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Influence of waves and horseshoe crab spawning on beach morphology and sediment grain-size characteristics on a sandy estuarine beach

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ABSTRACT

The effects of wave action and horseshoe crab spawning on the topography and grain-size characteristics on the foreshore of an estuarine sand beach in Delaware Bay, New Jersey, USA were evaluated using data collected over six consecutive high tides. Data were gathered inside and outside a 25 m long exclosure constructed to create a control area free of disturbance by crabs. The density of crabs in the swash zone outside the exclosure was 8·1 organisms m^{-2}. The maximum depth of sediment activation on the upper foreshore where spawning occurred was 0·103 m during periods characterized by low significant wave heights: < 0·08 m. This depth is greater than the depth of activation by waves alone during moderate significant wave heights of 0·16–0·18 m but less than the maximum depth (0·127 m) recorded when spawning occurred during periods of moderate wave heights. Spawning, combined with moderate wave heights, creates a concave upper foreshore that is similar to the type of profile change that occurs during storms, thus lowering the wave-energy threshold for morphological response. Spawning during low wave heights increases the mean grain size and sorting of surface sediments caused by the addition of gravel to the swash. Sedimentological differences are most pronounced on the upper foreshore, and data from this location may be most useful when using grain-size characteristics to interpret the effect of spawning in the sedimentary record. Depths of sediment reworking by horseshoe crabs can be greater than those by subsequent storm waves, so evidence of spawning can be preserved on non-eroding beaches. Greater depth of activation by horseshoe crab spawning than by waves alone, even during moderate-energy conditions, reveals the importance of crab burrowing in releasing eggs to the water column and making them available for shore birds.

Keywords Bioturbation, Delaware Bay, foreshore, gravel, horseshoe crab, sediment activation.

INTRODUCTION

Waves, tides and currents are significant geomorphic agents on sandy estuarine beaches that account for temporal variation in beach morphology and spatial variation in textural properties of sediments on the surface and down to the depth of wave reworking (Rosen, 1980; Sherman *et al.*, 1994; Armbruster *et al.*, 1995). The role of fauna in altering the topography and sediments on beaches is less well documented, but the body of research on their effect in other aquatic environments is increasing (Rhoads, 1967; Graf & Rosenberg, 1997; de Brouwer *et al.*, 2000; de Deckere *et al.*, 2001). Fauna alter sedimentary habitats by mechanically disturbing and transporting sediments, bonding them by chemical secretions, or altering boundary-layer conditions by changing bedform conditions (Rhoads & Stanley, 1965; Nowell *et al.*, 1981; Jumars & Nowell, 1984; Meadows & Tait, 1989; Fries *et al.*, 1999; Statzner *et al.*, 2003). The relative roles of physical and faunal processes differ depending on the amount of wave and current energy, the grain-size characteristics of sediments and species type. On intertidal foreshores, the relative effects of fauna should be greater where the energy of physical processes is lower, and the effects should be more persistent because waves and currents are often insufficient to disturb the surfaces under non-storm conditions. Accordingly, fauna may play a greater role in determining the surface characteristics of sandy estuarine beaches than exposed sandy ocean beaches.

Burrowing is the most common adaptation of species utilizing sandy beaches on exposed coasts or estuaries (Little, 2000). Horseshoe crabs (*Limulus polyphemus*) are one of the largest animals that physically alter sandy estuarine foreshores. Previous research on physical alteration of beach and near-shore environments by horseshoe crabs focused on the magnitude of sediment reworking by burrowing on the offshore bars on the low-tide terrace (Kraeuter & Fegley, 1994) and the depth to which eggs are buried in the sediment matrix on the foreshore (Botton *et al.*, 1992; Smith *et al.*, 2002). The ability of animals to disturb and transport sediment through bioturbation and the impact on beach morphology and textural properties of sediment on the surface of the beach have not been investigated. The large numbers of horseshoe crabs that spawn on some of these beaches, the great depth of sediment reworking relative to wave action and the intensity of spawning during late spring, when large storms are infrequent, imply that these fauna may be an important agent of change in beach and sediment characteristics relative to waves and currents. The purpose of this paper is to compare the effects of waves and horseshoe crabs on the spatial and temporal changes in topography and grain-size characteristics across the foreshore of a sandy estuarine beach to evaluate how the relative effect of these physical and biological processes differ with differences in wave energy and levels of horseshoe crab spawning.

BACKGROUND

The dominant waves on estuarine beaches are generated by local winds blowing across relatively short fetches, and estuarine waves are low in height and short in period. The foreshores of mesotidal and high microtidal estuarine beaches are characterized by a wave-energy gradient that decreases with distance offshore as water level falls (Fig. 1). Wave energy is dissipated in the shallow water on the low-tide terrace during low tide, and the heights of waves breaking on the lower foreshore are negligible, even during strong onshore winds. As a result, wave energy is insufficient to move sand and gravel deposited at the base of the foreshore further baywards. As water levels rise, waves pass over the low-tide terrace and break as plunging waves on the upper foreshore (Nordstrom, 1992).

Estuarine beaches may undergo cut and fill with slope changes on the upper and lower portions of the foreshore or exhibit parallel slope retreat (Fig. 1, inset) depending on the direction

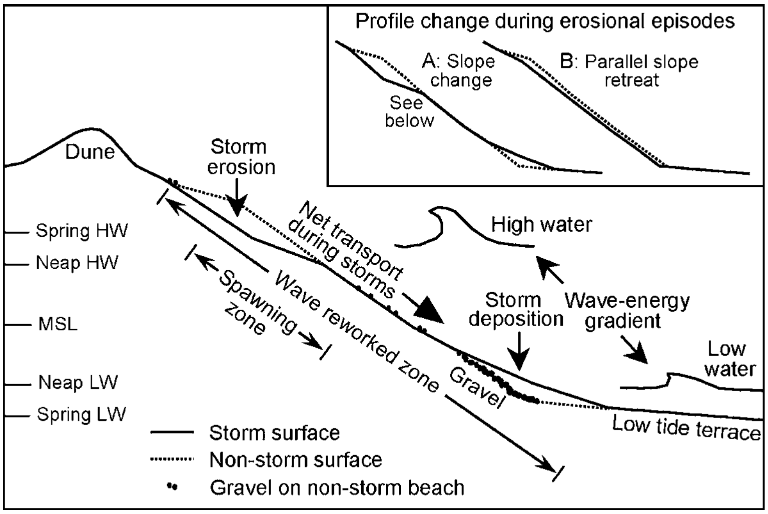

Fig. 1. Changes in beach profile and gravel distribution with changes in wave energy on meso-tidal and high microtidal estuarine beaches.

and magnitude of incident waves and the proximity of sediment sources and sinks (Nordstrom & Jackson, 1992). Cut and fill with slope change occurs during high-energy storm waves that remove sediment from the upper foreshore and deposit it on the lower foreshore, creating a concave-up profile high on the foreshore. Subsequent non-storm conditions then remove sediment from the lower foreshore and deposit it on the upper foreshore restoring the non-storm profile (Jackson, 1995). Parallel slope retreat occurs when breaking waves on the upper foreshore are lower and is enhanced when waves approach at large angles to the beach causing a net loss along the entire width of the foreshore.

Pebbles are often conspicuous on the surfaces of predominantly sandy estuarine beaches, especially during low wave-energy conditions (Nordstrom & Jackson, 1993). The proportion of gravel usually increases with distance downslope. Gravel is stranded just above the low-tide terrace on the falling tide when wave energy diminishes at low water under both storm and non-storm conditions. Finer particles deposited here during storms move onshore by low-energy, accretional waves, leaving gravel as a surface lag low on the beach. A portion of the pebbles is moved up the beach by the swash of low-energy waves or within the beach step in subsequent tidal cycles. Movement of surface pebbles can be enhanced under low-energy waves because there is insufficient energy in the backwash to bury the pebbles; they project into the flow of the swash and have low pivoting angles, increasing the probability of entrainment and movement over the sand particles (Nordstrom & Jackson, 1993).

Relatively high-energy waves (significant heights of 0·5–0·6 m associated with onshore winds $> 12{\cdot}0\ \mathrm{m\ s^{-1}}$) disturb the sediment to depths up to 0·15 m (Jackson & Nordstrom, 1993) and mix the sediments, causing the small amounts of gravel in the upper beach to be inconspicuous in the predominantly sand matrix. During these events, sediment is deposited over the more gravelly surface of the lower foreshore (Fig. 1). Thus, for a given beach, the number of pebbles on the surface of the foreshore is inversely related to wave energy and is at a minimum following high-energy events (Nordstrom & Jackson, 1993). Horseshoe crab spawning alters the effects of these physical processes by creating an additional process for mobilizing sediment, releasing sediment that would normally be buried below the depth of wave reworking and providing roughness elements within the breaking waves and swash.

Delaware Bay is host to the largest spawning horseshoe crab population on the mid-Atlantic coast of the USA. Spawning here occurs during the months of April, May and June, with rates being highest in late May and early June. Horseshoe crabs spawn in the highest densities on estuarine beaches with relatively high-wave energy regimes, but they choose times when incident wave heights are relatively low (Smith *et al.*, 2002). Most spawning occurs during the higher of the unequal diurnal high tides.

Crabs stay on the sub-tidal or intertidal portion of the low-tide terrace during low tide and migrate up the foreshore with the rising tide. They alter the beach substrate directly by crawling to change position and by burrowing to lay eggs and protect themselves during periods of inactivity (Vosatka, 1970). Crabs have their deepest penetration when they burrow into the substrate in the swash zone to bury their eggs. Females lay their eggs to a depth of *ca* 0·2 m (Botton *et al.*, 1992). These depths are greater than the sediment activation depths of *ca* 0·07 m that are associated with significant waves up to *ca* 0·3 m (Jackson & Nordstrom, 1993) that represent storm conditions expected to occur during the spawning months.

Crabs in the swash zone create obstacles to swash uprush and backwash, dissipating the velocity of the uprush but increasing turbulence. After spawning, most crabs migrate back to the low-tide terrace as water levels fall. Some crabs remain partially buried in the foreshore and return to the low-tide terrace at lower stages of the tide or remain stranded until the next high tide. The eggs released during spawning, including those initially buried but exhumed by the next spawning female, are abundant on the surface of the foreshore and provide food for birds that further alter the intertidal surface by walking and digging to excavate eggs (Botton & Harrington, 2003). The foreshore that is exposed at low tide after spawning reveals a hummocky topography above mean sea level, where spawning is most intense, and isolated pits lower on the profile.

Biological processes generally cannot be classified as having a stabilizing or destabilizing effect on sediments without conducting controlled experiments (Grant *et al.*, 1982). This study was undertaken to provide quantitative information on the topographical and sedimentological effects of horseshoe crabs by obtaining comparative data for multiple tidal cycles during the spawning season on a segment of beach subject to burrowing and a control area where crabs were excluded. These data are then compared with the changes in beach profile and sediment characteristics expected on an estuarine beach because of waves and wave-induced currents alone.

STUDY AREA

The field study was conducted on a beach in the Ted Harvey Conservation Area, Delaware on the west side of Delaware Bay (Fig. 2) from 22 to 25 May 2001. Tides are semi-diurnal with a mean range of 1·6 m and a spring range of 1·9 m [National Oceanic and Atmospheric Administration (NOAA), 2002]. Spring tide, associated with the new moon, occurred on 22 May. Dominant waves are generated within Delaware Bay by local winds. Prevailing winds are from the west and blow offshore, but low-pressure centres bring strong onshore winds from the NE and SE. The average number of days in May when onshore wind speeds are greater than 8·0 m $\sec^{-1}$ is 6·25 (Jackson *et al.*, 2002).

The foreshore that is normally reworked by waves during spring tides is *ca* 12 m wide and has a slope of 6·7°. A gently sloping low-tide terrace extends baywards of the base of the foreshore (Fig. 2). The beach is on a low-eroding sandy overwash barrier similar to many other barriers in Delaware Bay (Kraft *et al.*, 1979). A dike was built 1·0 m above the backshore elevation to protect the landward bird refuge from flooding, and the beach was sustained in 1995–1996 using 38,000 m^3 of sand and gravel obtained from an offshore source. Sediments are predominantly quartz and feldspar. The mean grain size of the surface sediment is in the range of medium to coarse sand; granules and pebbles comprise a small sub-population. The locally generated wave climate, morphology of the beach and its sediment sizes are similar to those of beaches in other portions of Delaware Bay and in meso-tidal and high micro-tidal environments in ria-type estuaries on the north-east coast of the USA, such as Raritan Bay and Chesapeake Bay (Nordstrom, 1992).

METHODS

A 25 m long exclosure (Fig. 2) was constructed on the foreshore to create a control area free of disturbance by crabs. A 1·2 m high fence was placed parallel to the break-in slope between the foreshore and low-tide terrace, with cross-shore ends extending 8·0 m landwards. The fence was made of wire mesh with openings of 0·1 m × 0·1 m, to allow waves and sediment to pass freely through it but prevent entry of crabs.

Process and topographic data were collected over six consecutive high tides and five low tides. Topography was measured at 1 m intervals along two parallel cross-shore transects. Line N (Fig. 2) was inside the exclosure and line S outside.

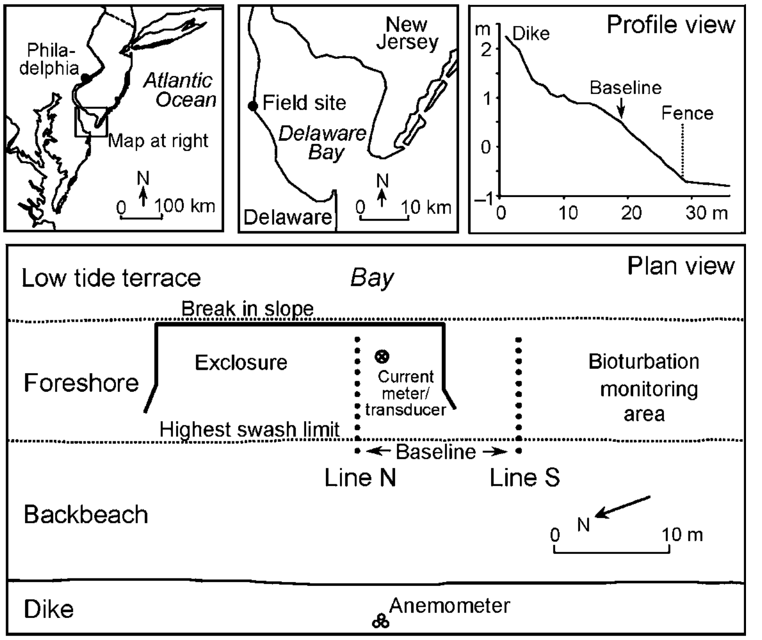

Fig. 2. Study area.

Measurements of surface elevation were taken from the tops of 10 mm diameter steel rods driven into the sand and tied into a common datum using transit surveys. The lines of rods extended from a baseline 1 m landward of the most recent storm wrack line to 1 m landward of the break-in slope between the low-tide terrace and foreshore. The rods enable measurement of changes in sand surface elevation to within 0·5 mm. A loose-fitting washer was placed over the rods to determine the depth of sediment activation according to the procedure described in Greenwood & Hale (1980). Measurements of surface elevation and depth of activation were taken during consecutive periods of low water to identify the effects of waves and currents during the previous high water. Activation depths are relative to the initial sand surface elevation prior to the high tide.

All spawning during the field deployment was at night, when the highest of the diurnal tides occurred. Many crabs remained on the foreshore after the swash zone receded down the beach with the falling tide. Their return to the low-tide terrace was indicated by elliptical pits in the beach, which were the dominant bedforms on the foreshore. Width, length and depth relative to the adjacent undisturbed beach surface were measured on the mornings of 23 May (11 pits) and 24 May (20 pits). Additional depth measurements were made where birds excavated holes at the bottoms of these pits.

Surface sediment samples, weighing *ca* 100 g each, were obtained from the top 5 mm of beach next to the rods at the 1 m stations inundated during the previous high tide. These sediments were gathered at the morning low tide on 23, 24, and 25 May to represent the surface characteristics following the night-time spawning peak and at the afternoon low tide on 23 and 25 May to reveal the effect of wave action during day-time high tide, when spawning did not occur. Sediments were also sampled at depth to reveal the effect of spawning on the bulk characteristics of the entire active layer. These samples were taken at three locations on the upper foreshore on each line in the afternoon of 23 May and the morning of 24 and 25 May, when an additional sample was obtained from the lower foreshore. Depth samples were gathered using a 50 mm diameter core inserted to a depth of 200 mm. Gravel was split from the sand and the total gravel fraction was sieved at 0·5 phi intervals. Ten gram splits of the sand fraction were sieved in a sonic sifter at 0·5 phi intervals, and the gravel and sand fractions were arithmetically combined. The mean (M_z) and sorting (σ_I) of sediment samples were calculated using inclusive graphic measures (Folk, 1974).

Wind speed was monitored using a Gill three-cup anemometer (R.M. Young Company, Traverse City, MI, USA) mounted 2·65 m above the crest of the dike (Fig. 2). Modal wind direction was noted using a hand-held compass. An electromagnetic current meter was deployed 0·10 m above the bed on the lower foreshore. Water-level data were collected using a pressure transducer co-located with the current meter. Data from these two instruments were used to calculate the wave angle using the method of Sherman & Greenwood (1986). Instruments were placed within the exclosure to protect them against damage by crabs moved by the breaking waves and swash. Data were recorded at high tide on all days at 2 or 4 Hz for 17·1 min. Wave heights reported are significant heights. Wave periods represent the peak-energy variance from spectral estimates of transducer data. Significant wave orbital velocities were estimated from linear wave theory (Dean & Dalrymple, 1991) and the threshold for sediment entrainment was estimated from the wave orbital velocities (Komar & Miller, 1973).

RESULTS

Observations from the night of 24 May reveal that the density of crabs on the beach in the swash zone near line S was 8·1 crabs m^{-2}. Crab activity in the swash zone is chaotic at these times, with crabs crawling over others in their attempt to move up or down the beach and some crabs being transported by swash against their will. The number of crabs is sufficient to break up the swash uprush and restrict its vertical extent, but no measurements were taken to quantify this effect.

Physical processes

Winds blew offshore during two of the six high-tide monitoring periods (Table 1). They blew onshore from south of shore normal during the other times, resulting in longshore transport to the north. Wave heights on the lower foreshore ranged from a high of 0·18 m during the night-time high tide on 22 May to a low of 0·07 m during the daytime high tide on 23 May. The highest waves occurred during the nights of 22 and 24 May, when wind speed exceeded 4·6 m sec^{-1}. These wave heights are termed moderate to distinguish them from the high waves that would be expected during easterly storms

Table 1. Mean wind speed (W_s), modal wind angle ($W\alpha$), water depth (h), wave height (H_{sig}), period (T_{pk}) and angle (α), wave orbital velocity (U_{sig}), and critical orbital velocity (U_{crit}) to the north and south, monitored at high water during May 2004.

Day/time	$W_{s\ (mean)}$ (m sec^{-1})	$W_{s\ (SD)}$ (m sec^{-1})	$W\alpha^1$ (deg)	h (m)	H_{sig} (m)	T_{pk} (sec)	α (deg)	U_{sig} (m sec^{-1})	$U_{crit\ N}$ (m sec^{-1})	$U_{crit\ S}$ (m sec^{-1})
22/21:57	5·58	1·17	47	0·64	0·18	2·2	0·4	0·30	0·22	0·23
23/10:24	3·78	0·90	157	0·49	0·07	2·7		0·15	0·20	0·19
23/22:43	1·76	0·28	121	0·80	0·08	2·9	2·4	0·13	0·21	0·20
24/11:16	2·82	0·45	26	0·49	0·07	3·1		0·16	0·20	0·21
24/23:29	4·68	0·94	36	0·71	0·16	2·8	3·5	0·29	0·23	0·24
25/11:58	3·35	0·46	20	0·53	0·08	2·9		0·20	0·23	0·20

[1] Wind angle is in degrees from shore normal with values > 90 approaching from land.

when wind speeds exceed 8·0 m sec^{-1}. Significant wave orbital velocities exceeded the critical threshold for sediment entrainment by waves (based on median size of the sand and granule fraction) during the evening high tide on 22 and 24 May but were lower than the critical threshold when wave heights were <0·10 m (Table 1).

Depth of sediment activation

Depth of sediment activation outside the exclosure was minimal (<0·03 m) following daytime high tides (Fig. 3B,D,F) when water levels were low and horseshoe crab spawning did not occur. Depth of sediment activation is enhanced by

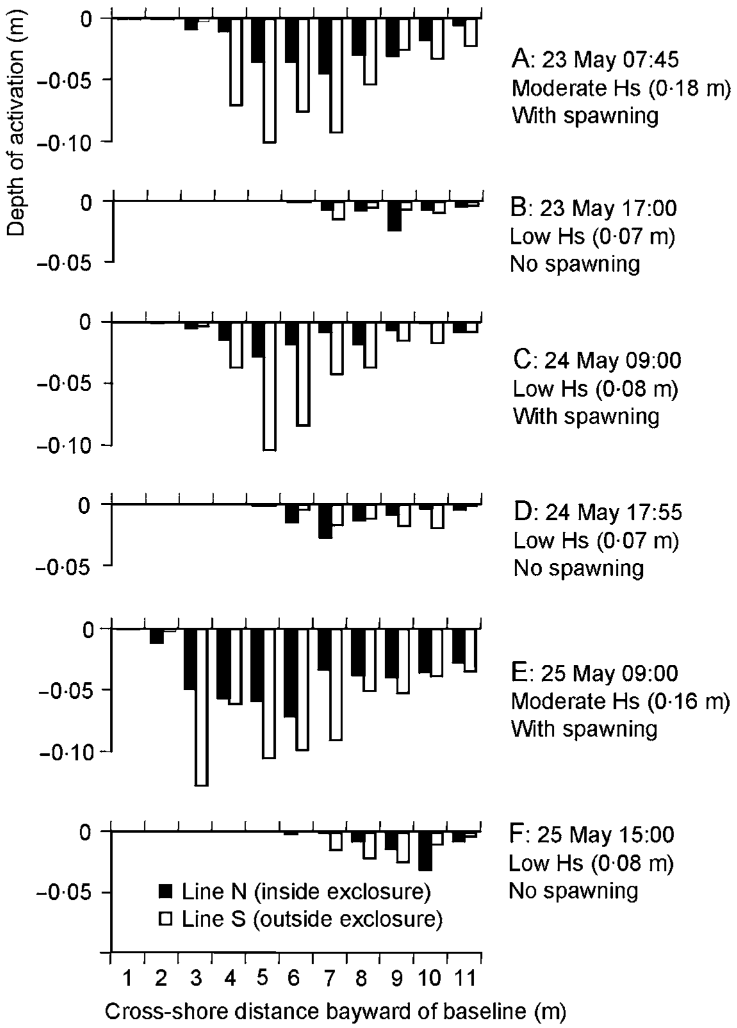

Fig. 3. Depth of sediment activation between baseline and fence line.

spawning under both the low and moderate wave heights that occurred at night (Fig. 3A,C,E). The maximum depth of activation on the upper foreshore outside the exclosure (line S) when low wave heights occurred during spawning (Fig. 3C) was 0·103 m, which is greater than the depth of activation by waves alone during moderate-energy conditions (line N, Fig. 3A,E) and nearly as great as the maximum depth of activation outside the exclosure (0·127 m) when wave heights were higher (Fig. 3E).

Surface elevation changes

No vertical accretion of sediment was conspicuous at the exclosure fence during the experiment, indicating that it functioned properly. Beach elevation changes outside the exclosure (line S) are greater and differences between locations of erosion and deposition across the profile are enhanced during periods of moderate wave heights and higher spawning (Fig. 4A,E). Cross-shore differences on line S are most pronounced on the mid- and upper foreshore, where spawning occurs. The magnitude of elevation change low on the profile and at the uppermost limit of swash uprush is greater on line N than on line S. Thus crab burrowing changes both the magnitude and location of surface change. The lack of conspicuous differences in magnitude of elevation change between lines N and S when spawning occurred under low-energy conditions (Fig. 4C) indicates that the increased sediment activation by horseshoe crabs (Fig. 3) does not increase the likelihood of surface change in the absence of high wave heights. During moderate wave heights (Fig. 4A,E) increased sediment activation by crabs results in a greater volume of sediment deposited on the lower foreshore over a tidal cycle.

Horseshoe crab spawning and wave action causes the beach profile to exhibit greater change through time (line S; Fig. 5A), especially within the zone of active spawning on the upper foreshore. Spawning, combined with moderate wave energies (line S; Fig. 5B) creates a concave upper foreshore, with deposition lower on the foreshore, similar to the kind of profile response seen on estuarine beaches during storms (Fig. 1), but the zone of deposition is not displaced as far bayward as it would be under high-energy storm waves. Profile change is less conspicuous when the

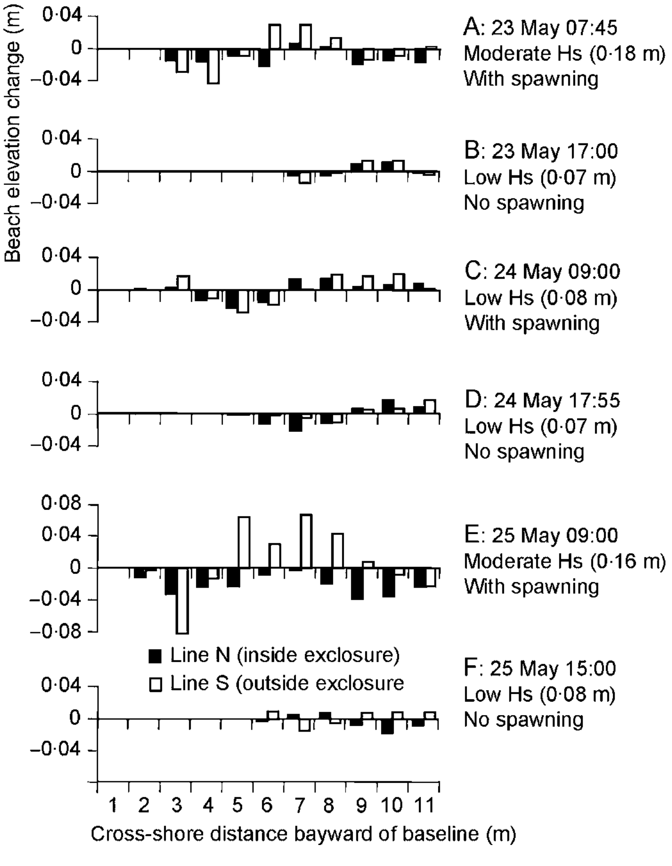

Fig. 4. Beach elevation changes between baseline and fence line.

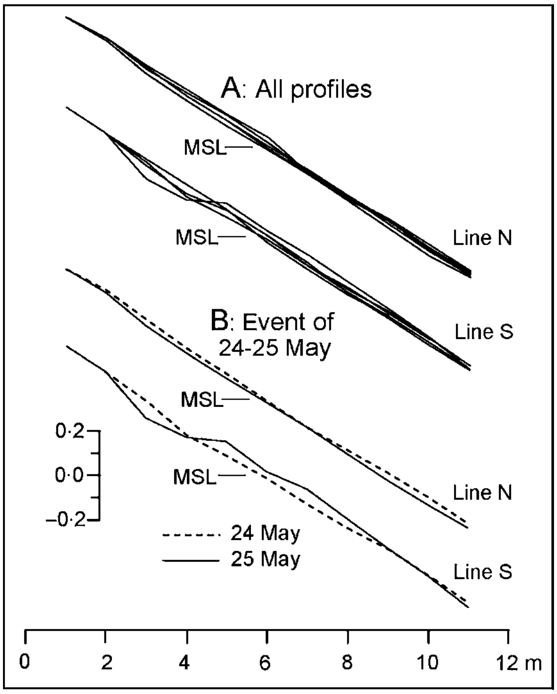

Fig. 5. Beach profiles taken at consecutive low tides.

beach is modified by waves alone (line N; Fig. 5b). The steeper slope that forms at the upper limit of spawning on line S (Fig. 5) and the interference of crabs with swash run-up reduce the height of the runup, causing less change than on line N at the upper limit of the active beach.

The majority of burrow pits occurred at mid-foreshore. Swash during the falling tide smoothes most burrow pits and furrows made by crabs that move down the foreshore right after spawning, but isolated pits remain where crabs delay their movement down the foreshore until only a few swash uprushes occur at their location. Crab pits monitored on the morning of 23 May following the moderate energy event during the previous night averaged 0·34 m wide by 0·45 m long and 0·04 m deep ($n = 12$). Pits monitored on the morning of 24 May, following the low-energy event, averaged 0·36 × 0·46 × 0·06 m ($n = 20$). A *t*-test reveals that the difference in mean depth measured on the 2 days is significant (d.f. = 30, $P < 0{\cdot}01$). The greater depth on 24 May appears to be due to less reworking and filling by the lower energy swash during falling water levels, but the pits are still less deep than when created because of swash filling. Smaller holes, created by birds attempting to excavate buried eggs at the bottoms of these pits, are cone shaped and reach a depth *ca* 18 mm deeper than the pits. Crab pits and bird-excavation holes are completely filled by swash uprush and backwash during the subsequent rising tide, even under low-energy conditions.

Textural properties of sediments

Grain-size data (Table 2) reveal the significance of crab spawning to delivery of gravel to the surface of the foreshore, changing the sorting characteristics of the surface sediments. Surface samples on line N, where spawning did not occur, are finer (higher ϕ values) and better sorted with lower percentages of gravel than surface samples at comparable cross-shore positions on line S during all sampling periods. *t*-Tests performed on mean grain size of surface samples along the two lines reveal that differences are significant ($P < 0{\cdot}01$; two-tailed test) for the periods of lower wave heights with and without spawning on 23 and 24 May but not on 25 May, when much gravel accumulated on line N. Differences in mean grain size are not significant at the 0·05 level for the two periods of moderate wave heights and intensive spawning. Differences in sorting and percentages of gravel are significant ($P < 0{\cdot}05$; two-tailed test) for the periods of moderate wave heights and spawning and are significant ($P < 0{\cdot}01$; two-tailed test) for periods of low wave heights, except on 25 May when gravel accumulated on line N.

The coarsest grain sizes and greatest percentages of gravel on line N occurred after low-energy events. Mean grain sizes and percentages of gravel generally increase with lower elevations on the foreshore on line N. This trend is obscured on line S, where coarser means and greater percentages of gravel can occur higher on the foreshore under both low and moderate wave-energy conditions. The upper limit of uprush was barely above the sampling point 2 m from the baseline, so no gravel was delivered to this location as a result of crab spawning.

Core samples (Table 3) reveal little difference between the two sites, and no differences were significant. Within sites, core samples on line N are coarser, more poorly sorted, and contain more gravel than the surface samples gathered at the same locations (6 m from the baseline at 17:00 hours on 23 May and 4, 5, 6, and 9 m from the baseline at 09:00 hours on 24 and 25 May). Core samples on line S are better sorted and contain less gravel than the surface samples.

t-Tests were run on the sand fractions of the samples to determine whether differences in mean grain size caused by crab burrowing are solely because of the preferential movement of gravel. The only significant differences in surface

Table 2. Grain size characteristics and % gravel of sediments within top 5 mm of surface along North and South sampling lines.

Date/time	Location (m)	Mean (ϕ)		Sorting (ϕ)		% Gravel	
		North	South	North	South	North	South
23 May/07:45; Moderate H_s – spawning	4	1·90	−0·32	0·34	2·11	0·0	27·2
	5	1·86	1·38	0·39	1·27	0·0	11·3
	6	1·28	0·35	1·00	2·14	5·3	18·4
	Mean (n = 3)	1·68	0·47	0·58*	1·84*	1·77*	18·97*
23 May/17:00; Low H_s – no spawning	6	0·85	0·18	1·24	2·23	6·3	22·9
	7	1·17	0·19	0·41	1·96	1·3	19·8
	8	0·62	−1·43	0·64	2·12	3·7	48·6
	9	0·48	−0·79	0·63	1·81	4·6	30·9
	10	0·46	−0·58	0·49	1·43	2·0	19·0
	11	−1·17	−1·99	1·08	1·74	22·6	47·5
	Mean (n = 6)	0·40†	−0·74†	0·75†	1·88†	6·75†	31·45†
24 May/09:00; Low H_s – spawning	2	1·93	1·63	0·33	0·39	0·0	0·0
	3	1·94	1·43	0·31	1·31	0·0	12·3
	4	1·92	0·17	0·31	1·90	0·2	18·5
	5	1·81	−0·70	0·38	2·42	2·2	35·2
	6	1·80	−0·39	0·35	2·27	2·7	35·7
	7	1·21	−1·89	0·79	2·44	0·6	64·1
	8	1·33	−1·59	0·66	2·30	0·3	54·1
	9	0·77	−1·43	0·75	2·16	3·9	51·9
	10	−0·14	−0·83	1·63	2·16	17·3	29·9
	Mean (n = 9)	1·40†	−0·40†	0·61†	1·93†	3·02†	33·52†
25 May/09:00; Moderate H_s – spawning	2	1·73	1·89	0·49	0·39	0·0	0·0
	3	1·68	1·25	0·34	1·56	0·0	11·6
	4	1·69	−0·27	0·33	2·08	4·7	27·2
	5	1·38	1·29	0·43	1·37	0·0	13·6
	6	1·39	0·24	0·41	2·29	0·0	18·0
	7	1·48	1·82	0·89	0·40	0·4	2·0
	8	0·62	−0·73	0·85	2·56	0·9	48·6
	9	0·57	−0·90	0·48	2·54	0·0	42·7
	10	−0·40	0·73	1·39	0·86	17·1	1·7
	11	−0·58	−0·51	1·28	0·95	15·4	9·6
	Mean (n = 10)	0·96	0·48	0·69*	1·50*	3·85*	17·50*
25 May/15:00; Low H_s – no spawning	6	1·46	0·16	0·46	2·44	0	24·1
	7	0·40	1·63	1·90	1·32	16·0	13·8
	8	−0·48	0·15	2·12	2·22	32·9	21·9
	9	−0·80	−1·94	1·85	1·93	35·2	66·7
	10	0·16	0·22	0·83	0·65	12·3	3·06
	11	−1·32	−1·74	1·44	1·40	38·0	53·6
	Mean (n = 6)	−0·10	−0·25	1·43	1·66	22·4	30·5

*Differences between North and South lines significant ($P < 0{\cdot}05$, two-tailed test).
†Differences significant ($P < 0{\cdot}01$, two-tailed test).

samples were in the sorting ($P < 0{\cdot}01$; two-tailed test) at 09:00 hours on 24 May following spawning during low wave heights on 23 May. There were no significant differences in the mean or sorting of the core samples.

DISCUSSION

Previous studies of the effects of organisms on substrate document their ability to: (i) alter sediment characteristics, bottom roughness, and entrainment thresholds; (ii) introduce sediment into the flow that would otherwise be unavailable for transport; and (iii) change the kinds of bedforms that can occur (Grant *et al.*, 1982; Fries *et al.*, 1999). Horseshoe crabs are only one of the organisms that alter sandy estuarine beaches in these ways, but their large size and numbers result in conspicuous changes in beach topography and grain size characteristics, determined by percentages of gravel.

Table 3. Grain size characteristics and % gravel of sediments from cores along North (N) and South (S) lines.

Date/time	Location (m)	Mean (ϕ)		Sorting (ϕ)		% Gravel	
		North	South	North	South	North	South
23 May/17:00	4	1·08	0·57	1·09	1·54	5·0	10·7
	5	0·15	0·69	1·53	1·40	11·6	8·5
	6	0·28	0·38	1·37	1·45	7·7	7·2
24 May/09:00	4	0·81	0·03	1·34	1·82	8·2	17·5
	5	0·39	0·70	1·48	1·37	8·9	8·0
	6	0·19	0·14	1·39	1·50	7·2	12·2
	9	−1·37	−0·97	2·00	1·70	38·4	27·0
25 May/09:00	4	0·45	−0·08	1·53	1·98	0·1	21·7
	5	−0·15	1·07	1·95	0·97	19·2	3·8
	6	−0·83	0·50	2·23	1·78	29·1	14·1
	9	−1·06	−0·40	2·26	1·84	35·3	22·3

Changes in sediment transport are difficult to relate to a single biological mechanism or process because several biogenic factors may operate simultaneously (Grant *et al.*, 1982). Disturbance of the foreshore during spawning results from the combined effects of crawling and burrowing that occur over multiple egg laying events during a single high tide (Brockmann, 1990). The greatest depths of disturbance during spawning are accomplished by burrowing to deposit eggs, so burrowing is assumed to be the dominant biogenic mechanism altering the upper foreshore.

Spawning changes the magnitude, location and type of surface change. Differences between lines N and S indicate that crab reworking can change beach-profile response from parallel slope retreat to erosion with slope change thus lowering the wave-energy threshold for conspicuous morphological response. The difference in morphological response is most pronounced after the event of the night of 24 May when the longshore transport potential was greatest because of relatively high waves and angles of approach (Table 1). Calculation of longshore sediment transport potential using the Coastal Engineering Research Center (CERC) (1984) equation reveals that the volume of sediment in transport alongshore during the night high tide on 24 May was 6·1 times greater than on 22 May and 8·2 times greater than on 23 May. The cut and fill and concave upward profile high on the foreshore that occur because of spawning during moderate-energy conditions, mimics the cut and fill profile that occurs during higher-energy storm waves (Fig. 1, inset), except that the sediment removed from the upper foreshore is deposited higher on the beach than it would be during storms. The high transport rate the night of 24 May is believed to be partly responsible for delivery of gravel from spawning areas to line N, leading to the high proportion of gravel there on 25 May (Table 2).

Biota alter surface grain-size characteristics by introducing new size fractions to the surface, including coarser fractions that can project into the bottom boundary layer (Jumars & Nowell, 1984; Luckenbach, 1986). Spawning by horseshoe crabs can result in significant differences in grain-size statistics on the foreshore surface when wave heights are low, because of the addition of gravel. As with profile changes, the effect of crab burrowing is manifest on the upper foreshore, where coarser grain size means and greater percentages of gravel can occur under both low and moderate wave heights. Use of the sand fraction alone to identify grain-size differences is less useful than use of both the sand and gravel fractions. Gravel is usually far less common on the upper foreshores of estuarine beaches than on the lower foreshores (Nordstrom & Jackson, 1993), so the proportion of gravel on the upper foreshore may be the most useful diagnostic feature in using grain-size characteristics to interpret the effect of crabs in the sedimentary record. The lack of significant differences in core samples with and without burrowing implies that sampling in layers rather than using bulk samples may provide better clues in the sedimentary record.

The direct effects of crab spawning are confined to 3 months of the year during the spawning season, but they are prominent over that time period. The tendency for crabs to spawn at the highest stages of the diurnal high tide during spring conditions increases the preservation potential of these features over periods of days to weeks. Subsequent reworking of the beach during storms will remove all surface evidence of spawning, but because depths of reworking by horseshoe crabs can be greater than depths of reworking by winter storm waves (Jackson & Nordstrom, 1993), evidence can be preserved at depth on beaches that are not undergoing long-term erosion. Crab pits and bird-excavation holes are filled by swash uprush and backwash during the subsequent rising tide, even under low-energy conditions, obscuring their changes to the beach surface. The depths of these features are similar to or less than those reached by storm waves, so they have less preservation potential.

The relative effect of physical versus biological processes in sediment activation is a function of wave exposure, beach morphology and the density of horseshoe crabs that spawn during a given tidal cycle. Depth of activation by waves is greater on steep beaches than on gently sloping beaches, and this difference can be the result of breaker type, with plunging waves resulting in greater sediment activation (Kraus, 1985; Ciavola *et al.*, 1997). The depth of activation when low wave heights occur during spawning is greater than the depth of activation by waves alone, even during moderate-energy conditions. Thus burrowing by successive sets of crabs will release more eggs to the water column and make more eggs available to shore birds than waves alone. Higher wave heights would increase the depth of activation and thus the potential to release larger quantities of eggs, but few horseshoe crabs will spawn if wave heights are too high (Smith *et al.*, 2002). Thus burrowing by horseshoe crabs is the primary mechanism for delivery to the sediment surface of newly deposited eggs located low in the substrate.

CONCLUSIONS

Spawning changes the magnitude, location and type of surface change and increases the likelihood of beaches undergoing cut and fill with slope change. Depth of activation by crabs relative to waves is accentuated during low wave heights, but crab burrowing at these times may not increase the magnitude of surface change. Activation depths are greatest when higher waves accompany spawning, and surface changes can be enhanced over the changes that would occur because of waves alone. Spawning during low wave heights can increase the gravel fraction and the mean and sorting of surface sediments. Morphological changes on the upper foreshore have preservation potential because the greatest amount of spawning occurs at the higher stages of the diurnal high tide during spring conditions, and intensive storms are infrequent in early summer. Winter storms can remove the surface evidence of spawning, but evidence can be preserved at depth on non-eroding beaches because reworking by crabs can be deeper than reworking by storm waves.

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