

Beach restoration improves habitat quality for American horseshoe crabs and shorebirds in the Delaware Bay, USA

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ABSTRACT: Beach nourishment is commonly conducted to protect human infrastructure but rarely for the primary purpose of improving wildlife habitat. To improve horseshoe crab spawning and shorebird feeding habitat in the Delaware Bay, New Jersey (USA), we removed 2000 t of shoreline rubble and placed sand on 16 ha of degraded shoreline spanning 8 beaches. Horseshoe crab egg cluster abundance varied annually, seasonally and spatially. Beaches restored using sand with grain size fractions similar to native sand had horseshoe crab egg cluster abundances matching or exceeding those of high-quality reference beaches. Deeper sand with a higher coarse-grain fraction resulted in the highest egg cluster abundance across all sites and beaches, while finer-grained sand used on a subset of restored beaches was associated with lower egg cluster abundances. These patterns were also reflected in shallow egg availability for shorebirds, with egg cluster abundance correlating positively with shallow egg abundance. Over time, sand placed on beaches moved cross-shore and longshore, and overwashed into marshes. Longshore sand movement nourished adjacent beaches and ebb shoals at creek mouths. Such shoals attract spawning horseshoe crabs and have high densities of surface eggs available for shorebird feeding, but experience high attrition of egg clusters. This study demonstrates that investments in beach restoration provide important benefits for horseshoe crabs and shorebirds. Outcomes can be further improved by expanding project scope and integrating other coastal restoration strategies. Restoration will be critical for the conservation of coastal species as sea levels rise and current and past coastal management practices continue to degrade habitats.

KEY WORDS: Horseshoe crab · *Limulus polyphemus* · Beach replenishment · Restoration · Shorebird habitat · Management

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1. INTRODUCTION

Coastal habitats are under threat worldwide as a result of both direct human impacts and accelerating sea level rise (Doody 2012). While shoreline management to protect human infrastructure spans centuries (French 2001), efforts to manage attributes of coastal habitats to sustain and improve wildlife habitat are still uncommon. This is likely because the high cost

and logistical challenges of shoreline restoration can only be justified if the action will reduce risk to human infrastructure or enhance recreational value (Coburn 2012). Increasingly, coastal habitat management will be critical for conservation as the separate and interacting effects of sea level rise and human shoreline development drive loss and degradation of the habitat available to coastal-dependent wildlife (Galbraith et al. 2002).

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One of the most common shoreline management practices is beach replenishment (Pilkey & Clayton 1989, Dean 2003). While there is a wide range of species, including plants, invertebrates, reptiles, mammals and birds that depend on beaches as primary habitat (Defeo et al. 2009), replenishment projects are rarely designed specifically to improve habitat quality for wildlife. Most projects are instead intended primarily for shoreline protection, with habitat enhancement occasionally included as a secondary goal (Maslo et al. 2011). Often beach replenishments have different dimensions and grain sizes from those of natural beaches (Speybroeck et al. 2006, Jackson et al. 2010, Nordstrom et al. 2011). As a result, ecological studies of sand replenishment are often geared toward measuring potential negative impacts to wildlife as opposed to benefits (Peterson & Bishop 2005). Managing sand volume and configuration on beaches has the potential to benefit beach-dependent wildlife, particularly in locations where human activities have degraded habitat by inhibiting or altering natural geomorphic dynamics. It is first critical to understand how physical parameters (e.g. grain size, moisture, slope, elevation) affect habitat quality for wildlife in order to maximize the benefit of habitat management projects.

Throughout their range, American horseshoe crabs *Limulus polyphemus* spawn primarily on sandy beaches (Walls et al. 2002). The beaches of the Delaware Bay host the largest spawning population of horseshoe crabs in the world (Shuster & Botton 1985), where the unique geomorphic setting provides extensive low-energy beaches (Jackson et al. 2002) that horseshoe crabs require for spawning. The synchronous spawning of millions of crabs each spring (primarily in May and June) offers a surplus of horseshoe crab eggs that numerous species of fish and birds feed upon (DeSylva et al. 1962, Tsipoura & Burger 1999, Botton et al. 2003). Most notably, a globally significant shorebird migration stopover on the Delaware Bay coincides with horseshoe crab spawning (Clark et al. 1993). Tens of thousands of red knots *Calidris canutus rufa*, ruddy turnstones *Arenaria interpres*, sanderlings *Calidris alba* and semipalmated sandpipers *Calidris pusilla* stop to feed on horseshoe crab eggs as they migrate from South America to Arctic nesting grounds. Loss and degradation of horseshoe crab spawning habitat thus affects not only horseshoe crabs, but also shorebirds (Tsipoura & Burger 1999, Baker et al. 2004, Duijns et al. 2017) and potentially many other constituents of the estuarine food web (Botton et al. 2003).

The 4 extant species of horseshoe crabs all face significant conservation threats, including habitat loss

and exploitation for food, bait and biomedical use of blood (Botton et al. 2015). The 3 species native to Asia (*Tachypleus tridentatus*, *T. gigas* and *Carcinoscorpius rotundicauda*) are experiencing habitat loss primarily through direct habitat conversion via coastal development (Mishra 2009, Cartwright-Taylor et al. 2011, Kwan et al. 2016, Nelson et al. 2016a, Fairuz-Fozi et al. 2018). Habitat loss and degradation for the American horseshoe crab can be more subtle, with degradation occurring as a result of past (Smith et al. 2017b) and present shoreline management practices (e.g. bulkheading and beach replenishment) which may interact with coastal dynamics and sea level rise to degrade beach habitat (Avisar 2006, Jackson et al. 2009).

The majority of Delaware Bay beaches rest on the shoreward edge of wide fringing tidal marshes (Lewis et al. 2005). Since the last ice age, these beaches and marshes have been transgressing inland in response to a rising sea level (Fletcher et al. 1993). As the beaches transgress into marsh, mud and peat outcrops appear in and around beaches. Across the landscape, this process results in a mosaic of sandy beaches (Lathrop et al. 2013) with varying depths of sand interspersed with peat and residual salt marsh at the foot of beach slopes. American horseshoe crabs appear to avoid areas of mud and peat (Botton et al. 1988), and high-quality habitat is characterized by continuous deep sand that offers adequate oxygen levels and minimizes exposure of developing eggs to hydrogen sulfide (Vasquez et al. 2015a). Given this pattern, horseshoe crab habitat availability is influenced by beach transgression, with temporal and spatial variation in habitat quality depending on both long-term (e.g. sea level rise) and short-term (e.g. storms) disturbances.

In addition to natural variation in habitat quality, horseshoe crab spawning habitat quality on beaches is affected by past human uses of the shoreline. From the colonial era through the early 20th century, much of the Delaware Bay shoreline was managed as an impoundment dike for farming on adjacent marshes (Phillip 1995, Smith et al. 2017b). When active management of these dikes ceased, shoreline in some places began to fragment and disintegrate (Weinstein et al. 2000). Past observations and predictions for the future show that the highest rates of habitat loss and shoreline transgression are in these formerly impounded areas (Smith et al. in press).

On both the New Jersey and Delaware sides of the bay, many settlements fringe the shoreline immediately inshore of beaches. Notably, numerous settlements in New Jersey have been abandoned as a

result of inland transgression of the shoreline. Prior to abandonment, these settlements introduced bulkheads and riprap to curb erosion, which reduced the habitat quality of the sites for horseshoe crabs and shorebirds (Jackson et al. 2009, 2015). Once the towns were condemned and demolished, these shoreline obstructions were left behind, degrading habitat for horseshoe crab spawning. This retreat and abandonment has occurred primarily along the New Jersey shoreline, in contrast with Delaware, which has invested in beach replenishment to protect such communities for the last 5 decades (PSDS 2017).

Storms can also degrade horseshoe crab habitat. Hurricane Sandy made landfall on 29 October 2012. Although it was not a direct hit to the Delaware Bay, high winds and storm surge generated uncharacteristically powerful waves that caused a pulse of beach sand over-wash across many Delaware Bay beaches. This triggered an instant decrease in the availability of high-quality habitat, as peat and formerly buried hard structures were unearthed. Sand was stripped from beaches and carried inland onto the adjacent marshes. In many places, the resulting shoreline was starved of sand, leaving extensive peat outcrops. This loss of sand on beaches translated to major degradation of horseshoe crab spawning habitat. Inventories of horseshoe crab habitat in the Delaware Bay in 2002 and again in 2010 indicated that the habitat had changed very little over this time period (Lathrop et al. 2013, Smith et al. in press). However, surveys immediately after Hurricane Sandy revealed a significant loss of habitat, including an estimated 70% decrease in optimal habitat and >20% decrease in suitable and less suitable habitat classes (Lathrop et al. 2013). This sudden decline in habitat quality provided the impetus to begin managing New Jersey Delaware Bay beaches to improve habitat quality for horseshoe crabs and shorebirds. Management involved both

replacing the sand lost during the storm to pre-Hurricane Sandy footprints and removing shoreline rubble and other material left behind during past human use of the shoreline and further exposed as a result of Hurricane Sandy.

In this study, we evaluated the impact of a multi-year beach restoration project designed specifically to improve beach habitat quality for horseshoe crabs and shorebirds. This evaluation is based on experimental tests of the effect of sand grain size and sand depth on horseshoe crab egg cluster abundance and the availability of eggs to shorebirds. In addition, we evaluated patterns of sand movement within project areas and its influence on habitat quality over time. This project evaluation is necessary to both assess current project outcomes and identify strategies that can improve future iterations of habitat management for horseshoe crabs and shorebirds within Delaware Bay and throughout the range of the American horseshoe crab.

2. MATERIALS AND METHODS

2.1. Beach designs

Overall, we adhered to a consistent design across all beaches, consisting of a 1.2 m North American Vertical Datum of 1988 (NAVD 88) berm height with a 15:1 slope down to mean low water. Berm width varied from 6–12 m, depending on the presence of upper dune features or human infrastructure. Sand was trucked in from nearby sand mines and graded with heavy equipment to design specifications. Total sand volumes placed on each beach ranged from 3400.5 to 30 582 m³, depending on the dimensions of the design template and initial condition of the site (Table 1). Total restored area was 16 ha, comprising 4.4 km of shoreline. Mean sand grain size varied by

Table 1. Total sand volumes placed on restored beaches and volume change within the design template over time. Dashes indicate where no sand placement occurred

Site	Hectares	Volume placed (m ³)				Volume change (m ³)		
		2013	2014	2015	2016	2014–2015	2015–2016	2014–2016
Moores Beach	2.5	4263	12 248	–	–	–6072	–3720	–9792
Kimbles Beach	1.3	6540	3647	–	4381	–2573	3203	630
South Reeds Beach	1.1	2325	1690	–	–	–922	186	–736
Cooks Beach	0.9	2235	1231	–	2898	–1812	1856	44
Pierces Point	1.2	3385	3181	–	–	–1495	–1979	–3473
Thompsons Beach	4.4	–	–	27 335	–	–	–3596	–
Dyers Cove	2.6	–	–	–	12 845	–	–	–
Fortescue	1.9	–	–	30 582	–	–	–6491	–

project site (0.36–0.91 mm, Table 2) to test the effect of grain size on project outcomes.

Sand was placed on 8 beaches between 2013 and 2016 (Fig. 1, Table 1). Where necessary, rubble and other exposed materials were removed prior to placing sand. Pierces Point (39.089° N, 74.902° W), Kimbles (39.105° N, 74.895° W), Cooks (39.109° N, 74.893° W), South Reeds (39.113° N, 74.892° W) and Moores Beaches (39.189° N, 74.950° W) each received sand in 2013 and again in 2014 to complete design templates. We added sand to Fortescue (39.224° N, 75.167° W) and Thompsons Beach (39.192° N, 74.995° W) in 2015 and to Dyers Cove (39.263° N, 75.208° W), Kimbles Beach and Cooks Beach in 2016 (Table 1). Sand was placed on beaches in February and March just prior to the start of horseshoe crab spawning in early May.

2.2. Horseshoe crab egg sampling sites

Sampling was tied to beach profile monitoring lines (described in Section 2.6) at the 8 sites in Table 1. In 2014, 2 reference beaches were monitored: Baycove (39.102° N, 74.900° W) and N. Reeds Beach (39.126° N, 74.892° W). In 2015 and 2016, we expanded monitoring to additional reference beaches including Villas

(39.028° N, 74.943° W), Sunray Beach (39.047° N, 74.930° W), Green Creek (39.058° N, 74.923° W), Cape Shore Lab (39.072° N, 74.913° W), Highs Beach (39.079° N, 74.909° W) and Gandys Beach (39.280° N, 75.243° W) along with unrestored sections of Thompsons Beach and Pierces Point. Sites extended across 60 km of bay shoreline and ranged in character from 'optimal' to 'suitable' in terminology proposed by Botton et al. (1988) and as mapped by Lathrop et al. (2013). Monitoring of physical and biological patterns began immediately after sand placement with the exception of the Thompsons Beach site.

For Thompsons Beach, we monitored egg abundance at restored and unrestored beach segments both before and after beach restoration (before–after–control–impact [BACI] analysis). The beach is divided into 4 segments separated by man-made headland structures composed of remnant bulkheading and riprap. The central 2 segments (comprising 0.9 km of beach) were the subject of sand placement, while the 2 flanking segments (comprising 0.55 km of beach) did not receive sand.

In response to changing intertidal morphology, in 2016 we established new sampling sites in areas of noticeable sand accumulation on ebb shoals. These areas are attractive to both horseshoe crabs (for spawning) and shorebirds (for feeding) and are gen-

Table 2. Results of sand grain size analysis for unreplenished reference beaches and for each interval of beach restoration by site. Data were unavailable in fields with dashes (–)

Beach type	Year	n	Restoration stage	Geo. mean (mm)	Sorting (µm)	Sand type	% Fine and very fine	% Medium	% Coarse	% Very coarse
Unreplenished Beaches										
Beaches	2016	61	Reference sites	0.83	2.09	Native	3.6	21.9	47.8	16.3
Shoals	2016	11	Reference sites	0.81	2.29	Native	3.1	23.8	47.6	15.8
Restored Beaches										
Cooks	2014	4	Immediately after sand placement	0.84	–	Coarse	6.7	18.1	47.2	13.5
Cooks	2016	5	3 mo after sand placement	0.41	2.84	Fine	36.3	39.7	10.7	4.5
Dyers Cove	2016	5	3 mo after sand placement	0.91	2.09	Coarse	3.7	19.1	37.1	26.1
Fortescue	2015	6	3 mo after sand placement	0.38	1.81	Fine	28.4	47.6	16.1	5.4
Fortescue	2016	5	1 yr after sand placement	0.94	2.12	Coarse	5.1	22.7	36.9	20.1
Kimbles	2014	4	Immediately after sand placement	0.55	–	Fine	29.2	19.5	28.6	11.1
Kimbles	2015	4	1 yr after sand placement	0.91	2.41	Coarse	4.2	21.8	37.5	21.8
Kimbles	2016	4	3 mo after sand placement	0.36	2.22	Fine	36.4	43.2	8.2	5.9
Moores	2014	6	Immediately after sand placement	0.54	–	Coarse	8.1	42.0	33.6	13.8
Moores	2016	5	2 yr after sand placement	0.96	2.59	Coarse	3.1	23.0	36.8	23.0
Pierces Point	2014	4	Immediately after sand placement	0.61	–	Fine	23.2	20.7	32.0	13.5
Pierces Point	2016	3	2 yr after sand placement	0.92	2.28	Coarse	2.8	14.2	54.9	18.0
South Reeds	2014	4	Immediately after sand placement	0.94	–	Coarse	2.3	15.5	48.9	18.1
South Reeds	2016	4	2 yr after sand placement	1.56	2.74	Coarse	0.2	4.4	37.9	27.9
Thompsons	2015	–	Immediately after sand placement	–	–	Coarse	–	–	–	–
Thompsons	2016	4	1 yr after sand placement	0.75	2.44	Coarse	3.0	30.4	45.8	11.4

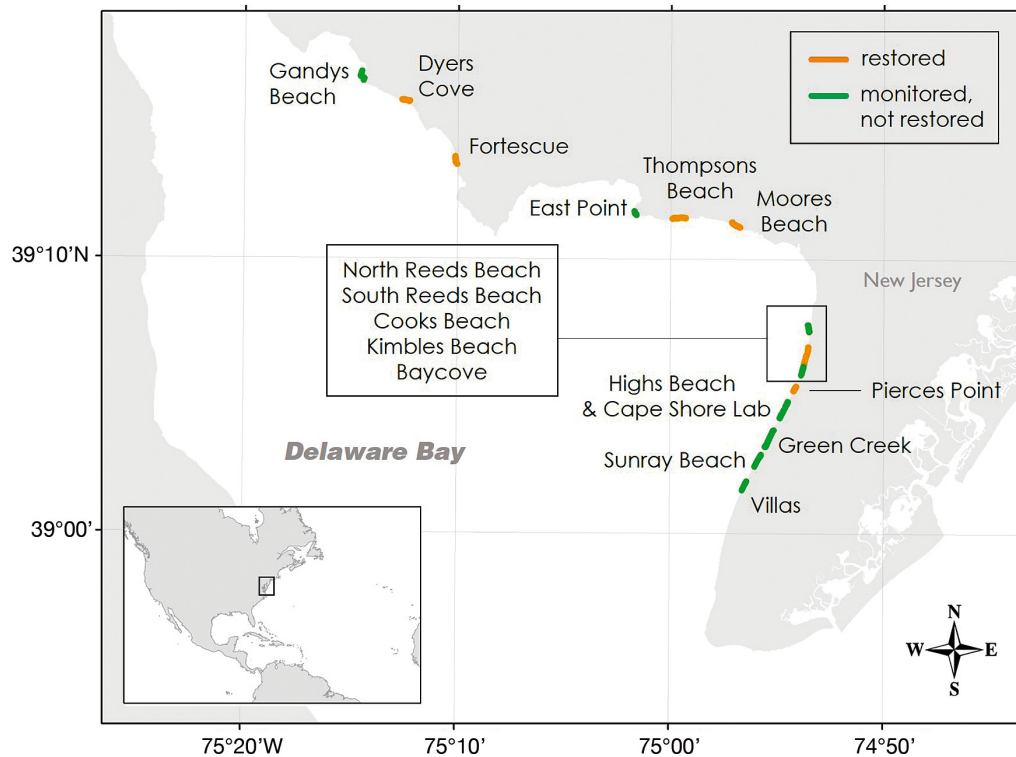


Fig. 1. Beaches that were the subject of monitoring and nourishment. Beaches symbolized by an orange line were restored as part of the project while beaches symbolized by a green line were monitored as reference beaches

erally just offshore of the main beach face near creek mouths. We sampled shoals at Green Creek, Pierces Point, Bay Cove, Cooks, Kimbles, South Reeds and Moores Beaches, Dyers Cove, Fortescue and Gandys Beach. Data from shoal sites were used to compare abundance patterns to that of the main beach face to examine their potentially unique role as habitat for horseshoe crabs and shorebirds.

2.3. Horseshoe crab egg cluster sampling

Sampling for both horseshoe egg cluster (i.e. clutch) abundance and surface egg abundance (see Section 2.4) occurred along 9 m cross-shore transects centered mid-slope on the beach profile. Transects were systematically distributed along the beach, with 5 to 10 transects per beach depending on beach size. To minimize repeated disturbance of the same sampling sites, the sampling transect was placed at a random offset within 25 m of the beach profile location. Monitoring occurred across a total of 47 transects in 2014 and 96 transects in 2015–2016. For both shallow egg and cluster sampling, 9 samples were taken at 1 m intervals along the transect on each sampling occasion.

We sampled horseshoe crab egg cluster density at each beach once per week starting in the second week of May. Sampling spanned 6 wk in 2014 and 9 wk in 2015 and 2016. Horseshoe crabs deposit egg clusters comprising an average of 3650 eggs per cluster (Shuster & Botton 1985) that are tightly adhered to each other when freshly deposited and remain in cluster form throughout development if undisturbed. We dug 9 cube-shaped pits ($20 \times 20 \times 20$ cm, 8000 cm³) with a small shovel. A side-trench was first dug to allow careful sideways excavation of the sample area to minimize disturbance of clusters prior to being counted. All aggregations of eggs that were at least 2.5 cm wide in one dimension were counted. Clusters within each sampling hole and those intersected by the sides of the hole were counted, and the predominant developmental stage of each cluster (egg, embryo and larva) was noted. We also recorded (in 2015 and 2016) when we observed clusters that died due to anoxia or desiccation (Penn & Brockmann 1994). At each sample pit, we continued digging to the 41 cm mark in order to determine the depth to underlying peat and mud. Clusters predominately occur between 10 and 20 cm deep in the sand (Weber & Carter 2009).

2.4. Horseshoe crab egg availability at the beach surface

To estimate horseshoe crab egg availability for shorebird feeding, we sampled shallow-depth horseshoe crab egg densities at each beach once per week. Sediment cores were taken at 1 m intervals along the transect parallel to the sample pits described above for egg cluster sampling. Sediment cores were 5 cm deep with a 5.7 cm diameter (255.17 cm³), similar to previous studies (Pooler et al. 2003). Cored sand samples were stored in polyethylene bags. Samples were processed by placing the sample in a shallow tray and adding a small amount of fresh water to create a thin layer of water in the bottom of the tray. A gentle shake of the tray causes eggs to settle above the veneer of sand. Eggs were then tallied with a click counter under a magnifying lamp. In 2014, sampling occurred for 2 wk starting in the second week of May at the same time as egg cluster sampling. In 2015 and 2016, the sampling period was extended to 5 wk.

We used 2015 and 2016 data to make comparisons among sites because the sampling period and range of sampling sites were more restricted in 2014. We used all 3 years of data to examine the correlation between simultaneously sampled egg cluster abundance and shallow egg availability (Spearman's ρ).

2.5. Sand grain analysis

For each transect, sand samples of approximately 100 g were collected at mid-beach face at a depth of 15 cm. Samples were dried to constant weight in a forced-air oven at 110°C. In 2014, sieving was carried out on a motorized sieve shaker using sieve sizes ranging from 2.8 to 0.063 mm. In 2015 and 2016, sieving was carried out with a Geotech Keck sand shaker using sieve sizes ranging from 6.35 to 0.053 mm. Sieved fractions were weighed to the nearest 0.1 g, and we ensured that total sieve weight was within 1% of the starting sample weight. Sample statistics were calculated using the 'GRADISTAT' statistics package (Blott & Pye 2001), and results of geometric means and sorting were calculated using the method of Folk & Ward (1957).

2.6. Beach profile change

On each restored beach, we established a baseline with uniformly spaced survey stations to determine sand placement and post-construction beach and

sand volume changes over time. Pre- and post-construction surveys were conducted at each station to document initial sand volume placement.

To conduct the surveys, we used a Leica RTK GPS 1200 system utilizing Leica's Smart Network and a Leica TS06 electronic total station. Data were processed and analyzed to generate sand volume and shoreline changes using both GIS and the 'Beach Morphology Analysis Package' (Sommerfeld et al. 1993). In addition to as-built measurements, restored beaches were measured at 3 and 6 mo intervals after restoration. Beyond this time frame, measurements were taken on a regular biannual schedule in the spring and fall.

We calculated sand volume change over 1 yr intervals measured in April of 2014, 2015, and 2016. XYZ coordinate data from beach profiles were used to create a triangular irregular network (TIN) representing elevation for each measurement phase. We calculated volume change across study areas by calculating areas of loss, gain and overall net change across TINs between each measurement interval.

2.7. Statistical analysis

We analyzed all horseshoe crab egg data (both clusters and surface eggs) with repeated-measures generalized estimating equation (GEE) regression models (Fieberg et al. 2009), fit using negative binomial regression to account for non-parametric count data with a log link function and first-order autoregressive working correlation structure. We chose this correlation structure because repeated measures show a decreasing correlation over time due to temporal variation in horseshoe crab spawning intensity and egg cluster attrition. Analyses estimating total egg cluster abundance and abundance at the egg stage used all sampling rounds. Because developed and dead clusters did not appear until later sampling rounds, we truncated the data for analysis to rounds 4–9 for the developed stage and rounds 6–9 for dead clusters. All analyses were conducted in SPSS software (IBM SPSS Statistics for Windows).

The response variable was the sum of 9 samples collected along a transect during weekly sampling. We tested for main effects of the following variables on egg cluster and shallow egg abundance: restoration status (reference beaches and restored beaches classified as being composed of either >30% coarse fraction or >20% fine fraction, Table 2), site, year, sampling round and the mean seasonal sand depth of the sampling transect.

We tested for differences among categorical variables by contrasting estimated marginal means using Wald chi-squared statistics with least significant difference adjustments to correct for multiple comparisons. We accounted for unbalanced sampling across sites and time intervals by including factors that control for site-level and temporal variation within and between seasons.

We conducted a separate analysis of the influence of continuous sand grain size data on total egg cluster abundance. We used 2016 data only because we analyzed grain size distribution of all sites in that year, whereas in other years sand grain size was only measured for restored beaches (Table 2). We examined the effect of mean grain size and grain size fractions on egg cluster abundance while controlling for the effect of sand depth and sampling round. Because of a lack of independence among grain size fractions, we fit a separate model for each fraction and evaluated model fit using quasi-likelihood under the independence model criterion (QIC) and model weights to select amongst model subsets (Burnham & Anderson 2002).

3. RESULTS

3.1. Patterns of horseshoe crab egg cluster abundance

Horseshoe crab egg cluster abundance varied significantly across years, sampling rounds, sites, sand depths and by restoration action (reference vs. restored), at the egg stage (Table S1 in the Supplement at www.int-res.com/articles/suppl/m645p091_supp.pdf), developed stages (Table S2) and when all live clusters were combined (Table S3).

Across the 3 years of sampling, the highest egg cluster abundance occurred in 2015 (Wald $\chi^2 = 50.74$, $df = 2$, $p < 0.001$) with equivalent abundances in 2014 and 2016 ($p = 0.78$). Egg cluster abundance followed a seasonal trajectory (Fig. 2), with egg-stage clusters peaking in late May (sampling Week 4) and declining through the rest of the sampling periods. Clusters that reached developed embryonic and larval stages began to appear in mid-May (Weeks 3 and 4) and peaked in mid-June (Week 7). Clusters that died from anoxia and desiccation typically began to appear in late June (Week 6) and increased through the last round of sampling. The proportion of clusters sampled that were in this condition ranged from 1 to 21%, depending on the year and sampling week. There were no significant differences in dead cluster

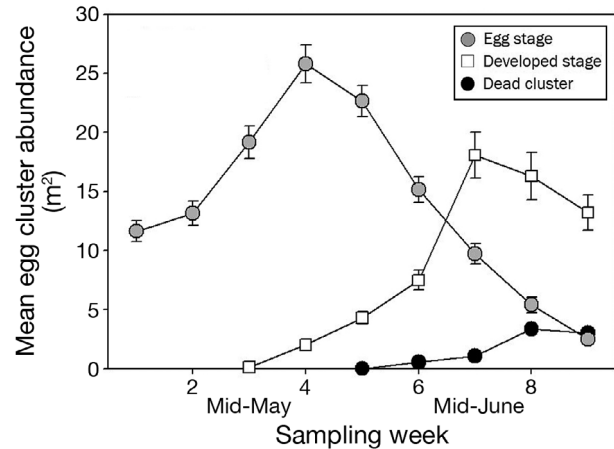


Fig. 2. Seasonal trajectory of horseshoe crab egg cluster abundance (\pm SE) at early (egg) and late (developed embryos and larvae) developmental stages. The prevalence of dead clusters that experienced desiccation and anoxia is also plotted

abundance among years (Wald $\chi^2 = 0.02$, $df = 1$, $p = 0.89$) or between restored and reference beaches (Wald $\chi^2 = 3.23$, $df = 1$, $p = 0.20$, Table S4).

There was a distinct spatial trend (Wald $\chi^2 = 53.2$, $df = 1$, $p < 0.0001$, Table S3) of decreasing egg cluster abundance with increasing distance from the mouth of the bay (Fig. S1). Across all sampled beaches, sand depth over underlying mud and peat was a strong predictor of egg cluster abundance (Wald $\chi^2 = 128.05$, $df = 1$, $p < 0.0001$, Table S3). Egg cluster abundance measured in the upper 20 cm of sand reached its maximum when sand depths to mud on beaches were at least 41 cm (Fig. 3). Sample holes that were at least 41 cm deep had significantly more egg clusters than all shallower depth categories (Fig. 3, Kruskal-Wallis rank sums test with post hoc comparisons, $\chi^2 = 691.9$, $df = 4$, $p < 0.0001$). The majority of sample holes (84%) were at least 41 cm deep.

3.2. Influence of sand grain size on egg cluster abundance

Across unrestored beaches and shoals, mean grain size was 0.8 mm, ranging between 0.62 and 1.04 mm, with a minor fine sand component (3%) and approximately 20% medium, 50% coarse and 15% very coarse sand grains (Table 2). Restored beaches had a finer mean grain size (0.62 mm, range 0.49–0.90 mm) and grain size fraction proportions that fell into 2 groupings, those with higher fine grain fractions (mean = 30.7% fine, 19.1% coarse, $n = 5$) and those with fine (mean = 5.2%) and coarse (mean = 41.7%) grain fractions that more closely matched natural

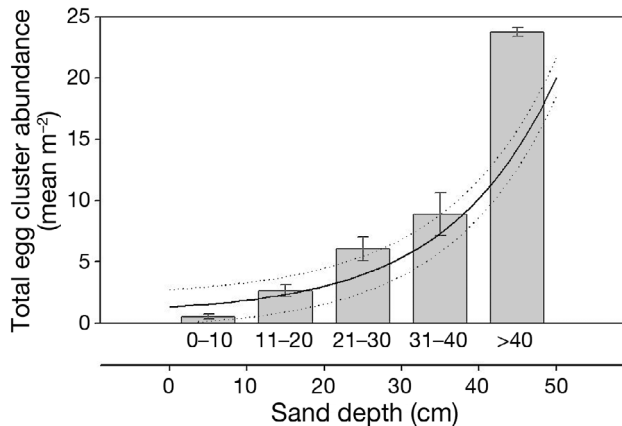


Fig. 3. Relationship between sand depth to underlying peat and mean horseshoe crab egg cluster abundance (\pm SE) sampled at 0–20 cm sand depths. Raw depth data are condensed into 10 cm bins for analysis and display. The modeled relationship that controls for variation due to year, sampling interval, sand depth and site and management (reference vs. restoration) is displayed on a continuous scale, with dotted lines representing 95% confidence intervals

beach conditions ($n = 5$, Table 2). Over time (1 and 2 yr after restoration), restored beaches showed increasing mean sand grain size (matched pairs t -test, $t = 6.83$, $p < 0.001$, $n = 22$ sample sites) and sand fraction proportions that tracked more closely with natural beaches (Table 2). Natural beaches showed no change in grain size over time (matched pairs t -test, $t = 1.1$, $p = 0.31$, $n = 12$ sample sites). For all sand samples, fine and medium grain size fractions correlated positively with each other (Spearman $\rho = 0.81$, $p < 0.0001$) and negatively with coarse (fine: Spearman $\rho = -0.53$, $p < 0.0001$; medium: Spearman $\rho = -0.43$, $p < 0.0001$) and very coarse fractions (fine: Spearman $\rho = -0.63$, $p < 0.0001$; medium: Spearman $\rho = -0.78$, $p < 0.0001$). There was no significant correlation between coarse and very coarse fractions (Spearman $\rho = 0.11$, $p = 0.3$).

Due to these correlations and lack of independence of grain size fraction variables, we created a separate GEE model for each grain size fraction (as well as mean grain size) while controlling for sampling period and sand depth. We evaluated the relative fit of models using the information-theoretic approach with QICc (corrected for small sample size) and model weights. The best-supported model (model weight = 1.0) included the coarse sand fraction, with increasing coarse sand corresponding with increasing egg cluster abundance (Fig. 4A, Table S5). The next-ranked model (Δ QICc = 18) included the fine grain fraction which showed decreasing cluster abundance with increasing proportions of the fine sand

fraction. This and all other models, including a null without a sand grain factor and a model with mean grain size (Fig. 4B) had little support, with Δ QICc > 10 (Burnham & Anderson 2002). The model with mean grain size showed no significant relationship between this measure and egg cluster abundance (Fig. 4B).

3.3. Egg cluster abundance on restored and reference beaches

Because of the strong effect of sand grain size on egg cluster abundance, we defined 2 restored beach categories ($>20\%$ fine sand and $>30\%$ coarse sand) and compared these with reference beaches while controlling for variation across sites, years, sampling intervals and sand depth (Tables S1–S3).

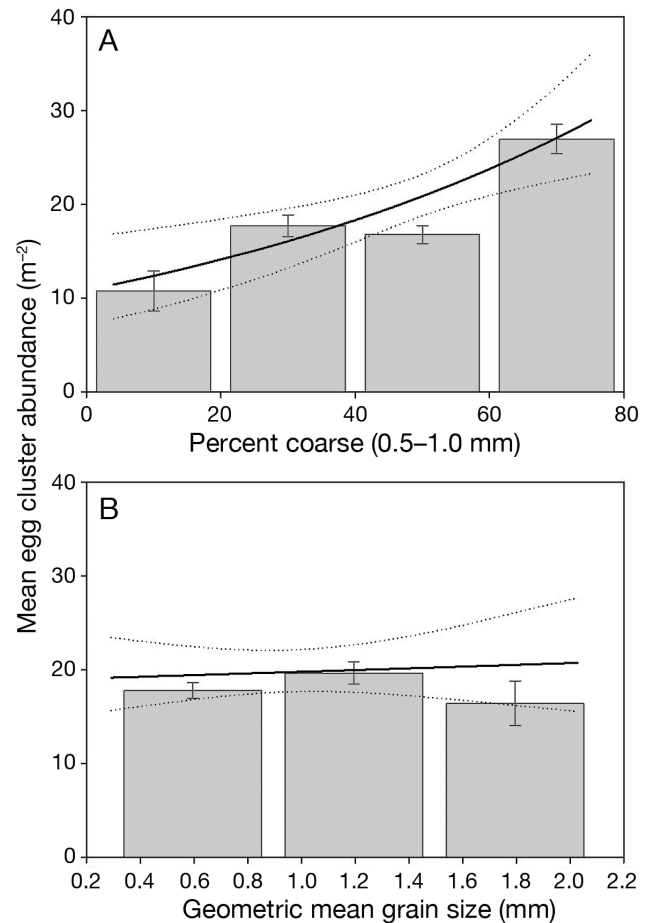


Fig. 4. Generalized estimating equation model predictions for total horseshoe crab egg clusters in 2016 displaying (A) the effect of coarse grain sand proportion and (B) mean grain size on egg cluster abundance, controlling for the effect of sand depth and sampling interval. Dotted lines represent 95% confidence intervals. Raw data are binned with means displayed as bars (\pm SE)

For clusters at the egg stage, abundance at restored beaches with >30% coarse sand was significantly greater (Fig. 5, Wald $\chi^2 = 13.74$, $df = 1$, $p < 0.0001$, mean \pm SE: $13.9 \pm 1.1 \text{ m}^{-2}$) than either reference beaches ($8.8 \pm 0.5 \text{ m}^{-2}$) or restored beaches with >20% fine-grained sand ($7.8 \pm 1.2 \text{ m}^{-2}$) which had equivalent abundances (Wald $\chi^2 = 0.47$, $df = 1$, $p = 0.49$).

For clusters at developed stages, abundance at restored beaches with >30% coarse sand ($8.0 \pm 1.2 \text{ m}^{-2}$) was equivalent to reference beaches ($p = 0.85$, $7.7 \pm 0.8 \text{ m}^{-2}$). Both coarse sand-restored (Wald $\chi^2 = 6.4$, $df = 1$, $p = 0.012$) and reference beaches (Wald $\chi^2 = 6.6$, $df = 1$, $p = 0.01$) had significantly greater abundance of developed clusters when compared with fine sand-restored beaches (Fig. 5, $3.5 \pm 1.0 \text{ m}^{-2}$).

3.4. Horseshoe crab shallow egg abundance

Horseshoe crab eggs in the top 5 cm of sand available for shorebird feeding varied significantly across years, sampling rounds, sites, sand depths and by restoration action (Table S6). There was no clear spatial trend in shallow egg abundance with distance up the bay as observed with egg clusters (Table S6). Site-level mean shallow egg abundance per round was positively correlated with egg cluster abundance (Spearman's $\rho = 0.57$, $p = 0.0003$).

There was a higher overall abundance of shallow eggs in 2015 (raw mean \pm SE = $8353.8 \pm 763.8 \text{ m}^{-2}$, model mean = $4720.1 \pm 582.1 \text{ m}^{-2}$) compared with 2016 (raw mean = $6752.1 \pm 764.6 \text{ m}^{-2}$, model mean = $2979.8 \pm 351.7 \text{ m}^{-2}$, Wald $\chi^2 = 15.9$, $df = 1$, $p < 0.0001$).

Controlling for all other variables, shallow egg abundance at restored beaches with >30% coarse sand ($6964.6 \pm 755.6 \text{ m}^{-2}$) was equivalent to reference beaches ($p = 0.20$, $5583.6 \pm 395.5 \text{ m}^{-2}$). Both coarse sand-restored beaches (Wald $\chi^2 = 34.5$, $df = 1$, $p < 0.0001$) and reference beaches (Wald $\chi^2 = 17.7$, $df = 1$, $p < 0.0001$) had significantly greater shallow egg abundances when compared with fine sand-restored beaches (Fig. 5, $1356.4 \pm 364.4 \text{ m}^{-2}$).

3.5. BACI comparison of sand addition on Thompsons Beach

On Thompsons Beach, total egg cluster abundance was equivalent at control and impact (restored) beach segments prior to restoration in 2014 (before control [BC]: 6.5 ± 1.6 vs. before impact [BI]: 5.2 ± 1.2 , Fig. 6A, $p = 0.47$). After sand addition, egg cluster abundance

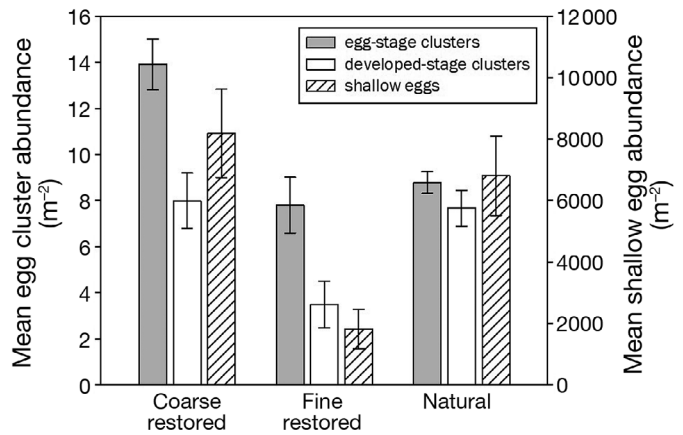


Fig. 5. Marginal means (\pm SE) from generalized estimating equations (controlling for variation due to year, sampling interval, sand depth and site effects) for horseshoe crab egg cluster (egg clusters and developed egg clusters both on left y-axis) and shallow egg abundance (right y-axis) on reference and restored beaches. Restored beaches with 'coarse' sand had at least 30% of samples in the coarse grain size fraction (0.5–1.0 mm) while restored beaches with 'fine' sand had at least 20% of samples in the fine grain size fraction (<0.25 mm)

in the restored section was significantly greater than the control section ($p < 0.001$) in both 2015 (after control [AC]: 23.6 ± 5.3 vs. after impact [AI]: 53.02 ± 8.6) and 2016 (AC: 7.2 ± 1.4 vs. AI: 27.1 ± 5.6) and when the 2 post-restoration years were lumped (overall BA \times CI contrast: Wald $\chi^2 = 34.6$, $df = 3$, $p < 0.001$).

Shallow egg abundance showed similar patterns, with equivalent abundance at control and treatment (restored) beach segments prior to restoration in 2014 (BC: 925.6 ± 402.8 vs. BI: 700.5 ± 194.9 , Fig. 6B, $p = 0.57$). After sand addition, shallow egg abundance in the restored section was significantly greater than the control section when 2015 and 2016 were lumped (overall BA \times CI contrast: Wald $\chi^2 = 27.9$, $df = 3$, $p < 0.001$) but within-year comparisons showed no significant difference (AC: 3397.8 ± 890.5 vs. AI: $4524.6 \pm 1,449.2$) and 2016 (AC: 2208.5 ± 746.8 vs. AI: 6027.1 ± 1751.5).

3.6. Egg abundance on shoals

Comparing both egg cluster and shallow egg abundances on beaches and nearshore shoals revealed significant differences between the 2 habitat types. During sampling weeks 4–10 (late May through early July) in 2016, total egg cluster abundance on shoals

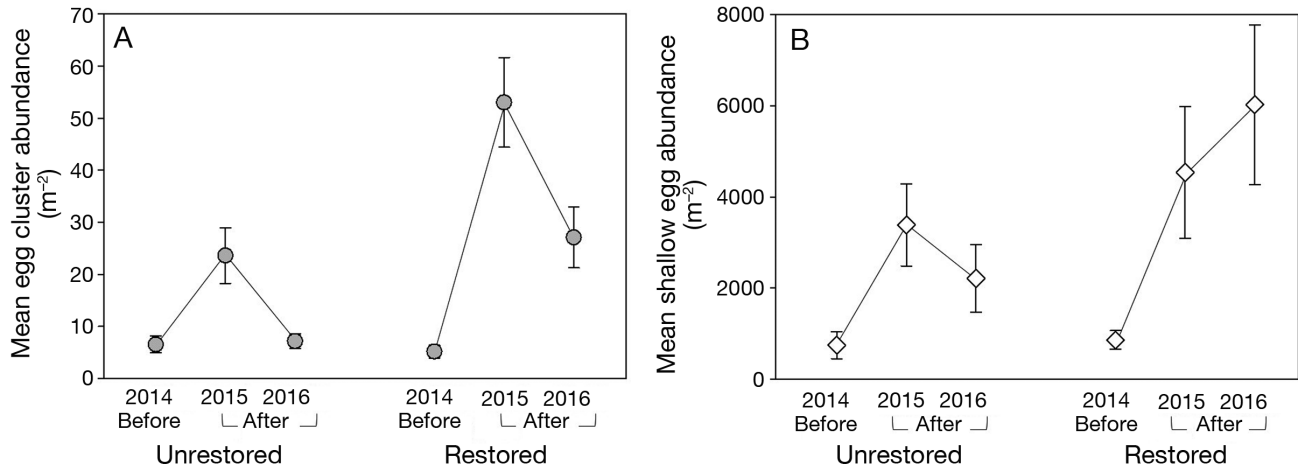


Fig. 6. Comparison of mean horseshoe crab abundance (\pm SE) of (A) egg clusters and (B) shallow eggs on unrestored and restored sections of Thompsons Beach before (2014) and after restoration (2015–2016)

(mean \pm SE: $33.3 \pm 7.2 \text{ m}^{-2}$) was 150% higher than that of beaches ($13.4 \pm 0.8 \text{ m}^{-2}$, Wald $\chi^2 = 7.5$, $df = 1$, $p = 0.006$, Fig. 7). Significant attrition of clusters occurred between the peak egg stage period (undeveloped clusters, Weeks 4–6) and the peak embryonic and larval stage period (developed clusters, Weeks 8–10) on both beaches (from 22.1 ± 1.5 to 14.2 ± 1.2 , $p < 0.001$) and shoals (from 50.7 ± 12.4 to 25.1 ± 8.3 , $p = 0.003$), based on a pairwise comparison of GEE-estimated marginal means. Shoals initially had significantly higher abundance of egg clusters compared with beaches ($p = 0.021$), but this difference dissipated at the developed stage, with no significant differences in cluster abundance between shoals at the developed stage and beaches at both the early egg stage ($p = 0.719$) and later developed stage ($p = 0.192$). These patterns indicate a higher attrition of egg clusters from shoals when compared with beaches. This attrition may have contributed to higher shallow egg abundance on shoals, which was 45% higher on shoals when compared to beaches (Fig. 7, $Z = 3.8$, $p = 0.0002$) during Weeks 4–6 (late May through mid-June).

3.7. Sand volume change over time

Across all beaches, volume of sand placed within the beach design template decreased by an average annual rate of 26% (Table 1). The beach com-

plex of Kimbles, Cooks and South Reeds illustrates some of the dynamics at work (Fig. 8D). These 3 sites were divided by small tidal creeks. Volume change analyses showed an accumulation of sand in the mouths of these creeks and only moderate sand loss at South Reeds Beach. This indicated an overall pattern of longshore drift from south to north, with creek mouth areas serving as sinks for sand, enlarging intertidal shoals. Sand movement was also from south to north at Pierces Point, where sand accumulated in the unrestored northern beach segment (Fig. 8E). Similarly, east to west sand movement

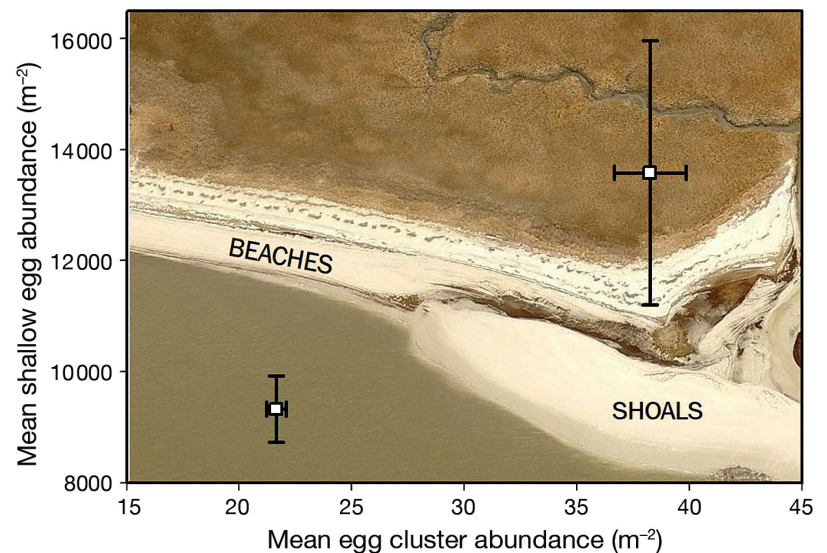


Fig. 7. Comparison of mean horseshoe crab egg cluster abundance (\pm SE) and shallow egg abundance (\pm SE) at 0–5 cm depths on the main beach face and on intertidal shoals just offshore of beaches. The image illustrates the 2 habitat types with a beach backed by saltmarsh on the left and an ebb shoal at a creek mouth on the right

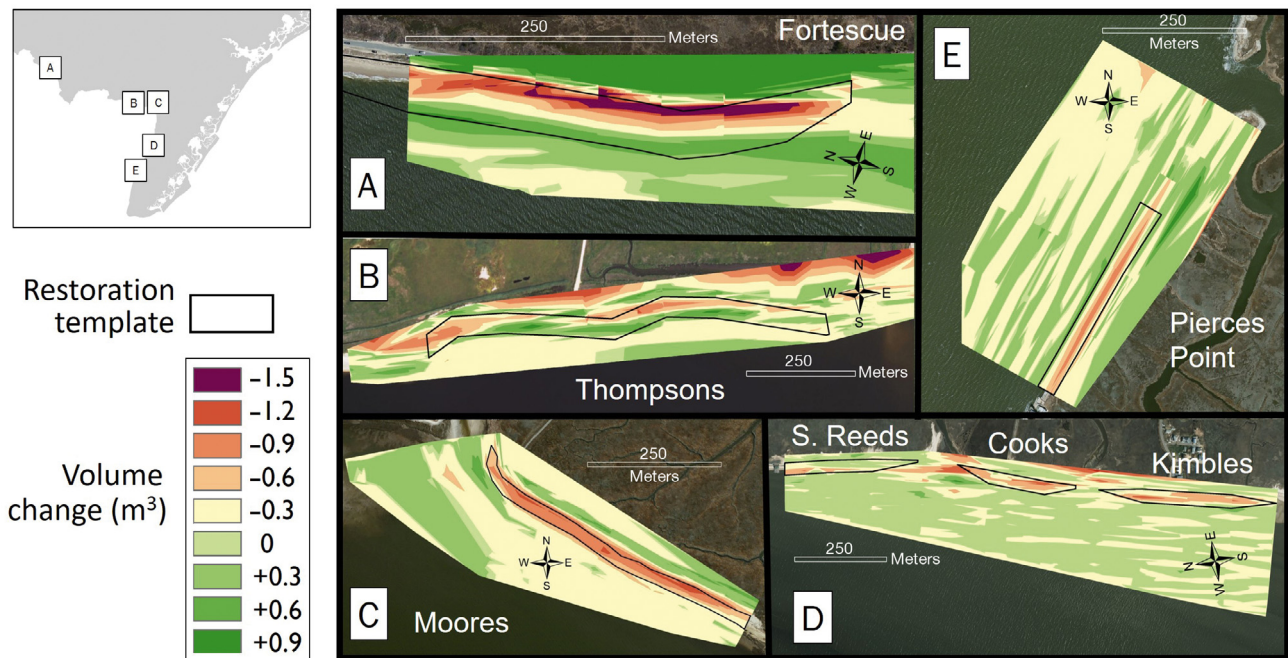


Fig. 8. Depiction of volume change over time for 7 restored beaches. (A) Fortescue, change between April 2015 and April 2016; (B) Thompsons Beach, change between April 2015 and April 2016; (C) Moores Beach, change between April 2014 and April 2016; (D) South Reeds, Cooks and Kimbles Beaches, change between April 2014 and April 2016; (E) Pierces Point, change between April 2014 and April 2016

along Moores Beach (Fig. 8C) stripped sand from the restoration template area and deposited it in the inner creek mouth and shoal. The pattern at Fortescue appeared to be primarily cross shore, with sand moving to the bayward portion of the restoration template and beyond (Fig. 8A). At Thompsons Beach, there was localized erosion of sand at the western end of each of the 2 restored beach cells (Fig. 8B).

4. DISCUSSION

This large-scale project was carried out with the primary purpose of improving horseshoe crab habitat for the benefit of horseshoe crabs and shorebirds. Previous efforts to examine the role of sediment nourishment to improve habitat quality for spawning horseshoe crabs were carried out as small-scale experiments (Jackson et al. 2007, Hsieh & Chen 2009) and larger nourishment projects for shore protection have rarely been evaluated for their impacts on horseshoe crab habitat quality (Botton et al. 2018). Our results indicate that habitat quality for horseshoe crabs and shorebirds can be directly enhanced through sand addition and beach restoration. Horseshoe crabs immediately spawned in sand that had been placed on beaches just a few weeks prior to

their arrival. BACI analysis at our Thompsons Beach project site showed clear benefits of sand addition, with significantly higher horseshoe crab egg cluster abundance compared with unrestored control sites in the year of, and 1 yr after, restoration. Across all sites, beaches restored with sand that matched native sand grain sizes had egg cluster abundances that consistently matched or exceeded that of high-quality reference beaches. Increasing egg cluster abundance likewise increased availability of eggs at the surface and at shallow sand depths where they are accessible for shorebird feeding.

The increase in egg cluster abundance we observed was related to deeper sand depth as a result of sand addition. This pattern could be the result of a redistribution of spawning horseshoe crabs that use restored sites at higher densities and/or due to enhanced egg cluster carrying capacity conferred by increased beach sand volume. There is evidence that horseshoe crabs avoid areas without sand (Botton et al. 1988), and it is likewise possible that they have the capacity to preferentially select high-quality spawning sites.

Sand grain size fractions played an important role in determining egg cluster abundance on beaches. Our results showed that egg cluster abundance increased with increasing proportion of coarse-grained sand on

beaches. An inverse relationship was evident for the proportion of fine-grained sand. Restored beaches with a greater proportion of fine-grained sand had significantly fewer eggs than those that employed coarser-grained material. In this study, mean grain size was not a sensitive indicator of beach habitat quality, with no relationship evident with egg cluster abundance across the range of grain sizes observed on natural and restored beaches. Most prior studies discuss the suitability of sand grain size for horseshoe crabs in terms of mean grain size (Brady & Schrading 1998, Avissar 2006, Jackson et al. 2007), and restored beaches in this study used sand with mean grain sizes that fell within previously published guidelines (Smith et al. 2002). Nonetheless, within this range, varying grain size proportions had marked effects on restoration outcomes. For this reason, we caution against the use of mean grain size metrics because it may not always be sensitive to variation in the proportion of coarse vs. fine grain fractions in samples.

Given that female horseshoe crabs work their entire bodies into the beach face when it is tidally inundated to deposit egg clusters (Brockmann 1990), the lower egg cluster abundance on beaches with a greater proportion of finer sand may indicate either that horseshoe crabs are actively selecting habitat based on grain size or that they have greater difficulty when attempting to position themselves to deposit eggs as a result of sediment compaction. Indeed, we noted during field work that it was more difficult to dig sample pits with shovels in beaches with a greater fine fraction. Greater surface hardness with finer sand has been observed in another study of beach replenishment in Jamaica Bay, New York, USA, also with resulting lower egg cluster abundances (Botton et al. 2018). Here it took several years for horseshoe crabs to spawn at the beach, and only did so after the grain size began to revert to background levels. Beaches in our study replenished using sand with finer-grained composition also reverted over time to a grain size composition that matched natural beaches. This is likely due to effects of wave and current conditions (Stockton University Coastal Research Center 2017) that determine the relative fractions settling along the shoreline, with finer fractions activated and moved from the beach face via cross-shore and longshore drift and via overwash. For projects that focus on property protection and employ larger sand volumes, the persistence and effects of finer-grained sand may be more long-lasting and, when redistributed by wave and currents, may impact other intertidal and subtidal habitats (Wilson & Madsen 2011).

Use of finer-grained sand also results in beach slopes that are less steep (Bascom 1951) and lower pore space that translates to lower interstitial dissolved oxygen, particularly in lower-energy wave environments (Avissar 2006, Vasquez et al. 2015b). Low dissolved oxygen levels can negatively affect the development of horseshoe crab eggs (Penn & Brockmann 1994, Vasquez et al. 2015a,b). Taken together, the results presented here caution against the use of sand with a fine grain (or smaller) fraction that is more than 10% for beach restoration and replenishment. Ideally, replenished sand should match native sand composition (Table 2), because restored beaches in this study that matched native composition had the highest horseshoe crab egg cluster abundances.

In the Delaware Bay, replenishment projects intended to protect human infrastructure may use grain sizes that are finer than native sands. For example, a study in Delaware that experimentally added coarser material to a previously replenished beach (Jackson et al. 2007) recorded mean grain sizes (at 15 cm depth) there of 0.33 mm at a control site and 0.40 mm, which is finer than native sand. Natural beaches on the Delaware side of the bay have a mean grain size of 0.7 mm, which is comparable to the 0.83 mm size documented for the New Jersey side in this study (Jackson et al. 2005). Between 1962 and 2007, Delaware had used 2.3 million m³ of material to replenish beaches (Jackson et al. 2007), and replenishment activity has continued steadily since then. It is not clear whether beach replenishment projects that prioritize property protection will perform in the same way as restoration projects with explicit habitat enhancement goals. While the New Jersey side of the bay has been the subject of no beach nourishment projects for property protection in recent times, replenishment for this purpose has been common on the Delaware side of the bay since the 1960s. Replenishment projects designed for property protection typically have dimensions that are considerably different from natural beaches, with higher and wider berm heights that have disrupted cross-shore sand transfer patterns (Jackson et al. 2010).

These disruptions (Jackson et al. 2010, 2013) may impact shorebirds and horseshoe crabs because there are clear patterns of association with beach geomorphic processes and horseshoe crab egg availability. Beach width, slope and grain size all may affect crab spawning site selection, egg survival (Jackson et al. 2008, Vasquez et al. 2015b) and the transfer of horseshoe crab eggs to the surface where they are available for shorebird consumption (Nordstrom et al. 2006, Jackson et al. 2014). An alternative ap-

proach to shoreline protection is to budget and plan for recurrent, programmatic management working with smaller volumes of sand in order to ensure that natural coastal dynamics will still function properly and to improve or sustain resource value.

The magnitude of sand loss from the restoration design templates in this study varied across sites. Sand moved cross-shore into intertidal areas, along-shore to accumulate in small tidal creek mouths that separate beach segments and into the adjacent marsh via wave overwash during high tide events. The greatest stability was seen at Thompsons Beach and South Reeds Beach, which were 2 sites that did not have a tidal creek mouth adjacent to the construction template. Where creek mouths interrupt longshore drift, ebb shoals form and can be significant sand sinks, particularly on low-energy shorelines like the Delaware Bay, where wave action is not sufficient to return sand to the beach face (Weggel 2011). Our findings from horseshoe crab egg sampling indicate that sand movement into tidal creek mouths was not necessarily a net loss for habitat value because sand transfer to shoals there sustains one of the most productive habitats for foraging shorebirds in the Delaware Bay.

Loveland & Botton (2015) proposed that these shoals represent a refuge habitat for horseshoe crabs as beaches degrade. Shoals instead appear to represent an 'attractive sink' (Delibes et al. 2001) in that they attract a high amount of spawning activity, but this reproductive effort is largely wasted because a relatively small proportion of clusters reach embryonic and larval stages. This is likely because wave and current dynamics cause frequent shifts in the location and size of shoals which results in egg exhumation. This process may also be responsible for the high surface egg availability that we documented on shoals. The differences in horseshoe crab egg abundance patterns between shoals and beaches suggest that the determinants of horseshoe crab spawning and shorebird feeding habitat quality in the Delaware Bay may diverge in some circumstances.

4.1. Recommendations for improving project outcomes

While the project described here had clear benefits for horseshoe crabs and shorebirds, several strategies can be employed to build upon these results to achieve higher rates of sand persistence within design templates while still allowing for natural coastal dynamics. These strategies include the incorporation

of living shorelines (Bilkovic et al. 2016), increasing dune-berm heights, increasing sand grain size and expanding project footprints. Shell reefs and other living shoreline structures can be installed in areas of high erosion. For example, preliminary results from a reef installed in 2015 at South Reeds Beach by the American Littoral Society showed that erosion was reduced low on the beach face, typically where peat is first exposed (unpubl. data collected by S. Hafner on behalf of the American Littoral Society). It is essential that living shorelines are designed and tested to ensure that they do not create barriers to movement or create impingement hazards for horseshoe crabs. Increasing dune heights reduces the frequency of overwash events which further minimizes the loss of sand over the berm into adjacent tidal marsh and likewise helps prevent horseshoe crab strandings in areas behind the beach. This also allows wave runup to pull sand from the upper beach face down to the mid and lower beach face, replacing sand lost from these areas during storm events and under normal wave and current processes (Jackson et al. 2010). Larger sand grain size also reduces the likelihood that sand is activated in the water column and transported from the beach face (Komar 1977) and provides higher-quality horseshoe crab habitat. Finally, carrying out more comprehensive projects along longer stretches of shoreline would help reduce post placement loss of sand into adjacent unmanaged beach cells. Ebb shoals that occur at shoreline discontinuities eventually reach a maximum sand capacity, and surplus sand will then continue to move along the shoreline (Weggel 2011).

An additional strategy for improving long-term maintenance of habitat quality is to expand the restoration focus to include adjacent salt marshes. Beaches in the Delaware Bay are part of a coupled system, where they are supported by underlying marsh along the majority of the shoreline (Lewis et al. 2005). These marshes have been impacted by the historic practice of marsh impoundment for farming (Phillip 1995, Weinstein et al. 2000, Smith et al. 2017b). The consequence of this practice was a dramatic loss of marsh platform elevation. As beaches transgress into lower than normal marshes, dunes flatten and breach, forming overwash fans, and ultimately the beach is more likely to fragment and disintegrate. A comprehensive, programmatic approach of restoring marsh elevation and managing beaches and dunes is needed to maximize the resilience and persistence of these habitats as sea levels continue to rise. The goal is to recover the resilience lost as a result of past human impacts to beaches and marshes

via restoration to ensure the long-term persistence of this coastal ecosystem.

4.2. Habitat management as a critical component of shorebird and horseshoe crab conservation

For the American horseshoe crab, habitat restoration complements other efforts to conserve this species (Smith et al. 2017a), which include harvest management and bycatch reduction (Atlantic States Marine Fisheries Commission 1998) as well as emerging efforts to assess and minimize the population impacts of increasing demand by the biomedical bleeding industry for horseshoe crabs (Krisfalusi-Gannon et al. 2018). Around the world, all horseshoe crab species are under urgent conservation threat from the cumulative impacts of habitat loss (Nelson et al. 2016a,b, Fairuz-Fozi et al. 2018) and use for food, bait and biomedical applications (Botton et al. 2015, John et al. 2018). Habitat restoration can play an important role in the recovery of both Asian and American horseshoe crabs.

For American horseshoe crabs, adding sand to beaches ultimately increases the potential habitat carrying capacity of a site for horseshoe crab spawning output. Additionally, increased horseshoe crab spawning effort on beaches translates to increased eggs available as food for red knots (listed as federally endangered in the USA) and other shorebirds. Egg availability is a critical limiting factor for red knots, influencing both survival and reproduction (Duijns et al. 2017), and overharvesting of horseshoe crabs in the Delaware Bay is considered to be a key driver of population declines of this shorebird (Baker et al. 2004) which triggered its eventual listing under the US Endangered Species Act (US Fish and Wildlife Service NJ Field Office 2014). Abundance estimates of shallow horseshoe crab eggs available for shorebird feeding reported in this study (7000 m^{-2}) and by long-term monitoring (Dey et al. 2019) are considerably lower than estimates from the early 1990s (35000 m^{-2}) for New Jersey Delaware Bay beaches (Botton et al. 1994) before horseshoe crabs were overharvested later in that decade (Smith et al. 2009). Egg abundance likely remains low because the Delaware Bay horseshoe crab population, although stabilized at its 1998 level when unregulated overharvesting was at its peak and management first began (Atlantic States Marine Fisheries Commission 2019), has not recovered to pre-overharvest levels during 20 yr of management (Niles et al. 2009, Millard et al. 2015, Atlantic States Marine Fisheries

Commission 2019). This suggests that, although beach management will be an increasingly fundamental component of efforts to conserve both horseshoe crabs and shorebirds, additional management interventions may be necessary to recover horseshoe crab populations.

The conservation of plants, fish and other wildlife that are dependent on beaches and dunes will increasingly need to incorporate habitat management as a strategy to maintain populations in the face of habitat loss driven by sea level rise (Schlacher et al. 2007, Brierley & Kingsford 2009, Defeo et al. 2009) and to restore habitats degraded by past coastal management actions. In most cases, this will require designs that explicitly account for the physical and biological characteristics that represent high-quality habitat for target species. This may entail, as with horseshoe crabs and shorebirds, simply matching restoration designs with that of an undisturbed natural shoreline so that key habitat attributes are maintained. The need to explicitly account for key habitat attributes in restoration comes with the recognition that such designs may not necessarily maximize shoreline protection for human infrastructure. Nonetheless, there will be an increasing need to identify opportunities for reaching design compromises that both restore and enhance habitat quality for species of conservation concern while also enhancing the protection of human infrastructure.

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