island. Vegetated stable foredunes reaching 5 m in height were removed entirely by Opal along Santa Rosa Island and Destin. Between 95–99% of the sediment eroded from the beach-dune system was redeposited to the island interior and along the northern bay shoreline, with overwash fans extending bayward by almost 100 m. Along the south shoreline of the island a notable coarsening of the quartz sand-beach sediments occurred. Considering the magnitude of the disturbances associated with the 1995 hurricanes, it is likely that the

macrobenthic biota in the Florida district of GUIS was everely impacted.

Study Design

The design of this impact assessment closely followed that for the comprehensive 1993 macrobenthic inventory (Rakocinski et al. 1995, 1998a), for which sites were distributed among the GUIS barrier islands both to allow historical comparisons and to provide a balanced baseline study. To achieve a balanced study design, at least one exposed beach site and one protected beach site were located on each GUIS barrier island (Figure 1). Three stations were placed at each beach site, including a mid-swash intertidal station, as well as 5-m and 15-m subtidal stations. Grassbed and lagoon sites also were established throughout the study region. Each grassbed site included 2 stations, while lagoon sites encompassed 3 or 4 stations.

The GUIS Florida district locations sampled for the 1993 inventory included 2 sand-beach sites (PK1, PK3), one grassbed site (PK2), and one lagoon site (PK4) at Perdido Key; 2 sand-beach sites (GB1, GB2), and one grassbed site (GB3) at Gulf Breeze; and 4 sand-beach sites (SR1, SR3, SR5, SR6), two grassbed sites (SR2, SR4), and one lagoon site (SR7) at Santa Rosa Island

(Figure 1, Table 1). The 1996 post-hurricane survey utilized the same configuration of study sites in the Florida district, but owing to the lack of seagrass at one station, only one of the 2 stations was sampled at site SR4 in 1996.

Field Sampling

The 1996 macrobenthic survey was completed over a 4-day period between 28 and 31 October 1996. At beach sites, samples were taken from the upper 20–25 cm of sediment using a 0.016 m² stainless steel box-corer (12.5 cm on a side) covered with 0.5 mm screen tops (Saloman and Naughton 1977). Stations at sand-beach sites were located at 0 m, 5 m, and 15 m from shore. From each station, 8 evenly spaced boxcores were taken every 1 m in a line parallel to the shore. Stations at the 2 Florida district lagoon sites were sampled with one epibenthic kicknet sweep each. A 0.45 m wide rectangular 0.5 mm mesh kicknet was swept along the bottom sediment surface for 20 m (9.0 m²). Stations at the 4 Florida district grassbed sites were sampled with duplicate 5 m epibenthic 0.5 mm mesh kicknet sweeps (4.5 m²) through submerged vegetation.

Small and/or light-bodied organisms were removed in the field by elutriating samples 5 times with a dilute formalin solution through a 0.5 mm sieve. Remaining material, including sediment, was washed through a 1.0 mm sieve to recover large and heavy organisms. This process has been shown to be effective in removing more than 95% of the organisms (Rakocinski et al

1991). Kicknet samples were first treated with 5% formalin and then passed through a 0.5 mm sieve. All processed samples were labeled, fixed with 5–10% formalin and returned to the laboratory.

LABORATORY METHODS

In the laboratory, macrobenthic invertebrates were sorted into major groups and transferred to 70% ethanol. As quality control, 5% of the samples were resorted to check for at least 90% accuracy. Grassbed and lagoon samples that contained vast numbers of organisms were split into 3 size fractions using nested sieves. The coarsest fraction was completely sorted visually using a lighted magnifying glass and finer fractions were subsampled using a MATODA plankton splitter. Following identification and enumeration of subsamples, abundance estimates were extrapolated by the appropriate split-factor. When superabundant, small snails were enumerated using a gridded petri-dish of 62.2 cm² within which organisms in 0.208 of the dish area (9 grid squares) were counted and extrapolated. Specimens were identified to the lowest practical taxonomic level and enumerated. Some organisms in poorly known groups were not identified to species. A voucher collection of all nominal taxa is maintained as part of The University of Southern Mississippi Institute of Marine Sciences Gulf Coast Research Laboratory Invertebrate Zoology collection, and a complete list of taxa occurring from this study is available upon request.

TABLE 1

Fourteen sites sampled during the Hurricane Opal/Erin macrobenthic impact study along with descriptions of locations and their position coordinates. Only one of the 2 grassbed stations from the 1993 inventory at site SR4 had seagrass present in 1996.

Island	Site	Habitat Type	Location	Latitude	Longitude
Perdido Key	PK1	Sand Beach	North Beach—FDNR range marker R63	30°19'08.6"	87°19'38.5"
Perdido Key	PK2	Grassbed	Grassbed adjacent to site PK1	30°19'08.6"	87°19'38.5"
Perdido Key	PK3	Sand Beach	South Beach—FDNR range marker R40	30°18'15.2"	87°23'31.9"
Perdido Key	PK4	Lagoon	Lagoon at Redfish Point—FDNR marker R51	30°18'57.0"	87°21'31.9"
Gulf Breeze	GB1	Sand Beach	North Beach—Naval Live Oaks campground	30°22'12.8"	87°08'36.1"
Gulf Breeze	GB2	Sand Beach	South Beach—east of Naval Live Oaks Visitor Center	30°21'49.5"	87°07'39.3"
Gulf Breeze	GB3	Grassbed	Grassbed adjacent to site GB2	30°21'47.6"	87°07'41.7"
Santa Rosa Island	SR1	Sand Beach	North Beach—Fort Pickens	30°18'49.1"	87°15'07.9"
Santa Rosa Island	SR2	Grassbed	Grassbed adjacent to site SR1	30°19'10.7"	87°15'24.8"
Santa Rosa Island	SR3	Sand Beach	North Beach—Santa Rosa	30°21'56.0"	86°58'05.8"
Santa Rosa Island	SR4	Grassbed	Grassbed adjacent to site SR3	30°22'01.9"	86°58'04.3"
Santa Rosa Island	SR5	Sand Beach	South Beach—Fort Pickens	30°19'06.8"	87°14'45.0"
Santa Rosa Island	SR6	Sand Beach	South Beach—Santa Rosa	30°21'41.9"	86°58'14.7"
Santa Rosa Island	SR7	Lagoon	Lagoon—Fort Pickens	30°19'19.9"	87°13'49.2"

Data Analysis

We used the Matrix Report feature of the Community Analysis System 4.0 (CAS) (Bloom 1992) to calculate organism abundances and summary community metrics for individual collections. Only 5-m and 15-m stations at beach sites were considered hereinafter. Summaries for box-core collections reflect combined abundances from all 8 cores per station (0.125 m²), whereas abundances represent each 20-m kicknet sweep (9.0 m²) for lagoon collections, or combined abundances for two 5-m kicknet sweeps (4.5 m²) for grassbed collections.

Species richness (S = number taxa per collection), total density, diversity (H'), evenness ($H'/H_{\max}$), and Simpson's Dominance Index (λ) were calculated (Magurran 1988). For box-core collections, species richness (S) was defined as the number of taxa collected by 8 cores (i.e., number taxa/0.125 m²). Diversity (H') was calculated on the $\log_e$ scale. $H_{\max}$ is the maximum value H' could take for a given number of taxa and organisms in a collection. The ratio of the 2 metrics then gives a normalized estimate of evenness.

Total density was presented as the total number of organisms per m². Geometric mean densities along with 2 standard errors (se) were calculated for individual taxa as well as for total numbers of organisms for each set of 8 cores per station and compared between sites in 1993 and 1996. Based on a sample size (n) of 8, two se gives >95% confidence limits for one-tailed tests of differences between years.

Principal Coordinate Ordination (PCO) provided a frame-of-reference for assessing variation in community structure, which incorporated historical reference samples from 1986/1987 and 1993, in addition to the 1996 post-hurricane samples. Through the use of an association matrix, PCO effectively translates differences in assemblage structure into intersample distances in ordination space. Twenty-three taxa used in former ordinations (Rakocinski et al. 1991, 1995, 1998a) were also used for this analysis. Case entries were geometric mean numbers per core ($\text{Inv}[\sum \ln(N+1)/\text{number cores per case}]$) for each of the 23 taxa. Every collection taken prior to 1996 from the same 1996 sand-beach stations was included, yielding 19 cases representing the 7 swash-zone stations and 20 cases representing the eight 15-m subtidal sand-beach stations.

Separate PCO analyses were performed for the 19 swash-zone cases and the twenty 15-m subtidal cases. The PCO was based on a dissimilarity matrix using Gower's Distance Index, where association values be-

tween each pair of samples are calculated for the i th taxa (Gower 1966). Following previous studies, abundance data were transformed by the e_{th} root and were not standardized, resulting in moderate weighting of the ordination according to the relative abundances of the various taxa. Sample coordinates were arrayed throughout PCO space so that possible sustained hurricane impacts on community structure could be assessed.

To detect possible hurricane effects at grassbed and lagoon stations, abundances of dominant taxa and faunal metrics were compared between the 2 groups of stations representing pre-hurricane (October 1993) and post-hurricane (October 1996) periods. Comparisons were based on the premise that changes in the same direction among all the stations likely represented real differences between the 2 periods. Where the normality assumption was met and the statistical power was ample (i.e., $b > 0.5$), differences in abundances between years were examined using paired- t tests; otherwise, non-parametric Wilcoxin Signed Rank (WSR) tests were used (Siegel 1956). Normality was checked with the Kolmogorov-Smirnov one-sample test and SigmaStat Version 2.0 was employed for all tests (Fox et al. 1995).

RESULTS

Sand-Beach Sites

Species Richness

Among swash-zone stations of both exposed and protected sand-beach sites, S patterns did not reflect sustained hurricane impacts on species composition. S was highly variable and ranged similarly among exposed swash-zone stations during both years (7–8 taxa in 1993 vs. 6–8 taxa in 1996) as well as among protected swash-zone stations (8–25 taxa in 1993 vs. 7–26 taxa in 1996) (Figure 2). Likewise, among 15-m subtidal stations at exposed beach sites, S ranged similarly (9–14 taxa in 1993 vs. 8–16 taxa in 1996), although S was higher at both Santa Rosa Island stations in 1993. In contrast, among the 5 eastern protected beach sites on Santa Rosa Island and Gulf Breeze, where the strongest hurricane impacts occurred, S was consistently and considerably lower in 1996. Indeed, S clearly ranged higher among protected 15-m subtidal beach stations in 1993 (39–55 taxa) compared to 1996 (24–46 taxa).

Faunal Diversity

H' at exposed beach sites was similar between 1993 and 1996, although values ranged somewhat higher among exposed swash-zone stations in 1993 (1.42–1.56) than in 1996 (0.97–1.39) (Figure 3). However,

Figure 2. Variability in species richness among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

among exposed 15-m subtidal stations, H' ranged similarly between 1993 (1.57–1.83) and 1996 (1.31–1.78).

Among protected swash-zone stations in 1993, H' ranged somewhat narrower (0.76–1.78) than in 1996 (0.24–1.83). Two protected swash-zone stations with notably low H' in 1996 included one at Santa Rosa Island site 3 (1.16 in 1993 vs. 0.24 in 1996), and one at Gulf Breeze site 2 (1.68 in 1993 vs. 1.00 in 1996). Among protected 15-m subtidal stations, H' ranged similarly between 1993 (1.62–3.10) and 1996 (1.48–2.96). However, H' was notably low in 1996 at 3 protected 15-m subtidal stations within the most severely impacted area, including Santa Rosa site 1 (3.10 in 1993 vs. 1.69 in 1996), Gulf Breeze site 1 (2.72 in 1993 vs. 1.48 in 1996), and Gulf Breeze site 2 (2.78 in 1993 vs. 2.33 in 1996).

Total Density

Among swash-zone stations at both exposed and protected sites, geometric-mean total density varied erratically between 1993 and 1996 (Figure 4). However,

among 4 of the 5 protected swash-zone stations, considerably higher densities occurred in 1993 than in 1996. Total densities at exposed swash-zone stations ranged similarly between 1993 (98–1,374 m^2) and 1996 (226–1,116 m^2), but densities ranged narrower among protected swash-zone stations in 1993 (1,197–10,658 m^2) than in 1996 (449–13,320 m^2).

Total densities generally ranged substantially lower in 1996 than in 1993 among 15-m subtidal stations from both exposed (491–1,312 m^2 in 1993 vs. 179–861 in 1996) and protected beaches (5,353–7,757 m^2 in 1993 vs. 3,109–4,857 m^2 in 1996). Subtidal total densities at the 2 exposed Santa Rosa sites were distinctly lower in 1996. Furthermore, total densities among protected subtidal sites were generally substantially lower in 1996 than in 1993 (Figure 4).

Sand-Beach Dominance Patterns

Differences in total densities between 1993 and 1996 subtidal sand-beach stations could not be attributed consistently to responses by particular dominant

Figure 3. Variability in faunal diversity among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

taxa. Dominant taxa occurring among the five 15-m subtidal stations from protected beaches in 1993 included oligochaetes, polychaetes (e.g., *Laeonereis culveri*, *Capitella capitata*, *Heteromastus filiformis*, *Paraonis fulgens*, *Streptosyllis pettiboneae*, and *Polygordius* sp. A), Nemerteans, Turbellarians, the lancelet (*Branchiostoma* cf. *floridana*), and several crustaceans (e.g., *Kalliapsuedes* sp. A, and *Acanthohaustorius uncinus*) (Rakocinski et al. 1998b). Several of these dominant taxa were lacking among the same subtidal stations in 1996, including *C. capitata*, *H. filiformis*, *A. uncinus*, *Kalliapsuedes* sp. A., and *B. cf. floridana*. Moreover, the haustoriid amphipod, *Lepidactylis* sp. A., became a dominant taxon at 2 of the 15-m subtidal stations of protected beaches in 1996, but was lacking at those same stations in autumn 1993 (Rakocinski et al. 1995, 1998a).

PCO Ordination

Most meaningful community variation among the swash-zone stations could be examined within the first

3 PCO dimensions, as implied by a cumulative vector efficiency of 85%. The first 3 PCO axes explained 42% of the variance in macrofaunal dissimilarity among the 19 swash-zone stations: Axis 1 represented 20.37% of the variance, Axis 2 represented 13.83% and Axis 3 represented 8.03%.

Swash-zone sample coordinates from protected beach sites were much more variable than variables from exposed beach sites, reflecting the more diverse macrofauna at protected sites (Figure 5A). Strongly aggregated groups of swash-zone stations representing protected and exposed sites also were evident. However, faunal-dissimilarity patterns among the swash-zone stations could not be attributed to hurricane effects, as PCO coordinates for the 1996 stations did not stand out from those of historical reference stations. Indeed, the most outstanding swash-zone PCO coordinate represented a protected Gulf Breeze site in 1993.

Most meaningful community variation among the twenty 15-m subtidal stations at sand beach sites could be examined within the first three PCO dimensions, as

Figure 4. Variability in geometric mean total density (± 2 se) among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

indicated by a cumulative vector efficiency of 63%. The first 3 PCO axes effectively explained 31% of the variance in macrofaunal dissimilarity among the twenty 15-m subtidal stations: Axis 1 represented 14.64% of the variance, Axis 2 represented 9.46%, and Axis 3 represented 6.82%.

The pattern of 15-m subtidal coordinates in 3-D PCO space revealed more variability in community structure among protected beaches than among exposed beaches. Coordinates representing protected and exposed sites were separated in PCO space, reflecting different faunal complements from protected and exposed beaches (Figure 5B). For exposed beach sites, differences in community structure attributable to hurricane effects were not apparent from the dispersion of 15-m subtidal coordinates. However, 2 of the PCO coordinates representing 15-m subtidal stations from protected beaches in 1996 fell outside the range of previously measured variability in faunal dissimilarity, including one at Gulf Breeze and another at Santa Rosa Island.

Grassbed and Lagoon Sites

Faunal Summary Metrics

WSR tests failed to reveal any overall directional changes in S , H' , $H'/H_{\max}$, λ , or total density ($0.469 > P_{\text{exact}} > 0.156$) among grassbed stations between 1993 and 1996. However, the lowest metric values occurred in 1996. S ranged lower among the 7 grassbed stations in 1996 (31–72) than in 1993 (48–84); H' ranged similarly in 1993 (1.17–2.82) and 1996 (0.58–2.54); $H'/H_{\max}$ and λ paralleled H' in 1993 ($H'/H_{\max} = 0.27$ – 0.64 ; $\lambda = 0.48$ – 0.87) and in 1996 ($H'/H_{\max} = 0.15$ – 0.61 ; $\lambda = 0.22$ – 0.83); and total densities varied widely and overlapped among stations in 1993 (779–5,865) and 1996 (358–7,126).

WSR tests did not indicate any overall directional changes in S , H' , $H'/H_{\max}$, λ , or total density ($1.0 > P_{\text{exact}} > 0.688$ among lagoon stations. Wide ranges for some summary metrics reflected the relatively high habitat heterogeneity among lagoon stations. However, ranges of most metrics overlapped between 1993 and

Figure 5. Principal Coordinate Ordinations of sand-beach stations from before hurricanes Opal and Erin, in October 1986/1987 and 1993, and the same stations in October 1996, one year after hurricane impacts occurred. Coordinate labels denote the station numbers and years. (A) Swash-zone ordination; (B) 15-m subtidal ordination. Solid = exposed sites; open = protected sites.

1996. Among the 6 lagoon stations, S ranged similarly in 1993 (17–69) and 1996 (16–81); H' overlapped in 1993 (1.84–2.91) and 1996 (2.11–2.87); $H'/H'_{\max}$ and λ paralleled diversity in 1993 ($H'/H'_{\max} = 0.50$ – 0.78 ; $\lambda = 0.66$ – 0.91) and in 1996 ($H'/H'_{\max} = 0.59$ – 0.82 ; $\lambda = 0.73$ – 0.92). Total density also varied widely among lagoon stations and overlapped broadly in 1993 (10–809) and 1996 (11–274).

Grassbed and Lagoon Dominance Patterns

Comparisons of relative abundances of taxa from grassbed and lagoon stations between years showed that the same taxa were generally dominant during both pre- and post-hurricane periods (Rakocinski et al. 1995, 1998b). Comparisons of infaunal taxa among the grassbed stations for each sampling period did not reveal any overall directional shifts. For example, total abundances of syllids ranged similarly in 1993 (0–52) and 1996 (0–139); and a WSR test showed that these estimates were not different ($P_{\text{exact}} = 0.84$).

Comparisons of epibenthic micrograzer gastropods from grassbed stations also failed to show any overall directional shifts in abundances between sampling periods. Numbers of *B. varium* ranged similarly in 1993 (307–8,618) and 1996 (289–28,345), and numbers of *A. lunata* also ranged similarly in 1993 (109–2,679) and 1996 (83–1,414), and WSR showed no difference between sampling periods ($P_{\text{exact}} = 0.94$ for both taxa).

Remarkably, abundances of several epifaunal crustaceans were lower at grassbed stations between 1993 and 1996 (Figure 6). Total numbers of amphipods, *Hippolyte* spp., *Pagurus* spp., and palaemonids were reduced in 1996. Numbers of amphipods in grassbed kicknet samples averaged and ranged higher in 1993 (127.1 ± 35.6 se; 5–246) than in 1996 (36.6 ± 18.0 se; 0–116) (paired-t test = 2.54, $P = 0.04$) (Power = 0.50 at $\alpha = 0.05$). Numbers of *Hippolyte* in grassbed samples also averaged and ranged higher in 1993 ($5,224 \pm 1,292.5$ se; 1,266–10,363) than in 1996 (447.9 ± 165.8 se; 73–1,125) (paired-t test = 7.57, $P < 0.001$; ln transformed) (Power = 1.0 at $\alpha = 0.05$). Again, numbers of *Pagurus* in grassbed samples averaged and ranged higher in 1993 (103.1 ± 20.9 se; 27–183) than in 1996 (25.0 ± 6.0 se; 0–44) (paired-t test = 3.85, $P = 0.008$) (Power = 0.88 at $\alpha = 0.05$). Finally, numbers of palaemonids in grassbed samples averaged and ranged higher in 1993 (47.4 ± 15.2 se; 6–124) than in 1996 (10.6 ± 5.0 se; 0–33) (paired-t test = 2.75, $P = 0.03$) (Power = 0.57 at $\alpha = 0.05$).

DISCUSSION

Sustained hurricane effects were evident in some habitats based on comparisons of 1993 and 1996 macrobenthic surveys, notwithstanding insufficient sampling frequency. One year after the hurricane impacts, lower species richness usually occurred at the protected beach stations and lower total densities usually oc-

Figure 6. Abundances of important epifaunal crustaceans from grassbed stations in 1993 before hurricanes Opal and Erin and in October 1996 one year after hurricane impacts.

curred at protected swash-zone as well as at both protected and exposed subtidal stations. The lowest faunal metric values in 1996 were generally from the stations hardest hit by the hurricanes. PCO showed that 2 of the most impacted subtidal protected stations in 1996, including one at Gulf Breeze and another at Santa Rosa Island, fell outside the range of previously measured variability in faunal dissimilarity. *Lepidactylis* sp. A is usually a dominant subtidal organism in spring. However, this amphipod became dominant at the 2 stations in October 1996, although it was lacking at those same stations in autumn 1993 (Rakocinski et al. 1995).

Differences in total densities between 1993 and 1996 at subtidal sand-beach stations did not reflect consistent responses by the dominant taxa, indicating that density differences reflected individualistic responses by various taxa. For example, several dominant taxa from 1993 were lacking among protected 15-m subtidal stations in 1996, including *C. capitata*, *H.*

filiformis, *A. uncinata*, *Kalliapsuedes* sp. A., and *B. cf. floridana*. Interestingly, *B. cf. floridana* usually is abundant in stable subtidal habitats (Rakocinski et al. 1993, 1996). The lack of *Capitella* and *Heteromastus*, and the increase in *Lepidactylis* sp. A, may reflect relatively low availability of organic matter in the newly disturbed and overwashed sandy sediments of the impacted protected beaches since opportunist capitellids colonize organically rich sediments following a disturbance (Boesch et al. 1976). Finally, epibenthic crustacean taxa in seagrass habitats were generally lower in 1996 than in 1993, although abundances of many grassbed taxa were similar for each sampling period. Evidence that grassbed habitats incurred sustained hurricane effects included significant decreases in total ampithoids, *Hippolyte* spp., *Pagurus* spp., and total palaemonids. Thus sustained hurricane effects were apparently selective on certain taxa. The same trends were upheld by data from lagoon stations in which grassbed habitat

occurred (Rakocinski et al. 1998b). Posey et al. (1996) noted selective effects of storm disturbance on vulnerable surface sediment-dwelling organisms as opposed to deep sediment-dwelling taxa. The finding that such benthic effects are selective and individualistic supports the currently accepted Gleasonian concept of community organization, which views assemblages as associations of organisms that are individually adapted to live under particular conditions (Ricklefs 1983).

Although effects of severe meteorological events on macrobenthic assemblages are often difficult to ascertain, documented impacts of hurricanes on the biota include burial by sediment deposition, turbidity effects, suffocation from the decomposition of organic matter, scouring, osmotic stress, physical stranding, and thermal shock (Saloman and Naughton 1977). In a thorough study of the effects of Hurricane Eloise on the swash-zone macrofauna of several exposed beach sites at Panama City Beach, Florida, Saloman and Naughton (1977) failed to find any major differences between pre- and post-hurricane periods, despite substantial erosional alteration of the beach. Using the same type of box-corer as this study, the authors found that abundances of swash-zone organisms were inherently variable. They mainly attributed the lack of measurable hurricane effects to the adaptations of organisms inhabiting this high-energy environment as well as to inherent faunal variability. They also cited other studies that found little evidence of hurricane impacts on the biota inhabiting exposed beach sites (Keith and Hulings 1965, Croker 1968). Thus, despite the large extent of the hurricane disturbance in this study, it is not surprising that we found less evidence of sustained effects on the fauna of exposed beaches.

Various factors noted in other studies of hurricane effects on macrobenthos also may have played some role in our study, including hydrography, sediment disturbance, and depletion of dissolved oxygen. In a study of hurricane effects on the aquatic fauna of north Florida Bay, Tabb and Jones (1962) found that both direct disturbance and subsequent oxygen depletion greatly impacted seagrass associated organisms. Moreover, fish and invertebrates remained scarce for several months in the area of greatest oxygen depletion. Similar detrimental impacts may have been responsible for the effects we observed on epifaunal crustacean populations of grassbed habitats. Boesch et al. (1976) found that many species declined from drastic storm-induced decreases in salinity and dissolved oxygen, followed by irruptive increases in several opportunistic species within one year. Moreover, the deep and relatively stable mud-

bottom community in the lower York estuary still had not recovered after 2.5 years, suggesting low community resilience. This time frame for recovery is comparable to that inferred from our study, as possible effects on grassbed macrofauna were still apparent one year after the storm impact. The resiliency of estuarine populations is thought to be related both to the spatial extent of impact as well as to the life-history characteristics of impacted species (Dauer 1984). The larger the area impacted and the longer-lived the species, the longer the expected recovery time.

The extent of inferred sustained effects of Hurricanes Erin and Opal corresponded inversely to the degree of disturbance typically experienced by resident assemblages. Exposed swash-zone stations showed the least evidence of faunal effects, followed by progressively greater effects at exposed subtidal, protected swash-zone, protected subtidal, and grassbed stations. Assemblages of relatively stable habitats like protected subtidal sand-beaches and grassbeds are richer and presumably less resilient than simpler assemblages of exposed sand beaches and shorelines. After one year, the post-hurricane assemblages of exposed beaches and swash-zone habitats were indistinguishable from those of pre-hurricane conditions. By contrast, abundances of epifaunal crustaceans of grassbed habitats were still low one year after the hurricanes. Thus, apparent differences in faunal recovery between protected and exposed sites might reflect differences in adaptations of resident taxa to typical disturbance regimes.

In a study of the effects of extensive beach restoration on macrobenthic assemblages across exposed-beach transects, Rakocinski et al. (1993, 1996) hypothesized that diverse offshore subtidal assemblages are less resilient than contiguous nearshore sand-beach assemblages. Faunal recovery near the beach was rapid, with complete colonization in less than one year. Indeed, Grant (1980, 1981) found that small patches of azoic beach sand could be completely colonized within one month. Being adapted to frequent disturbance from high energy conditions confers considerable resilience to macrobenthic assemblages of exposed sand beaches (Nelson 1993). Other studies of the impacts of beach nourishment also usually find rapid and complete macrobenthic recovery within the course of one year (Nelson 1989, 1993; Baca et al. 1991). However, like exposed offshore macrobenthos, assemblages of relatively stable habitats like protected subtidal sand-beaches and grassbeds appear to be less resilient than assemblages of exposed sand beaches (Rakocinski et al. 1991, 1995).

CAVEATS

Despite infrequent sampling, inadequate pre- and post-disturbance sampling, and the lack of an unimpacted reference area, the existence of GUIS baseline information from the 1993 macrobenthic inventory and the faunal survey of sand beaches in 1986/1987 provided a standard frame-of-reference for considering environmental impacts. The scope of the 1993 inventory furnished a preexisting balanced arrangement of study sites throughout GUIS and built-in spatio-temporal redundancies afforded by the inclusion of multiple sites and years. Established standard quantitative and semi-quantitative sampling methods and protocols also ensured comparability. This study demonstrates the utility of building a comprehensive and current database on macrobenthic resources to facilitate sound management decisions.

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