Exploiting beach filling as an unaffordable experiment: Benthic intertidal impacts propagating upwards to shorebirds

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Abstract

Cold-season filling using much coarser sediments than the native caused dramatic suppression of beach macroinvertebrates, demonstrably degrading habitat value for foraging shorebirds. As a dual consequence of persistent steepening of the foreshore, which translated to reduction in habitat area by 14–29%, and disturbance-induced depression of invertebrate densities on filled beaches, abundances of *Donax* spp. and haustoriid amphipods averaged less than 10% of control levels. *Donax* spp. is the biomass dominant and a key prey for higher trophic levels. Haustoriids lack pelagic larvae. Recovery on filled beaches was not initiated by either taxon during the March–November sampling. *Emerita talpoida*, an order of magnitude less abundant than *Donax* spp. on control beaches, exhibited a pattern of initial depression on filled beaches but recovered by mid summer. Polychaetes, mostly the small *Scolelepis squamata*, experienced a warm-season bloom of equal magnitude on filled and control beaches. Summertime recruitment of predatory ghost crabs appeared inhibited on filled beaches, perhaps by persistent shell hash. Intertidal shell cover on filled beaches averaged 25–50% in mid summer as compared to 6–8% on control beaches. Largely in response to prey depression, but perhaps also to surface shell armoring and/or coarsening of sediments, shorebird (mostly sanderling) use plummeted by 70–90% on filled beaches until November. Thus, despite likely adaptations to natural sediment dynamics, the high intensity of sediment deposition, cumulative spatial scope (10.8 km), and unnaturally coarse shelly character of the Bogue Banks beach nourishment resulted in a perturbation that exceeded biotic resistance and degraded the trophic transfer function of this highly productive habitat for at least one warm season.
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Keywords: Beach nourishment; Habitat function; Intertidal invertebrates; Sediment grain sizes; Shorebird use; Suppressed recovery

1. Introduction

The past 30 years have revealed many dramatic changes in the focus of ecological research within academia. A generation ago, applied ecology was largely scorned by university scientists, and untenured faculty members at major research universities risked denial of tenure if they pursued applied research. Over the subsequent decades, new ecological sub-disciplines and scientific journals, especially in conservation biology and restoration ecology, have arisen and flourished, reflecting both the societal importance of ecological applications and their acceptance into academia (Lubchenco et al.,

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1991). In marine ecology, a few visionaries have contributed disproportionately to this sea change in attitudes. Tony Underwood in Australia stands tall among them, legitimizing applied marine ecology by his influential emphasis on experimental designs that can bring statistical rigor to environmental assessment and his frequent demonstrations of how well conceived environmental assessment studies can provide opportunity for novel insight into marine ecological processes of broad significance (e.g., Underwood, 1997).

Ocean beaches represent an ecological system where exploiting management schemes to test hypotheses about processes at large scales is particularly important because of the difficulty and unaffordable expense of conducting large-scale experiments in this energetic system. Ecological understanding of factors that dictate composition and dynamics of sandy beach communities has remained rudimentary because of the limited capacity to conduct experimentation on appropriate scales. Correlative approaches have been applied to establish relationships among physical environmental variables (especially beach slope, sedimentology, and tidal range) and biological characteristics of populations and communities of intertidal invertebrates on sandy beaches (McLachlan, 2001; Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005). Although such correlations represent one giant step towards understanding mechanisms that drive dynamics and produce pattern in ecological communities, interpreting even a tight correlation between a physical and biological factor can be seriously misleading (Dayton and Oliver, 1980) because of confounded covariates, including especially biological intermediates (Connell, 1975). Establishing the mechanism by which a pattern is generated requires further insight often not attainable through correlation. The few instances in which managerial decisions, such as the opening and closing of fisheries (Defeo, 1998; Brazeiro and Defeo, 1999) or the removal of wrack from a beach (Dugan et al., 2003), have been utilized as experiments has greatly increased our understanding of processes that organize sandy beach systems.

Here, we take advantage of a beach fill ("nourishment") project and the development of rigorous statistical approaches for inferring impacts of such planned environmental interventions (Underwood, 1993, 1994) to provide experimental tests of hypotheses about impacts and complex recovery dynamics of sandy beach habitat function after large-scale physical disturbance. The overwhelming dominance of the literature by correlations between physical variables and ecological characteristics of sandy beach communities, in recognition of the often intense wave and storm disturbance of the beach substrate, has led to a common assumption that recovery following any disturbance of the sediments should be rapid in this community (NRC, 1995). However, the intensity of sedimentation, the seasonal timing of disturbance, and the physical nature of the added sediments in a beach fill project may not match the natural conditions to which the sandy beach biota has adapted. Utilizing a beach fill project, we test the hypothesis that recovery of the intertidal-to-shallow-subtidal invertebrate community and trophic functions of the beach habitat after massive sediment deposition during the cold season of late fall to early spring will occur rapidly over a period of weeks to months within the first warm season. We also assess whether timing of the disturbance to match the typical winter season of storminess and biological inactivity produces more rapid recovery than filling in early spring, when wave climate has moderated and seasonal recruitment of invertebrates has begun. By conducting synoptic assessment of physical habitat conditions, benthic invertebrate abundances, and predatory crab and shorebird abundances, we infer mechanisms that drive recovery dynamics in this poorly understood system.

2. Methods

2.1. Study sites and design

We took advantage of plans for a winter 2001–02 beach nourishment project on Bogue Banks (North Carolina, USA) to design an evaluation of ecological impacts and recovery from large-scale sedimentation during the subsequent warm season as a function of month of filling. Our possession of previous quantitative sampling data from 1998 (Manning, 2003) for beach macroinvertebrates at several localities along Bogue Banks, including areas to be filled and a control area outside but near the fill zone, made possible a rigorous design that could use a "beyond BACI" (Underwood, 1994) approach to control for natural temporal and spatial variation. Peterson and Bishop (2005) reported from a synthesis of the literature that only 11% of previous monitoring studies of environmental impacts of beach nourishment had applied any test using before–after contrasts of control and putative impact locations. Bogue Banks is an east–west oriented barrier island 45 km long located on the central coast of North Carolina (Fig. 1). Mean tidal range is about 1 m and mean wave height 1.2 m (Brooks and Brandon, 1995). Except for five smaller beach fill projects at Fort Macon and Atlantic Beach from 1973–1994 to dispose of spoils from channel and harbor dredging (Valverde et al., 1999) and spoil disposal in spring 1990 along two 0.5–
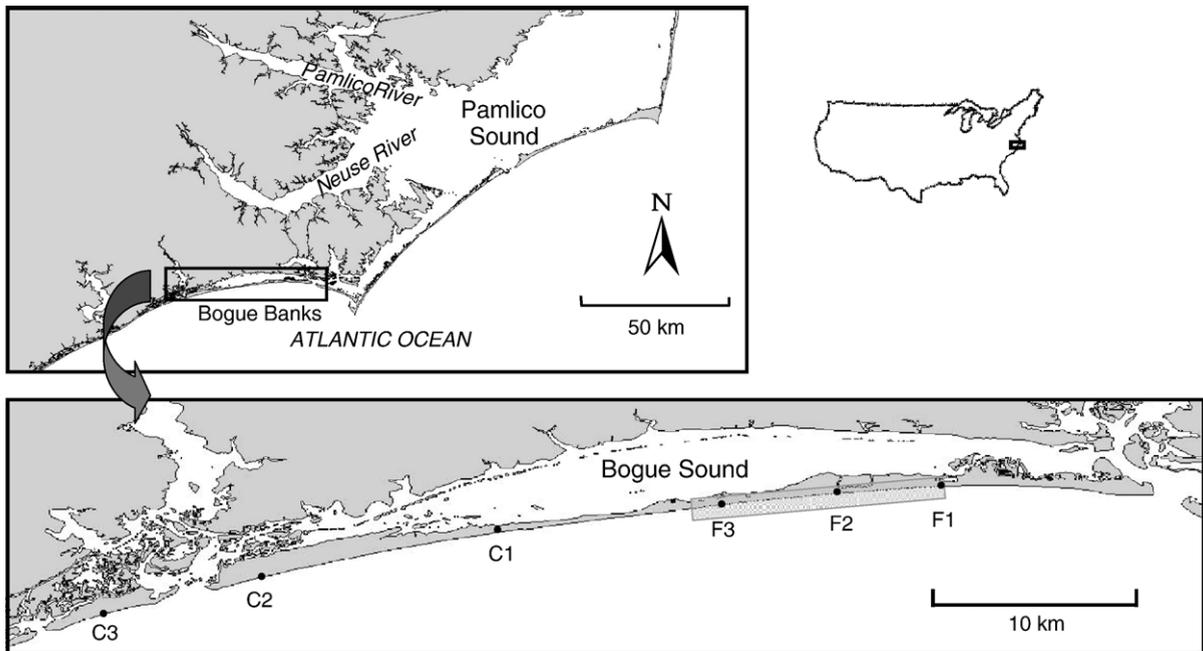
Fig. 1. Map of the North Carolina coast showing study locations (circles) relative to the section of Bogue Banks beach filled in 2001–02 (boxed and shaded). C1 = control 1 (Pierpoint), C2 = control 2 (Spinnaker's Reach), C3 = control 3 (Bear Island), F1 = beach filled in early December 2001 (Royal Pavilion), F2 = beach filled in early February 2002 (Dogwood Circle); F3 = beach filled in early April 2002 (Trinity Center).

1.0-km stretches of beach in Pine Knoll Shores (Peterson et al., 2000), the Bogue Banks beaches had not been modified by filling prior to the 2001–02 beach nourishment. This new project dredged materials from offshore to place 100–176 m^3 of sediment per linear m along 10.8 km of shoreline from the western edge of Atlantic Beach to near the western boundary of Indian Beach at the center of the island (Fig. 1). Filling began in late November 2001 and moved progressively east to west until 11 April 2002. The temporal progression allowed us to contrast study sites that were filled in early December, early February, and early April to test for differences in impacts and rate of recovery as a function of date of disturbance. By sampling at two-month intervals, biotic samples can be compared holding date of sampling constant or time since filling constant.

We selected six locations for documenting widths of beach zones and sampling sediment size composition, benthic macroinvertebrate densities, ghost crab burrow abundances, and shorebird use after completion of the nourishment project. Three study locations were established on filled and three on undisturbed control beaches (Table 1). We chose to use as many locations (three) from our previous sampling in 1998 as possible and to employ identical sampling methods to allow a subset of our data to be used in beyond BACI tests of ecological impacts (Underwood, 1994). Because filling covered a

continuous stretch of shoreline interspersion of filled and control locations was impossible, as in virtually all beach nourishment projects (Nelson, 1993). Nevertheless, sampling results indicated that, despite substantial biological differences between filled and control beaches, patterns did not simply follow an east–west gradient. Within each location, we sampled each of two study sites, separated by ∼0.8 km, using three replicate vertical transects 40 m apart. Our sampling design was constrained to match the design used for the 1998 sampling, in which the 40 m separation between transects was chosen to avoid sampling within individual patches of *Donax* spp. or *Emerita talpoida*, which can be observed during calm low tides to extend along the shoreline for 0.5–14 m. The distance between sites reflects analysis of pilot sampling data suggesting a lack of correlation in macrobenthic densities at 0.5–1.0 km scales on Bogue Banks, potentially allowing us to treat sites as independent or nested within location in analyses.

Sediment sampling was conducted on three occasions, in March, July, and November 2002, whereas biological sampling (intertidal–shallow subtidal macroinvertebrates, ghost crab burrows on the high beach, and shorebird use) took place bimonthly from March through November 2002 (Table 1). Corresponding sampling of sedimentology, benthic invertebrates, and ghost crab burrows had been previously conducted in

Table 1
Sampling design for tests of impact and recovery over the subsequent warm season after beach filling on Bogue Banks, NC, in 2001–02

Sampling location	Treatment	Sampling months for:					
		Sedimentology		Benthic invertebrates[c]		Shorebirds	
		Before	After	Before	After	Before	After
Royal Pavilion	Filled — Dec (F1)	None	3,7,11	None	3,5,7,9,11	None	3,5,7,9,11
Dogwood Circle	Filled — Feb (F2)	3,5[d],7[d],9[d]	3,7,11	3,5,7,9	3,5,7,9,11	None	3,5,7,9,11
Trinity Center[a]	Filled — Apr (F3)	4,5[d],7[d],9[d]	7,11	5,7,9	5,7,9,11	None	5,7,9,11
Pierpoint	Control (C1)	3,5[d],7[d],9[d]	3,7,11	3,5,7	3,5,7,9,11	None	3,5,7,9,11
Spinnaker's Reach	Control (C2)	None	3,7,11	None	3,5,7,9,11	None	3,5,7,9,11
Bear Island[b]	Control (C3)	None	3,7,11	None	3,5,7,9,11	None	3,5,7,9,11

Before dates apply to 1998 and after dates to 2002. At each sampling location, there were two nested study sites separated by ≈0.8 km. Locations F1, F2, and F3 are in Pine Knoll Shores, whereas C1 and C2 are in Emerald Isle. Months of sampling are indicated by numerals, with March = 3, May = 5, etc.
[a] Because beach filling did not occur at Trinity Center until April, there was no March 'after' sampling possible.
[b] On Bear Island, shorebird counts were made on only 1 morning within each sample period, not 2 as at all other locations. All shorebird counts were made over a 1.5-km stretch of beach, which covered both sites.
[c] Benthic invertebrates include infauna sampled by coring and a separate data set on ghost crabs sampled by burrow counts.
[d] Sediment data for these months lack samples for the supratidal zone and lack replication of transects.

March, May, July and September 1998 (only May and July at all three locations) at Dogwood Circle, Trinity Center, and Pierpoint, providing information prior to the nourishment project (Table 1). No biological sampling took place in January because of the dramatic seasonal depression of macrobenthic invertebrate abundances on Bogue Banks during winter (Diaz, 1980; Leber, 1982).

All benthic sampling was stratified along vertical transects perpendicular to the shoreline so as to integrate across the strong environmental gradients associated with tidal elevation, as in most previous studies of sand-beach macroinfauna (James and Fairweather, 1996). We identified five separate elevation zones on the beach and conducted stratified sampling of surface sediments and of beach macroinvertebrates, with equal effort in each zone. Zones were defined by physical factors at low tide, when all sampling was conducted. The supratidal zone (1) extended from the toe of the dune to the drift line marking the high tide mark. The high intertidal zone (2) extended down slope from the drift line to include the complete region where surface drying took place during low tide. The mid-intertidal zone (3) extended across the zone where sand remained wet throughout the low tide and down to the upper limit of where low-tide wave run-up extended. The low intertidal or swash zone (4) included the complete region of low-tide wave run-up from lowest retreat to maximum reach. And finally, the shallow subtidal zone (5) extended from the bottom of the swash zone to −1 m depth in the surf zone at low tide. On every date of sampling for invertebrates, the boundaries of each zone were marked by surveyor's flags and the width of each zone on each transect measured.

2.2. Sedimentology

For sediments, we created a composite sample combining the contents of three 4.8-cm diameter cores taken to 10 cm within each elevation zone. The three cores were haphazardly located within the top, middle, and bottom of each zone, with specific placement blind to surface sediment appearance. In the laboratory, each sediment sample was subdivided by coning and quartering to a weight of ~250 g by traditional methods (Folk, 1974). Then this smaller subsample was repeatedly rinsed with de-ionized water to remove salt and the rinse waters filtered through pre-weighed 0.7-µm filter papers, which were then dried for 15 h at 90 °C and reweighed to compute weight of the silt/clay fraction. Remaining coarser sediments were also dried for 15 h at 90 °C before sieving by hand on a 2-mm (-1Φ) screen to remove and weigh the gravel-sized fraction. The remaining sand sample was split down to a weight of 30–70 g (Folk, 1974), which was passed through a nested series of −0.5 to 3.5Φ screens at 0.5Φ intervals using a Rotap sieve shaker. Each of these samples was weighed, allowing computation of mean sediment size by weight by traditional methods (Folk, 1974) and thus percentage composition of silt/clay ($\Phi>4.0$), fine ($2.0<\Phi<4.0$), medium ($1.0<\Phi<2.0$), and coarse ($-1.0<\Phi<1.0$) sand, and gravel ($\Phi<-1.0$). Because surface shell could inhibit shorebirds and surf fish from gaining access to infaunal invertebrates, we also conducted an assessment of the percent cover of the surface of the lowest two intertidal zones by shell of gravel size and larger in July 2002. This sampling was achieved by

haphazardly repeatedly placing a weighted 0.25-m^2 PVC quadrat 30 times in zone 3 (mid-intertidal) and 30 times in zone 4 (swash) at every site during a single low tide and estimating percent shell cover. Such visual estimates of percent surface cover have been shown to be unbiased and efficient (Dethier et al., 1993). Breaking waves prevented analogous sampling from being done in zone 5 (shallow subtidal), also an area of great ecological significance.

2.3. Biota

We sampled separately for infauna and for predatory ghost crabs along each vertical transect. Macroinfaunal densities were estimated within each of the five vertical zones used for sediment sampling, although only zones 3–5 were routinely occupied. We created a composite sample of infauna within each zone comprised of three core samples 82 cm^2 in surface area and 15 cm deep, haphazardly located within the top, middle, and bottom of each zone and placed blind without regard to surface appearance. Pooling was done because densities, especially of amphipods, were so low that a surface area of 3 times that of a single core was deemed necessary to comprise an adequate sample. Contents retained on a 1.0-mm sieve were preserved in labeled jars with 10% formalin and stored in the lab until the benthic macroinvertebrates could be sorted, identified, and counted. Infaunal data are reported here for each of four dominant taxa, the bivalve *Donax* spp. (mostly *D. variabilis* Say 1822, but also *D. parvula* Philippi, 1849), the mole crab *Emerita talpoida* (Say 1817), amphipods – almost all haustoriids, and polychaetes – mostly *Scolelepis squamata* (Müller 1789). Ghost crab (*Ocypode quadrata* Fabricius 1787) densities were estimated by counting numbers of active burrow openings along a transect 4-m wide beginning in the mid-intertidal zone and extending to the top of the dune, where the crab distribution ended on these beaches (see Wolcott, 1978 for the justification of using active burrows as proxy for ghost crab abundances). Each transect was split into two components, one covering the relatively flat beach and the other the steeper dune face. This separation was done because this beach nourishment project stopped at the base of the dunes, leaving the dune face undisturbed. One ghost crab transect was established in association with each coring transect.

Counts of feeding shorebirds by species were conducted in 2002 on two consecutive days during each bimonthly sampling of invertebrates. The days selected for sampling were clear, with early morning low tides, winds less than 25 km/h and wave heights of less than 0.5 m. Within two hours of low tide, counts of feeding shorebirds were made at every location except Bear Island (C3), which could not be easily accessed. Along a 1.5-km stretch of beach, which covered both study sites at each location, feeding shorebirds were counted through binoculars and identified. So as not to introduce temporal bias in sampling, on each day the five sampling locations were visited in random order. No bird counts were made during the 1998 data collection, so inferences of impacts of filling must be based upon spatial contrasts afterwards.

2.4. Statistical analyses

Two sets of ANOVAs were employed for benthic invertebrates, differing by time periods included. One set contrasted all study sites in 2002 after beach filling as the most spatially comprehensive and replicated means of determining impacts of filling, assuming that beaches were intrinsically similar prior to treatment. The second set employed beyond BACI analyses to control simultaneously for both natural spatial and temporal variation (Underwood, 1994). This second set was necessarily restricted to the limited set of locations (3 of 6) and months (2 of 5) possessing data from 1998 before the beach filling, so the power to detect impacts was lower.

Following the recommendation by James and Fairweather (1996) for generic sampling of beach infauna, the first analyses, examining only spatial patterns, were nested. These had three factors: treatment (filled vs. control); location (3 levels, nested within treatment); and site (2 levels, nested within location). Because of the large seasonal changes in the abundance of fauna, separate analyses were conducted for each month of sampling. Analyses for May–November included each of the six locations sampled. Because filling at Trinity Center (F3) was not completed until April 2002, analyses for March necessarily included only two filled locations. To balance the design we consequently omitted the Bear Island control (C3) from March analyses, resulting in two locations within treatment. Due to the intrinsic spatial variability of infaunal populations, data were transformed to ranks prior to analysis. Where location proved significant ($p < 0.05$), hypotheses about the effect of timing of nourishment on impact were tested using post-hoc Student–Newman–Keuls (SNK) contrasts.

The beyond BACI analyses included the spatial factors location (3 levels) and site (2 levels, nested within location), as well as the orthogonal temporal factor, year (two levels: pre-[1998] vs. post-[2002] nourishment), and time (2 levels, nested within year). To enable

asymmetrical tests of impact, interactions between location and temporal terms were partitioned into sources of spatial variability (see Underwood, 1993, 1994).

The experimental unit for post-nourishment ANO-VAs was the transect total that weighted zone-specific density by the width of the zone along that transect (Brazeiro and Defeo, 1996). We deemed this to be the most appropriate method of determining impact given that separate analyses of beach width and faunal abundance by zone indicated that impacts of nourishment resulted from a combination of changing habitat area and changing density of fauna. For infauna, only the three lowest elevations (mid intertidal, swash zone, and shallow subtidal) were included to form the sum because the two higher zones proved almost invariably empty. Ghost crab analyses were conducted on the sum total of active burrows for the complete transect as well as for the separate portions on the flat beach and the dune face. Because zone widths were not measured prior to filling, weighting of infaunal densities by transect width was not possible for 1998 data. Consequently, beyond BACI analyses utilizing pre-fill densities of invertebrates used the average densities of taxa recorded for each transect across zones 3–5 as replicates. Abundances per transect of infauna were sqrt $(x+1)$ transformed and counts of shorebirds and ghost crab burrows ln $(x+1)$ transformed prior to ANOVA. Cochran's test was conducted on each data set following transformation to evaluate the ANOVA assumption of homogeneity of variances.

A single set of ANOVAs, utilizing only post-fill data, tested for differences by month in the abundance of feeding shorebirds between control and filled locations. The bimonthly analyses, which had two orthogonal factors day (2 levels, random) and treatment (2 levels: control vs. filled), utilized locations as replicates. In response to omitting Bear Island from analysis because day was not replicated there, it was necessary to randomly exclude a filled location (Trinity Center, F3) from analyses, resulting in a balanced design ($n=2$). Use of locations as replicates was justified by ANOVA results indicating no effect of timing of nourishment on other faunal components.

No geostatistical analyses like kriging were conducted on biotic variables (as shown valuable even for density estimation by Defeo and Rueda, 2002) because patterns were so dramatic that the simpler approaches sufficed. We did apply a multivariate analytic approach to the sedimentology, using non-metric multidimensional scaling (nMDS; Field et al., 1982) to generate two sets of two-dimensional ordinations of the location averages of the five sediment fractions (silts/clays, coarse-, medium- and fine-grained sands and gravel). Separate nMDS ordina-

tions were done for each elevation zone and were based on Euclidean distances, calculated from untransformed data. One set of ordinations considered only spatial differences in post-fill data. The second set, which used only locations sampled in both 1998 and 2002, incorporated a temporal factor in addition to the spatial one. Percent surface cover by shell (arc-sine transformed) was compared between control and filled areas using three-factor nested
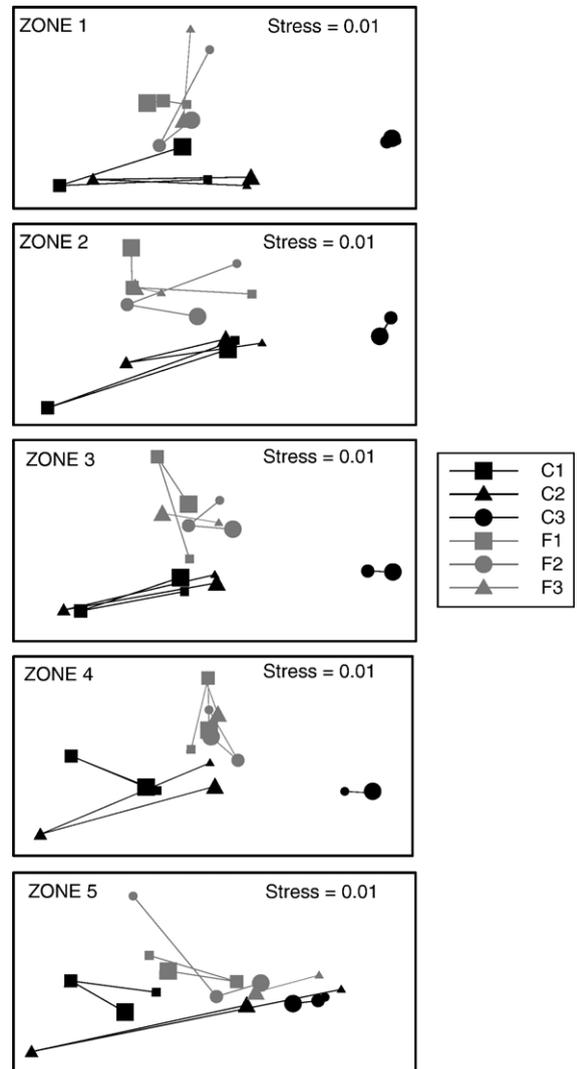

Fig. 2. nMDS plots showing average ($n=6$) granulometry of sediments following completion of beach nourishment in 2002, at locations inside (F1 = filled in December 2001; F2 = filled in February 2002; F3 = filled in April 2002) and outside (C1, C2, C3) the fill area. Zone 1 = supratidal; zone 2 = high intertidal; zone 3 = mid intertidal; zone 4 = low intertidal (swash zone); zone 5 = shallow subtidal. Small symbols denote samples collected in March 2002, medium symbols, July 2002, and large symbols, November 2002. Lines connect time series for each location. In March, only the December and February fill treatments had been completed.

ANOVAs, analogous to those used for the analysis of beach infauna.

3. Results

3.1. Beach sedimentology

Despite regulatory "sediment compatibility" requirements, sediment granulometry was grossly altered by beach filling. nMDS of the five sediment fractions (silts/clays, coarse-, medium- and fine-grained sands, and gravel) indicated that within each of the zones not only did filling change sediment granulometry (evidenced in Fig. 2 by the separation of points representing control and filled locations into distinctive and non-overlapping groups), but it also decreased spatial and temporal variability (spread was much less within the cluster of points representing filled locations; Fig. 2). Tracking of
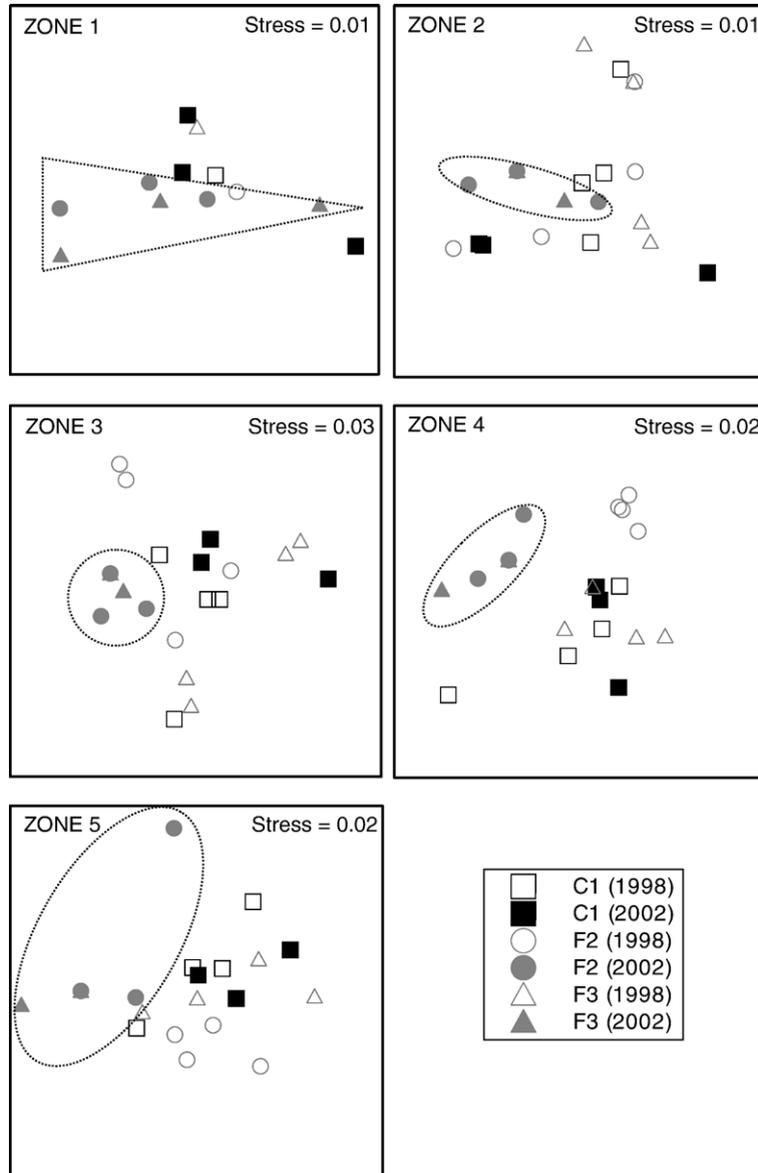

Fig. 3. nMDS plots showing average granulometry of sediments at locations on a control beach (Pierpoint, C1), a beach nourished in February 2002 (Dogwood Circle, F2) and a beach nourished in April 2002 (Trinity Center, F3), before (1998, open symbols) and after (2002, closed symbols) beach nourishment. Sampling was done on 4 occasions in 1998 prior to and 3 in 2002 after filling. On each 1998 sampling date, 2 replicate transects were used to calculate location averages. In 2002, 6 replicate transects were measured at each location, at each time. Dotted lines enclose data points for filled sites following nourishment. Zones are as defined for Fig. 2.

temporal trajectories of change in sediment composition at each location across the three post-nourishment dates of sampling did not reveal any consistent pattern of convergence between filled and control beaches that would indicate recovery (Fig. 2). A second set of nMDS plots (Fig. 3) utilizing pre- and post-fill data from the subset of locations sampled in both 1998 and 2002 confirmed that post-fill differences in the granulometry of control and filled locations was a consequence of nourishment, not pre-existing differences among locations. Within each of the five zones, samples collected from nourished beaches in 2002 were generally more similar to one another than to any of the samples collected in 1998 or samples collected in 2002 from control beaches (Fig. 3).

Multivariate changes in the sediment granulometry of filled locations following beach nourishment appear to be driven by increases in the percent contribution of the two coarsest sediment fractions (Table 2). The fill differed from the native beach in having far more gravel-sized and coarse-sand sized particles, virtually all of which were observed in the sieves and on the beach to be shell hash. Within the five zones sampled, the percent contribution of gravel to total sediment weight was up to 13 times greater and the percent contribution of coarse sand nine times greater at filled than control locations. The proportionate increases in the two coarsest fractions corresponded to reductions in fine- and/or medium sand contributions at filled beaches (varying between high elevations 1–2 and low elevations 3–5; Table 2). Silts and clays constituted a greater proportion of the sedi-

ment size distribution by weight at filled than at control sites. At filled locations silts and clays accounted for 0.6–1.1% of the total weight of sediment samples, as compared to 0.3–0.6% at control locations (Table 2).

Quantification of percent shell cover in July 2002 demonstrated enhanced shell armoring (cover of the substrate surface by shell) within zone 4 (swash) of filled beaches (ANOVA, $F_{1,4}=45.07$, $p=0.003$). Within zone 4, the percent shell cover on filled beaches ($50.0\pm$ [1 SE] 2.8%, $n=180$) was six times greater than at controls ($8.0\pm1.2\%$, $n=180$). Although within zone 3 (mid-intertidal), percent shell cover was also greater on filled (mean$=25.0\pm2.7\%$, $n=180$) than control beaches ($5.9\pm0.7\%$, $n=180$), this pattern was not statistically significant (ANOVA $F_{1,4}=3.53$, $p=0.134$) because of large spatial variation at the scale of sites ($F_{6,348}=7.67$, $p=0.000$).

3.2. Beach macroinvertebrates

Differences in abundances of benthic macroinfauna between nourished and control beaches in 2002 after the beach filling were dramatic, although variable among taxa (Fig. 4). Because of its body size and density *Donax* spp. comprised the vast majority of the infaunal biomass (unpublished data) and exhibited much lower abundances on filled beaches, approaching convergence only by November, when abundances on control beaches had fallen toward their winter minimum (Fig. 4). In the first three months of sampling, ANOVA revealed that the average abundance of *Donax* spp. per running m of shoreline was

Table 2

Mean (±1 S.E.) percent contribution of size fractions to total sediment weight within each of five beach zones surveyed on three dates (March, July, November) in 2002, after completion of beach nourishment, outside (control) and inside (filled) the area of filling

Fraction	Zone 1		Zone 2		Zones 1–2 (average)	
	Control	Filled	Control	Filled	Control	Filled
Gravel	0.7 (0.2)	9.9 (1.3)	0.2 (0.1)	3.7 (0.7)	0.5 (0.1)	7.1 (1.1)
Coarse sand	4.1 (0.8)	19.0 (0.9)	1.4 (0.3)	13.2 (1.1)	2.8 (0.7)	16.2 (1.1)
Medium sand	36.6 (3.8)	38.6 (1.7)	33.2 (4.1)	45.5 (1.7)	36.2 (4.6)	41.5 (1.9)
Fine sand	58.0 (4.3)	31.5 (1.1)	64.7 (4.2)	36.9 (2.2)	60.0 (5.0)	34.4 (1.8)
Silt/clay	0.6 (0.1)	1.1 (0.1)	0.5 (0.1)	0.7 (0.1)	0.5 (0.1)	0.9 (0.1)

Fraction	Zone 3		Zone 4		Zone 5		Zones 3–5 (average)	
	Control	Filled	Control	Filled	Control	Filled	Control	Filled
Gravel	1.0 (0.2)	13.1 (1.3)	2.6 (0.4)	14.3 (1.1)	3.2 (0.6)	8.8 (1.1)	2.9 (0.6)	11.6 (0.9)
Coarse sand	8.9 (1.0)	22.8 (1.2)	15.4 (1.4)	23.6 (1.1)	13.1 (1.3)	19.6 (1.7)	13.4 (1.2)	21.5 (1.1)
Medium sand	43.5 (3.3)	33.7 (1.3)	42.4 (2.4)	28.9 (1.2)	38.6 (2.6)	27.8 (1.2)	41.5 (2.6)	30.6 (1.1)
Fine sand	46.3 (4.0)	30.0 (1.4)	39.2 (3.5)	32.3 (1.8)	44.7 (3.7)	43.1 (2.7)	41.9 (3.5)	35.7 (1.9)
Silt/clay	0.3 (0.1)	0.6 (0.0)	0.4 (0.1)	0.8 (0.1)	0.4 (0.0)	0.6 (0.1)	0.4 (0.0)	0.6 (0.1)

Averages were calculated across all three times and across each of the three locations within each zone, with 6 replicate transects per location and sampling date. Zone 1 = supratidal; zone 2 = high intertidal; zone 3 = mid intertidal; zone 4 = low intertidal (swash zone); zone 5 = shallow subtidal. Sediment fractions are defined in Section 2.1.
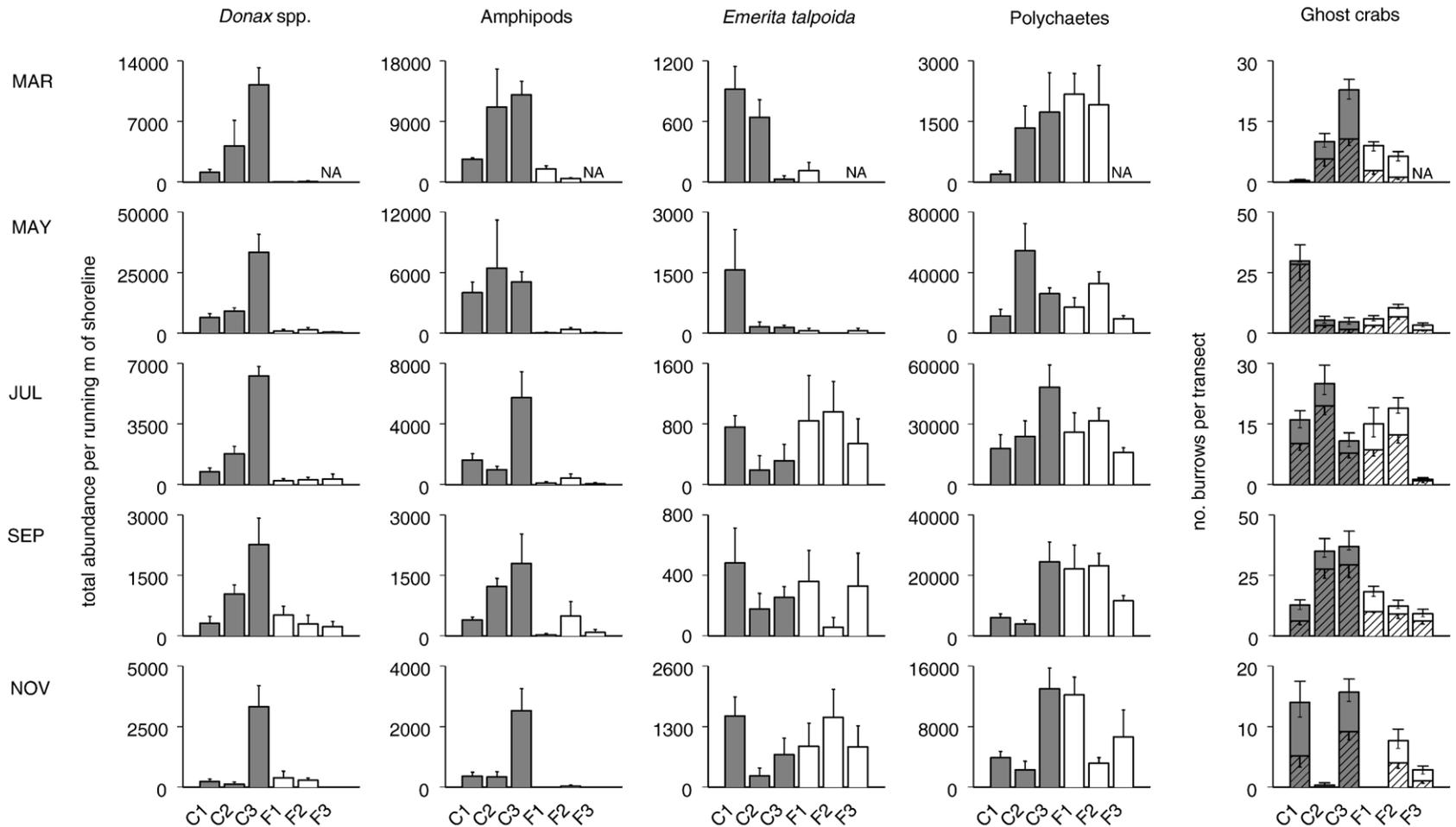
Fig. 4. Mean (±1 S.E.) abundances of macroinvertebrates per linear m of shoreline inside (grey) and outside (white) the fill area in 2002, after completion of beach nourishment. C1, C2, C3 = control locations; F1 = filled in December 2001; F2 = filled in February 2002; F3 = filled in April 2002. $n=6$. In March, only the December and February fill treatments had been completed at F3, so NA indicates datum unavailable. Burrow counts for ghost crabs are partitioned into those on the flat beach (patterned bars) and those on the dune face (plain bars).

Table 3
Summary of P-values from three-factor nested ANOVAs and post-hoc Student–Newman–Keuls (SNK) comparisons testing for spatial variation in the average abundance of each intertidal macroinfaunal taxon following beach nourishment of Bogue Banks

Date	Tr	Lo(Tr)	Si(Lo(Tr))	SNK tests	
Donax spp.					
Mar [a]	**0.005**	0.857	**0.048**		Tr: C>F
May	**0.006**	**0.009** [b]		Lo(Tr): C3>C1=C2; F1=F2=F3	Tr: C>F
Jul [c]	**0.017**	0.176	0.098		Tr: C>F
Sep	0.147	**0.003** [b]		Lo(Tr): C3>C1=C2; F1=F2=F3	
Nov	0.456	**0.000** [b]		Lo(Tr): C3>C1=C2; F1=F2>F3	
Amphipods					
Mar [a]	0.085	0.093	0.219		
May	**0.002**	0.062 [b]			Tr: C>F
Jul [c]	**0.009**	**0.008** [b]		Lo(Tr): C3>C1=C2; F1=F2=F3	Tr: C>F
Sep	**0.013**	0.087 [b]			Tr: C>F
Nov	0.094	**0.001** [b]		Lo(Tr): C3>C1=C2; F1=F2>F3	
Emerita talpoida					
Mar [a, c]	**0.036**	0.604	**0.026**		Tr: C>F
May	0.065	0.128 [b]			
Jul	0.418	0.106 [b]			
Sep	0.203	0.698	**0.011**		
Nov	0.651	0.574	**0.003**		
Polychaetes					
Mar [a]	0.227	0.310	0.091		
May	0.604	**0.000**		Lo(Tr): C2>C3>C1; F2>F1=F3	
Jul	0.820	0.246	**0.036**		
Sep	0.221	**0.000** [b]		Lo(Tr): C3>C1=C2; F1=F2=F3	
Nov	0.841	**0.000** [b]		Lo(Tr): C3>C1=C2; F1>F2=F3	

Total abundances of fauna were calculated by multiplying the width of each elevation zone times the faunal density and summing for each transect sampled. Tr = treatment (2 levels: C = control, F = filled), Lo(Tr) = location (3 levels: C1, C2, C3 within control; F1 [filled Dec 2001], F2 [filled Feb 2002], F3 [filled Apr 2002] within filled), Si(Lo(Tr)) = site (2 levels; random). $n=3$. Bold font indicates terms significant at $\alpha=0.05$. Data were converted to ranks prior to analysis to satisfy the assumption for ANOVA of homogeneity of variances.

[a] Because beach filling at Trinity Center (F3) was not completed until April 2002, this location was not sampled in March. To balance the ANOVA, the control location Bear Island (B3) was also omitted from March analyses, leaving 2 locations nested within each zone.

[b] MS_{Lo}/MS_{Si} was not significant at $\alpha=0.25$, allowing MS_{Lo} to be pooled with MS_{Si} (Underwood, 1997).

[c] Variances remained heterogeneous even after transformation. Analyses were done on untransformed data anyway because ANOVA is relatively robust to heterogeneous variances, but because of elevated risk of Type I error, one may wish to consider results significant only at $\alpha=0.01$.

significantly greater on the undisturbed control beaches (Table 3). Amphipod abundance (all haustoriids) exhibited a similar pattern of lower counts on filled beaches without a suggestion of convergence even as abundances on control beaches progressively declined to a low in November (Fig. 4). The differences among beaches in amphipod abundance per running m of shoreline were statistically significant in three of the five sampling months and marginally significant ($0.05 < p < 0.10$) in the other two (Table 3). Abundances of both *Donax* spp. and amphipods were generally greater on Bear Island (where sedimentology also diverged: Fig. 2) than on the other two control sites on Bogue Banks (Table 3; Fig. 4). Recalculation of the average percent differences in abundance across all sampling months between filled sites and control sites but excluding Bear Island resulted in 85%

fewer *Donax* spp., as compared to 93% fewer with Bear Island included, and 89% fewer amphipods, as opposed to 91% with Bear Island included.

The two other taxa of benthic intertidal infauna exhibited responses to filling that differed from those of *Donax* spp. and amphipods. The mole crab, *Emerita talpoida*, displayed significantly lower abundances on filled beaches only in the first post-fill sampling month (March: Table 3), although abundances remained greatly depressed on fill beaches in May (Fig. 4) and the pattern was marginally significant (Table 3). Recovery of the mole crab was evident from July onwards and its abundance reached annual highs by November on both filled and control beaches (Fig. 4). The final taxon of numerical importance on these beaches, the polychaetes, dominated by *Scolelepis squamata*, demonstrated

almost co-incident mean abundances at control and filled locations over the entire 2002 sampling period (Fig. 4) and accordingly no hint of a significant effect of filling (Table 3).

Every case of significantly lower mean abundance of a macroinfaunal taxon on filled beaches was comprised of contributions from reductions in both habitat area and organism density per unit area. In all instances, however, the density reduction was the greater contributor (26–100% reduction at filled beaches for *Donax* spp., 58–100% for amphipods, and 89–97% for *Emerita talpoida*). Across all months, the combined width of the occupied habitat area, zones 3–5, averaged 14–29% less at filled locations than at control beaches.

In contrast to differences in intertidal macroinfaunal abundances between control and nourished beaches, differences among locations that were filled in different months were small, variable, and inconsistent with the hypothesis that filling in spring (April) would depress biotic recovery rates (Table 3, Fig. 4). Whereas ANOVAs indicated a significant location effect on *Donax* spp. at three and amphipods at two of the five sampling dates, SNKs showed that these patterns were primarily a consequence of differences among control locations. Neither taxon exhibited a location effect in May, the first sampling month after all treated locations had been filled and thus when depressed recovery at F3 would be expected to be most serious. Although in

Table 4

Summaries of asymmetrical analyses comparing spatial variation in the density of macroinfauna and ghost crab burrows (using an unweighted average across zones) between filled (F) and control (C) beaches

Source	df	*Donax* spp.			Amphipods			*Emerita talpoida*			Polychaetes		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Yr	1	316.6			926.5			2.58			37.4		
Ti(Yr)	2	39.8			96.6			3.66			33.7		
Lo	2	6.9			5.8			1.09			9.7		
Si(Lo)	3	9.9			3.6			0.65			12.4		
Yr×Lo	2	11.0			6.8			1.04			2.6		
C vs. F	1	17.3	4.18	0.290	13.6	27276.40	**0.004**	0.55	0.36	0.655	3.7	2.44	0.363
Among F	1	4.7			0.0			1.52			1.5		
Yr×Si(Lo)	3	9.0			2.9			0.19			9.0		
Ti(Yr)×Lo	4	4.0			28.2			0.38			46.9		
C vs. F	2	7.9	37.33	**0.026**	1.9	0.03	0.966	0.52	2.27	0.373	93.6	406.87	**0.002**
Among F	2	0.2			54.5			0.23			0.2		
Ti(Yr)×Si(Lo)	6	3.7			5.1			0.20			17.7		
Res	48	7.2			3.4			0.57			7.1		
Cochran's test		C=0.50 (P<0.01)			C=0.23 (NS)			C=0.26 (P<0.05)			C=0.19 (NS)		

Source	df	Ghost crabs [a]		
		MS	F	P
Yr	1	0.02		
Ti(Yr)	2	0.15		
Lo	2	9.03		
Yr×Lo	2	6.80		
C vs. F	1	1.20	0.10	0.808
Among F	1	12.41		
Ti(Yr)×Lo	4	5.14		
C vs. F	2	2.57	0.33	0.750
Among F	2	7.71		
Res	24	0.43		
Cochran's test		C=0.55 (P<0.01)		

Yr = year (2 levels: 1998 [before nourishment], 2002 [after nourishment]), Ti(Yr) = time (2 levels; random), Lo = location (3 levels: C1 = control, F2 = nourished in February 2002, F3 = nourished in April 2002), Si(Lo) = site (2 levels; random). $n=3$. Bold font indicates interpretable terms significant at $\alpha=0.05$.
Data were sqrt $(x+1)$ transformed prior to analysis.
[a] The factor Si(Lo) was omitted from analyses on ghost crabs because in 1998 this taxon was sampled at only one site per location.
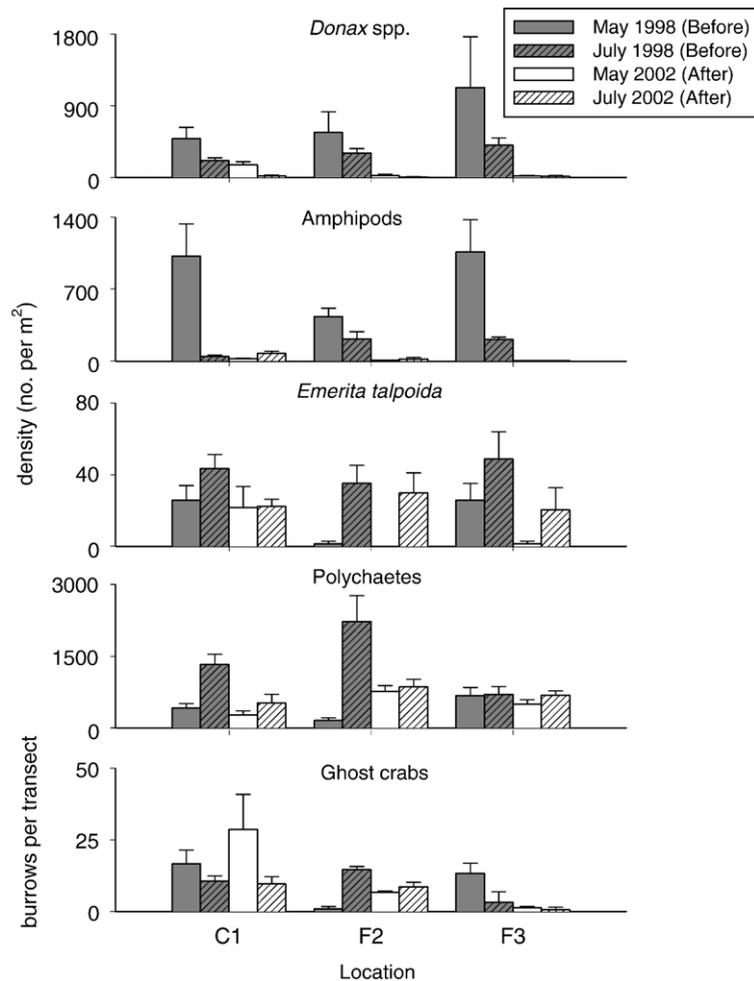
Fig. 5. Mean (+1 S.E.) densities per transect of macroinvertebrates in 1998, before beach filling, and 2002, after beach filling, outside (C1) and inside (F2, F3) the fill area. $n=6$.

November *Donax* spp. and amphipod abundances were lower at F3 than at F1 and F2, this pattern followed a temporal decrease in abundance at F3 between September and November and not greater recovery at F1 and F2, so is inconsistent with the hypothesis that springtime filling suppresses recovery. Observed differences among locations in the abundance of polychaetes, evident at three sampling months, were inconsistent in direction (Table 3). Although polychaetes did exhibit a pattern of lowest abundance among all filled locations at F3 from May through September (Fig. 4) and may reflect negative consequences of filling in spring, the difference was not statistically significant in any month (Table 3). *Emerita talpoida* did not display significant location effects in any of the five months (Table 3).

Our beyond BACI contrasts, done to control simultaneously for both natural spatial and temporal variation, indicated that depressed densities of amphipods on filled

beaches following the 2001–2002 nourishment cannot be attributed to pre-existing differences among these beaches (Table 4, Fig. 5). Asymmetrical analyses revealed that the magnitude of change from before to after filling varied more between control and filled treatments than between the two filled locations that were sampled in both years. Although a similar pattern of greater temporal change at filled than control beaches was also evident for *Donax* spp. (Fig. 5), the difference was not significant at the scale of years because of low power and high seasonal variability at the control location (Table 4). Interactions between treatment and year were similarly absent from the analysis of *Emerita talpoida* and polychaete densities (Table 4). The BACI pattern of differences in *Emerita talpoida* density do imply a possible, but statistically undetected, reduction from filling in May relative to pre-fill differences among beaches (Fig. 5) but no similar pattern in July, which
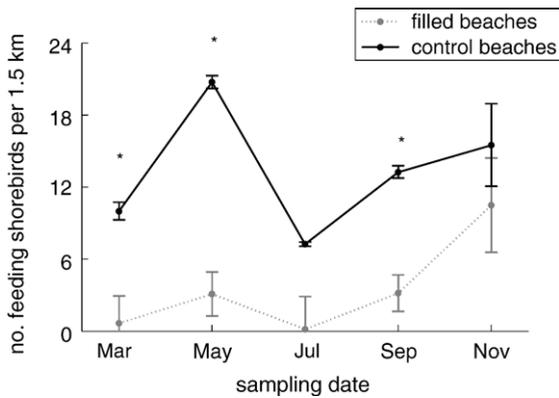
Fig. 6. Mean (±1 S.E.) numbers of foraging shorebirds per 1.5-km stretch of shoreline in 2002, after completion of beach nourishment, at multiple locations inside (filled) and outside (control) the fill area. Symbols indicate results of ANOVAs comparing the total counts of foraging birds between stretches of filled and control beaches. *$P<0.05$ in test of fill impact. $n=2$ locations, each sampled on two dates for the control treatment. $n=3$ locations, each sampled on three dates for the filled treatment.

matches results of our spatial analyses of 2002 data only, which showed a marginally significant depression on filled beaches in May but full recovery of *Emerita talpoida* by July (Fig. 4, Table 3). Thus, except for the inability to detect the larger temporal reductions in density of *Donax* spp. on filled beaches than on the control beach as an impact of filling, the beyond BACI testing confirmed results of post-fill spatial analyses.

3.3. Predators — ghost crabs and shorebirds

Our ability to detect impacts of filling varied between the two types of predators, ghost crabs and shorebirds. Despite the 90–113% greater width on filled beaches of the elevation zone most abundantly occupied by ghost crab burrows, the high beach zone 1, tremendous spatial variation at the level of both location and site within location dominated results of our nested ANOVAs on ghost crab burrow counts along vertical transects in 2002 (statistical results not shown). In two of five sampling months, abundances of ghost crab burrows on the dune face varied significantly among locations and, on the flat beach, variability at this scale was detected in all five months. Both control and filled locations contributed to this variability, which was temporally inconsistent in direction (Fig. 4) and precluded any effect of filling from being detected, even when pre-fill data were incorporated in beyond BACI analyses (Table 4). Variation between sites was also significant or marginally significant in nine of the fifteen nested ANOVAs done on ghost crab burrow counts (five months of counts for

flat beach, dune face, and also total counts). Despite greater areas of high beach habitat at filled locations, total burrow counts on vertical transects across the flat beach were on average up to twice as high on control beaches, with the largest, but still non-significant, differences in September after recruitment (evidenced by large numbers of small-diameter burrow openings) had increased abundances (Fig. 4).

Feeding shorebirds exhibited large and readily detectable reductions of use of filled beaches, with counts up to seven times greater on control than filled beaches in 2002 (Fig. 6). The dramatic depression of abundance of feeding shorebirds persisted from March through September, but by November 2002, seven to twelve months after the completion of nourishment, the difference between counts on filled and controlled beaches was no longer statistically significant and convergence was nearly complete (Fig. 6). ANOVAS demonstrated no significant or marginally significant effect of day or day × treatment interaction for any month, so the treatment effects remained constant over the two days of sampling within each sampling period. Shorebird counts averaged over all months of the entire 2002 sampling were comprised of sanderling (75%), willet (10%), ruddy turnstone (5%), red knot (5%), and five rarer species.

4. Discussion

Because intertidal sandy beaches frequently experience erosion, transport, and deposition of the sediments that constitute the habitat for benthic invertebrates, these organisms are often assumed to be adapted to disturbances that mobilize sediments (NRC, 1995). A limited literature indeed supports this presumption of adaptation to sediment dynamics by showing little change in abundances of sandy beach macroinfauna after intense storms (e.g., Saloman and Naughton, 1977). Nevertheless, experimental studies and field observations after natural sedimentation events (Peterson, 1985; Peterson and Black, 1988; Lohrer et al., 2004) demonstrate that sedimentation can cause high mortality of infaunal invertebrates on intertidal sand flats of coastal lagoons. Consequently, it is reasonable to conclude that sandy beach invertebrates can also suffer mass mortality from beach filling that exceeds some threshold intensity. Such an immediate effect of sedimentation represents a "pulse disturbance" (Bender et al., 1984). Presumably magnitudes of impacts of such pulse disturbances on sandy beach invertebrates would depend mostly on depth of sediment burial per unit time but also on sediment type, which is known to affect burrowing rates (Alexander et al., 1993) and, if too fine, cause suffocation (Peterson, 1985; Lohrer et al., 2004).

Effects of such a pulse disturbance are evident in our study for *Donax* spp., amphipods, and *Emerita talpoida* but not for polychaetes because of their seasonal absence until after March.

Recovery of the sandy beach invertebrates from this mass mortality event is dependent upon the potential for recolonization by reproduction and/or immigration and probably also suitability of the sedimentary habitat. Benthic infaunal invertebrates are known to be highly sensitive to sediment size and associated properties (e.g., Gray, 1974). Consequently, even under conditions of high potential rates of recolonization, persistently large deviation away from the natural sedimentology could depress recovery, acting as an ongoing "press disturbance" (Bender et al., 1984).

Absent an experimental test of recovery as a function of composition of fill, isolating the press disturbance component of beach filling impacts is a challenge. Several lines of evidence imply that it played an important role in inhibiting full recovery of the benthic community during the post-fill year examined in our study. First, the coarse, shelly sediments, which were incompatible with those naturally occurring on Bogue Banks beaches, persisted throughout the entire study period. Second, if a press disturbance were involved, one would expect it to be taxon-specific as a function of variable biotic preferences for sediment grade. In our study, *Emerita talpoida* abundance recovered rapidly within months, whereas the numerical and biomass dominant, *Donax* spp., and amphipods failed even to initiate recovery. Despite virtual convergence in abundance between filled and control beaches for *Donax* spp. and amphipods by November, this pattern was driven by seasonal declines toward winter minima on control beaches and cannot be assumed to imply recovery on fill. *Emerita talpoida* is known to prefer relatively coarse sand sediments (Bowman and Dolan, 1985), whereas the congeneric *Donax serra* has been virtually eliminated by persistent coarsening of sediments on a Namibian beach from deposition of diamond mine tailings (McLachlan, 1996) and burrowing rates of *Donax* spp. and other bivalves are slowed by elevated coarse components of sediments, including shell hash (Alexander et al., 1993; Manning, 2003). Thus, the contrasting patterns of recovery of *Emerita talpoida* and *Donax* spp. on Bogue Banks seem best explained by the persistent displacement of fine and medium quartz sands by shell hash in coarse sand and gravel size classes (King, 2004).

How long the fill effects on *Donax* spp. and amphipods will last is unclear from our sampling of just a single warm season and from the literature on past responses of *Donax*

spp. and other infaunal invertebrates to beach nourishment. Four previous studies where beach fill appears, based on limited information, to match natural granulometry and mineralogy have demonstrated limited initial impacts on macroinvertebrate abundances and recovery within days to weeks (Hayden and Dolan, 1974; Naqvi and Pullen, 1982; Gorzelany and Nelson, 1987; Burlas et al., 2001). In contrast, several other studies have shown large depressions of macroinfaunal densities induced by deposition of sediments in which the fine fraction composed of silts and clays was unnaturally elevated (e.g., Reilly and Bellis, 1983; Rakocinski et al., 1996; Peterson et al., 2000; Manning, 2003; Versar, 2003). Although none of these studies lasted long enough to document complete recovery of *Donax* spp. and other invertebrates, sampling extended in some cases throughout the warm season, thereby indicating effects lasting as long as on Bogue Banks. Assuming that large modifications to sedimentology represent a press disturbance that inhibits recovery of the benthic infauna, the duration of the impact would be expected to last as long as the sedimentological deviation persists. Nelson (1993) concludes from his review that enhancing the fine fraction of sediments during beach nourishment retards recovery. McLachlan (1996) presumes that the coarse fill on the Elizabeth Bay beach in Namibia will last indefinitely: coarse sediments are less readily eroded and transported off the beach than finer materials and often become concentrated in the swash and shore break zones (King, 2004), where benthic invertebrate abundances should be the highest.

The biotic potential for recolonization also must influence recovery rates after beach filling. Those studies that have failed to demonstrate substantial and long-lasting impacts of beach filling on the benthic invertebrates (Hayden and Dolan, 1974; Naqvi and Pullen, 1982; Gorzelany and Nelson, 1987; Burlas et al., 2001) appear not only to have used more compatible sediments but also to have been done on beaches characterized by high rates of long-shore sediment transport. In contrast, examples of large and long-lasting impacts (Reilly and Bellis, 1983; Rakocinski et al., 1996; Peterson et al., 2000; Manning, 2003; Versar, 2003) come from sites of low long-shore transport. High long-shore transport not only carries sediments and so has the capacity to dilute and disperse any unnatural sedimentological signal but also can enhance immigration of benthic invertebrates. Each of these effects implies a potential to speed up biotic recovery relative to more physically quiescent environments. A likely explanation for the failure of haustoriid amphipods to initiate recovery during the first warm season on Bogue Banks is their lack of pelagic larvae to disperse propagules combined with the low long-shore

transport, which can limit immigration. This explanation implies a serious consequence of disturbing such a long stretch of beach, 10.8 km, in that cumulative impacts of multiple contiguous km of disturbance would be greater than the sum of impacts of filling multiple isolated km, where nearby sources of colonists could initiate recovery.

Concerned by potential interference with reproduction through burial of new recruits or through insufficient time since filling to render the sediments biogeochemically attractive to larvae, we designed our study to include a test of whether the timing of the fill disturbance affects the rapidity of recovery. A contrast of beaches filled in early December, February, and April showed no detectable difference in benthic macroinfaunal recovery. This result comes as a surprise, but it may be best understood by recognition that neither of the two taxa that experienced the largest impact of the fill disturbance (*Donax* spp. and amphipods) had even initiated recovery by the final sampling period in November, perhaps because of the ongoing press disturbance by unnaturally coarse substrate. Only *Emerita talpoida* initiated (and completed) recovery during the year of sampling and its recolonization occurred sometime between May and July, after the last (early April) date of filling (consistent with seasonality shown by Diaz, 1980). Ghost crabs recruited through reproduction between July and September, long after the last fill date, and so the possible late summer depression in their recruitment on filled beaches was not influenced by timing of filling. Polychaete worms, largely the spionid *Scolelepis squamata*, exhibited a pattern of seasonal increase in abundance after March with an autumn decline that did not differ between filled and control beaches. Polychaete abundances on the beach filled in early April did lag for several months abundances on the two beaches filled in winter months, suggesting a possible suppression of recruitment by spring filling, but low power rendered this pattern nonsignificant. Consequently, extending beach filling into spring may slow benthic recovery rates, but our study of responses to sedimentologically incompatible sediments did not reveal any recovery for two most affected taxa against which to test this hypothesis.

Ours is the first study to assess and document impacts of beach nourishment on intertidal habitat quality propagating upwards to a higher trophic level, namely shorebirds feeding on benthic invertebrates. The shorebird counts were dominated by one species, the sanderling, although willets and ruddy turnstones also made meaningful contributions. Sanderlings foraged mostly by probing the sediments, supplemented by picking up surface items in the drift. Their greatly depressed use of filled beaches implies reduction in habitat value after filling, which has at least three plausible explanations. First, the foraging area of intertidal–shallow subtidal habitat was reduced by 14–29% on filled beaches. Second, densities of the prey taxon of greatest abundance and biomass, *Donax* spp., were dramatically depressed. Infaunal prey density has frequently been shown to affect habitat use in shorebirds (e.g., Goss-Custard et al., 1991). Third, presence of coarse shell material armored the substrate surface against probing bills, further reducing foraging habitat by 33%, and probably also inhibited manipulation of prey when encountered by a bill, as shown experimentally to be an important factor in shorebird feeding by Quammen (1982). Shorebird use of filled beaches increased by November almost matching that on control beaches, despite unabated persistence of large sedimentological modifications, but consistent with near convergence of filled and control beaches in abundances of large infaunal prey, when the seasonal crash of *Donax* spp. everywhere had left a recovered *Emerita talpoida* as the only abundant large infaunal prey at similar densities on filled and control beaches. Consequently, changes in either prey density per unit area or abundance per running length of shoreline appears to represent the most parsimonious explanation of patterns, including the fill-related decline, in shorebird usage of beach habitat.

By extension, the degradation of habitat value probably also affected surf fishes, which use the same prey invertebrates from the same intertidal–shallow subtidal habitat of such high productivity (McLachlan, 2001). For example, *Donax* spp. is targeted not only by feeding shorebirds, like sanderlings (Loesch, 1957) and ruddy turnstones (Schneider, 1982), but also surf fishes, like Florida pompano and flounders (Leber, 1982). Manning (2003) demonstrated experimentally that feeding on *Donax* spp. by Florida pompano is inhibited by shell augmentation in surface sediments because the fish are confused by and often ingest surface shell instead of living clams. Amphipods and other small crustaceans represent the sole prey for many postlarval and small juvenile fishes, including juvenile pompano (Bellinger and Avault, 1971), which recruit in spring to the surf zone habitat. Based on our study of habitat function of the sandy beach using beach filling as a large-scale experiment, it seems clear that permitting of beach nourishment projects should demand matching sedimentology at both the fine and coarse tails of the size spectrum to minimize habitat degradation and facilitate recovery. However, our inference that rapid biological recoveries appear to have occurred only under application of compatible sediments to beaches with high longshore drift means that these two environmental features seem confounded in present data and need to be isolated

in subsequent tests of determinants of recovery dynamics on sandy beaches.

References

Alexander, R.R., Stanton, R.J., Dodd, J.R., 1993. Influence of sediment grain size on the burrowing of bivalves. Palaios 8, 289–303.

Bellinger, J.W., Avault, J.W., 1971. Food habits of juvenile pompano, *Trachinotus carolinus*, in Louisiana. Trans. Am. Fish. Soc. 100, 486–494.

Bender, E.A., Case, T.J., Gilpin, M.E., 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65, 1–13.

Bowman, M.L., Dolan, R., 1985. The relationship of *Emerita talpoida* to beach characteristics. J. Coast. Res. 1, 151–163.

Brazeiro, A., Defeo, O., 1996. Macroinfauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments. Estuar. Coast. Shelf Sci. 42, 523–536.

Brazeiro, A., Defeo, O., 1999. Effects of harvesting and density-dependence on the demography of sandy beach populations: the yellow clam *Mesodesma mactroides* of Uruguay. Mar. Ecol. Prog. Ser. 182, 127–135.

Brooks, R.M., Brandon, W.A., 1995. Hindcast wave information for the U.S. Atlantic coast: update 1976–1993 with hurricanes. WI Report 33, Waterways Experiment Station, U.S. Army Corps of Engineers, Vicksburg, Mississippi.

Burlas, M., Ray, G.L., Clarke, D., 2001. The New York District's biological monitoring program for the Atlantic coast of New Jersey. Asbury Park to Manasquan Section Beach Erosion Control Project: Final Report. U.S. Army Corps of Engineers, Vicksburg, Mississippi.

Connell, J.H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard Univ. Press, Cambridge, Massachusetts, pp. 460–490.

Dayton, P.K., Oliver, J.S., 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore, K.R., Coull, B.C. (Eds.), Marine Benthic Dynamics. Univ. of South Carolina Press, Columba, pp. 93–120.

Defeo, O., 1998. Testing hypotheses on recruitment, growth and mortality in exploited bivalves: an experimental perspective. Can. Spec. Publ. Fish. Aquat. Sci. 125, 257–264.

Defeo, O., McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. Mar. Ecol. Prog. Ser. 295, 1–20.

Defeo, O., Rueda, M., 2002. Spatial structure, sampling design and abundance estimation in sandy beach macroinfauna: some warnings and new perspectives. Mar. Biol. 140, 1215–1225.

Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations — objective is not always better. Mar. Ecol. Prog. Ser. 96, 93–100.

Diaz, H., 1980. The mole crab *Emerita talpoida* (Say): a case of changing life history pattern. Ecol. Monogr. 50, 437–456.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast. Shelf Sci. 58, 25–40 (Suppl S).

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.

Folk, R.L., 1974. Petrology of Sedimentary Rocks. Hemphill Publishing Company, Austin, Texas.

Goss-Custard, J.D., Warwick, R.M., Kirby, R., McGrorty, S., Clarke, R.T., Pearson, B., Rispin, W.E., Durell, S.E.A.L.D., Rose, R.J., 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. J. Appl. Ecol. 28, 1004–1026.

Gray, J.S., 1974. Animal–sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12, 223–261.

Gorzelany, J., Nelson, W., 1987. The effects of beach replenishment on the benthos of a sub-tropical Florida beach. Mar. Environ. Res. 21, 75–94.

Hayden, B., Dolan, R., 1974. Impact of beach nourishment on distribution of *Emerita talpoida*, the common mole crab. J. Waterw., Harbors Coastal Eng. Div., Am. Soc. Civ. Eng. WW2, 123–133.

James, R.J., Fairweather, P.G., 1996. Spatial variation of interidal macrofauna on a sandy ocean beach in Australia. Estuar. Coast. Shelf Sci. 43, 81–107.

King, S.B., 2004. Sedimentological impacts of a beach nourishment project: Bogue Banks, North Carolina. MS thesis, University of North Carolina, Chapel Hill, North Carolina.

Leber, K.M., 1982. Seasonality of macroinvertebrates on a temperate high wave energy sand beach. Bull. Mar. Sci. 32, 86–98.

Loesch, H.C., 1957. Studies of the ecology of two species of *Donax* on Mustang Island, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 4, 201–227.

Lohrer, A.M., Thrush, S.F., Hewitt, J.E., et al., 2004. Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. Mar. Ecol. Prog. Ser. 273, 121–138.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J., Risser, P.G., 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology 72, 371–412.

Manning, L.M., 2003. Ecology of ocean beaches: the importance of human disturbances and complex biological interactions within a physically rigorous environment. PhD thesis, Univ. of North Carolina, Chapel Hill.

McLachlan, A., 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. Mar. Ecol. Prog. Ser. 131, 205–217.

McLachlan, A., 2001. Coastal beach ecosystem. In: Lewin, R. (Ed.), Encyclopedia of Biodiversity. Academic Press, New York, pp. 741–751.

McLachlan, A., Dorvlo, A., 2005. Global patterns in sandy beach macrobenthic communities. J. Coast. Res. 21, 674–687.

Naqvi, S.M., Pullen, E.J., 1982. Effects of Beach Nourishment and Borrowing on Marine Organisms. Misc. Rep., vol. 82-14. U.S. Army Corps of Engineers, CREC, Springfield, Virginia.

Nelson, W.G., 1993. Beach restoration in the southeastern U.S.: environmental effects and biological monitoring. Ocean Coast. Manag. 19, 157–192.

NRC (National Research Council), 1995. Beach Nourishment and Protection. National Academy Press, Washington, DC.

Peterson, C.H., 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11, 139–153.

Peterson, C.H., Bishop, M.J., 2005. Assessing the environmental impacts of beach nourishment. Bioscience 55, 887–896.

Peterson, C.H., Black, R., 1988. Density-dependent mortality caused by physical stress interacting with biotic history. Am. Nat. 131, 257–270.

Peterson, C.H., Hickerson, D.H.M., Johnson, G.G., 2000. Short-term consequences of nourishment and bulldozing on the dominant large invertebrates of a sandy beach. J. Coast. Res. 16, 368–378.

Quammen, M.L., 1982. Influence of subtle substrate differences on feeding shorebirds on intertidal mudflats. Mar. Biol. 75, 339–343.

Rakocinski, C.F., Heard, R.W., LeCroy, S.E., McLelleand, J.A., Simons, T., 1996. Responses by macrobenthic assemblages to extensive beach restoration at Perdido Key, Florida, USA. J. Coast. Res. 12, 326–353.

Reilly, F.J., Bellis, V.J., 1983. The ecological impact of beach nourishment with dredged materials on the intertidal zone at Bogue Banks, North Carolina. Misc. Rept., vol. 83-3. U.S. Army Engineer Coastal Engineering Res. Center, Fort Belvoir, Virginia.

Saloman, C.H., Naughton, S.P., 1977. Effect of hurricane Eloise on the benthic fauna of Panama City Beach, Florida, USA. Mar. Biol. 42, 357–363.

Schneider, D., 1982. Predation by ruddy turnstones (*Arenaria interpres*) on a polymorphic clam (*Donax variabilis*) at Sanibel Island, Florida. Bull. Mar. Sci. 32, 341–344.

Underwood, A.J., 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Aust. J. Ecol. 18, 99–116.

Underwood, A.J., 1994. On beyond BACI-sampling designs that might reliably detect environmental disturbances. Ecol. Appl. 4, 3–15.

Underwood, A.J., 1997. Experiments in Ecology: their Logical Design and Interpretation using Analysis of Variance. Cambridge University Press, Cambridge, UK.

Valverde, H.R., Trembanis, A.C., Pilkey, O.H., 1999. Summary of beach nourishment episodes on the U.S. east coast barrier islands. J. Coast. Res. 15, 1100–1118.

Versar, 2003. Year 2 Recovery from Impacts of Beach Nourishment on Surf Zone and Nearshore Fish and Benthic Resources on Bald Head Island, Caswell Beach, Oak Island, and Holden Beach, North Carolina: Final Study Findings. U.S. Army Corps of Engineers, Wilmington, North Carolina.

Wolcott, T.G., 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: scavengers or predators? J. Exp. Mar. Biol. Ecol. 31, 67–82.