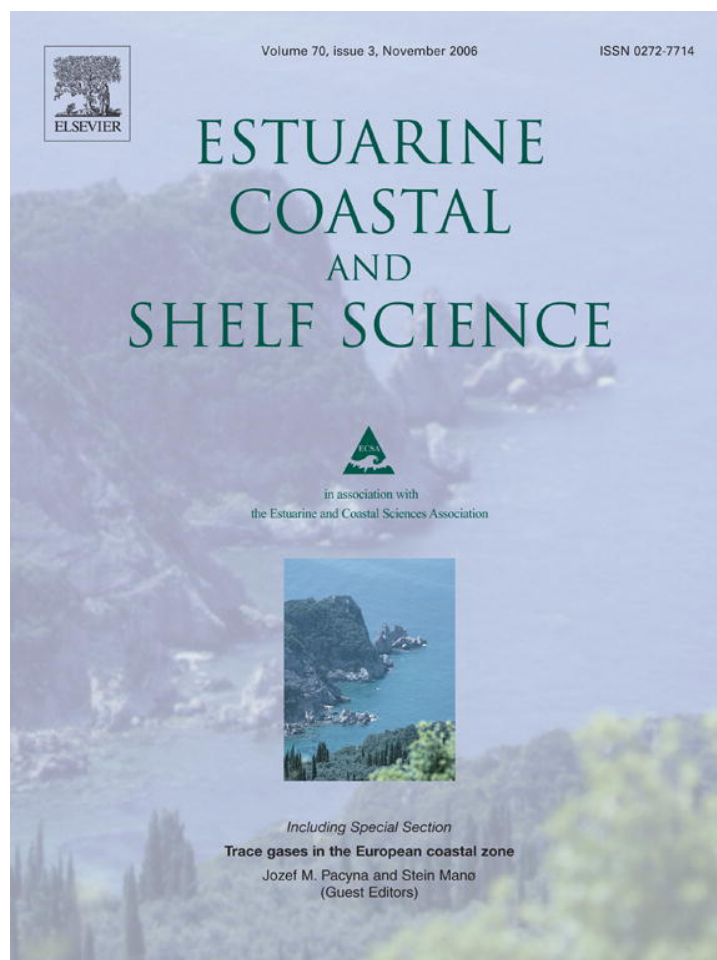


Provided for non-commercial research and educational use only.  
Not for reproduction or distribution or commercial use.



This article was originally published in a journal published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues that you know, and providing a copy to your institution's administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

# Transport of horseshoe crab eggs by waves and swash on an estuarine beach: Implications for foraging shorebirds

Karl F. Nordstrom<sup>a,\*</sup>, Nancy L. Jackson<sup>b</sup>, David R. Smith<sup>c</sup>, Richard G. Weber<sup>d</sup>

<sup>a</sup> Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901, USA

<sup>b</sup> Department of Chemistry and Environmental Science, New Jersey Institute of Technology, Newark, NJ 07102, USA

<sup>c</sup> United States Geological Survey, Leetown Science Center, Kearneysville, WV 25430, USA

<sup>d</sup> Delaware National Estuarine Research Reserve, 818 Kitts Hummock Road, Dover, DE 19901, USA

Received 21 November 2005; accepted 26 June 2006

Available online 28 August 2006

## Abstract

The abundance of horseshoe crab eggs in the swash zone and remaining on the beach after tide levels fall was evaluated to identify how numbers of eggs available to shorebirds differ with fluctuations in spawning numbers of horseshoe crabs, wave energies and beach elevation changes. Field data were gathered 1–6 June 2004 at Slaughter Beach on the west side of Delaware Bay, USA. Counts of spawning crabs and process data from a pressure transducer and an anemometer and wind vane were related to number of eggs, embryos and larvae taken at depth and on the surface of the foreshore and in the active swash zone using a streamer trap. Beach elevation changes and depths of sediment activation were used to determine the potential for buried eggs to be exhumed by waves and swash.

Mean significant wave heights during high water levels ranged from 0.08 to 0.40 m. Spawning counts were low (50–140 females km<sup>-1</sup>) when wave heights were low; no spawning occurred when wave heights were high. Vegetative litter (wrack) on the beach provides local traps for eggs, making more eggs available for shorebirds. Accumulation of litter on days when wave energy is low increases the probability that eggs will remain on the surface. High wave energies transport more eggs in the swash, but these eggs are dispersed or buried, and fewer eggs remain on the beach. Peaks in the number of eggs in the swash uprush occur during tidal rise and around time of high tide. The number of eggs in transport decreases during falling tide. Many more eggs move in the active swash zone than are found on the beach after water level falls, increasing the efficiency of bird foraging in the swash. Greater numbers of eggs in the swash during rising tide than falling tide and fewer eggs at lower elevations on the beach, imply that foraging becomes less productive as the tide falls and may help account for the tendency of shorebirds to feed on rising tides rather than on falling or low tides on days when no spawning occurs.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** horseshoe crab eggs; estuarine beach; Delaware Bay; shorebirds; wave runup; wrack

## 1. Introduction

Knowledge of the movement of eggs and larvae from spawning areas to nursery areas and feeding areas for predators is critical in determining the viability and suitability of habitat for fish and invertebrates (Garvine et al., 1997; Roman and Boicourt, 1999; Brown et al., 2004) and animals that feed

on them (Botton et al., 1994; Burger et al., 1997). The location and timing of egg entrainment, dispersal and deposition have important implications for the migration patterns, feeding behavior and life cycles of some of these organisms. The effect of egg movement on predators can be great, even when the temporal and spatial scales of movement are small. One example is found in the significance of horseshoe crab eggs in Delaware Bay (Fig. 1A, B) to western hemisphere shorebirds that migrate thousands of kilometers from South America to the Arctic (Myers, 1986; Castro and Myers, 1993; Baker et al., 2004; Morrison et al., 2004). Delaware Bay is the most

\* Corresponding author.

E-mail address: [nordstro@marine.rutgers.edu](mailto:nordstro@marine.rutgers.edu) (K.F. Nordstrom).

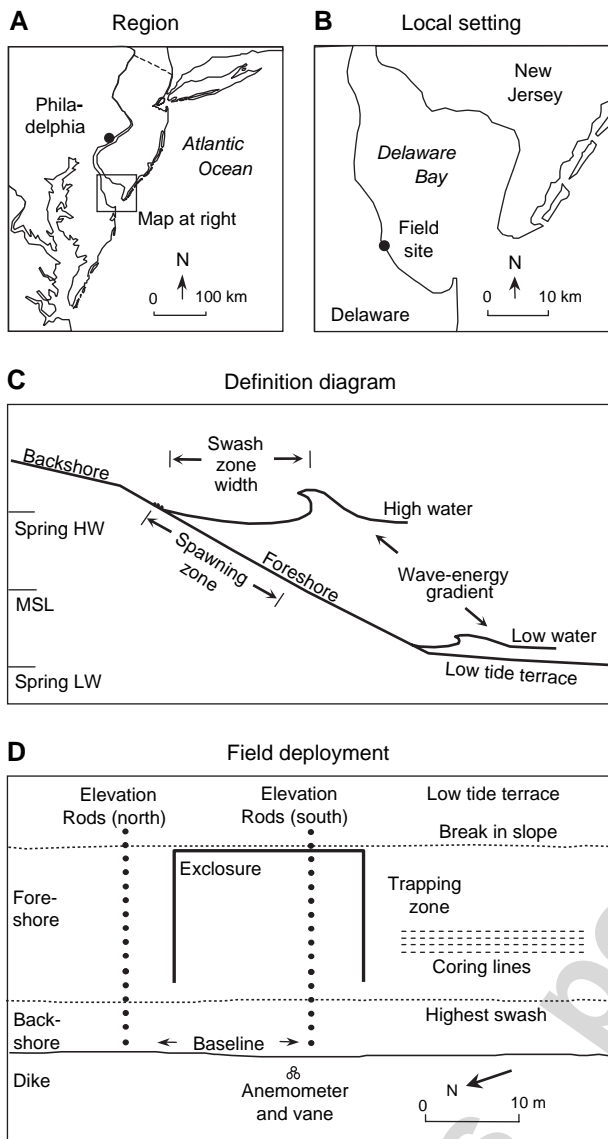


Fig. 1. Study site and location of instruments and trap sampling. The pressure transducer 35 m bayward of the break in slope is not depicted in Block D.

important stopover site on the east coast of North America during the spring (northward) shorebird migration. Horseshoe crab eggs in Delaware Bay are locally abundant only on some beaches and only for short periods in the late spring and early summer (Botton et al., 1994; Smith et al., 2002). On beaches where horseshoe crab spawning occurs, differences in rates of delivery of eggs to shorebirds differ according to fluctuations in spawning numbers, wave energy and beach elevation changes (Smith et al., 2002; Jackson et al., 2005). Tidal cycles are also important, because tidal elevation determines locations of crab spawning (Penn and Brockmann, 1994) and the amount of wave energy delivered to the foreshore (Jackson and Nordstrom, 1993) that, in turn, affect abundance of horseshoe crab eggs.

Local temporal and spatial patterns of foraging activity by migrating shorebirds have been related to temporal changes within the zone of swash uprush and backwash (wave runup

zone) and on the dryer beach above it over the tidal cycle (Burger et al., 1977). Most shorebirds feed in a narrow zone just above the swash limit to a few meters into the water, although Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Caldris alba*) often feed on the beach above the active swash limit (Burger et al., 1977). Burger et al. (1997) observed that shorebirds on a Delaware Bay beach used the beach for foraging at all tidal stages but fed more on rising tides than on falling tides or low tides. These results contrasted with time of foraging on an estuarine beach north of Delaware Bay after the period of horseshoe crab spawning (Burger et al., 1977). Botton et al. (1994) found no difference in shorebird abundance during high tide, mid-tide and low tide, although flock size was larger at high tide. Birds were concentrated at the edge of the water and fed on horseshoe crab eggs in the swash zone at high tide and mid-tide; at low tides, birds dispersed over tidal flats and sand spits at mouths of tidal creeks. Eggs remain on the beach at these times, but foraging is limited.

Knowledge of the number of eggs exhumed and moved in the zone of breaking waves and swash as it moves up and down the beach with the tide and the number of eggs remaining on the beach can help explain the timing and abundance of foraging birds as well as their likelihood of success in using the beach under different weather conditions. Weather conditions are critical to the delivery of eggs because the dominant waves on most estuarine beaches are locally generated by winds blowing across the bay (Nordstrom, 1992), and the amount of horseshoe crab eggs on the surface of the beach is related to the energy of the waves (Smith et al., 2002) and the characteristics of the waves during and after breaking as well as bioturbation by the crabs.

The foreshores of estuarine beaches are relatively steep, and plunging waves are converted to swash without the intervening surf zone that is characteristic of many ocean beaches. The width of the swash zone and the energy of the swash are determined by wave height and period (frequency of arrival of successive wave crests) that are, in turn, determined by wind speed and direction. Under a relatively constant wind direction and speed, swash energies are at a minimum at low tide when wave energies are dissipated on the broad, flat, shallow low tide terrace and at a maximum near high tide, when wave energy dissipation is minimized (Fig. 1C).

The movement of eggs across the foreshore occurs within the swash uprush and backwash. The specific mechanics of egg transport in the swash are not known, but mixing of eggs within the active sediment layer suggests that transport processes of eggs may be similar to non-biogenic sediment. Transport of non-biogenic sediment in the swash zone is a two-stage process, where entrainment and subsequent transport can occur due to (1) turbulence from wave collapse in the breaker zone and interaction of the breaker with the backwash of the previous swash; and (2) bed shear stresses associated with the swash front that then advances across the subaerial beach during the uprush (Puleo et al., 2000). Eggs and sediment deposited in each uprush excursion are subject to removal and transport during the backwash, so more eggs may be in transport than are permanently deposited on the surface

of the beach inundated by the swash. Differences in wave heights and periodicities determine the locations of the seaward and landward limits of the swash zone, the location where the backwash meets the subsequent uprush, and the quantity of sediment and eggs transported in any given swash excursion. The rise and fall of the tide determines where the swash zone intersects the foreshore. Differences in the abundance of eggs at different locations within the beach matrix and differences in the energy of the swash determine the number of eggs released at a given time.

This study was conducted to determine the number of eggs made available to shorebirds in the active swash zone and remaining on the surface of the beach above the active swash zone on an estuarine beach during the rise and fall of the tide. The number of eggs is related to tidal stage and the energy of waves. The field site is Slaughter Beach on the west side of Delaware Bay near the mouth of the estuary (Fig. 1 A, B). This study is one of the several experiments conducted to evaluate the characteristics of the beach prior to implementation of a nourishment operation designed to provide shore protection. The site and the timing of the experiment reported here were not chosen specifically to evaluate the delivery of eggs to shorebirds, but spawning levels were sufficient to evaluate the significance of egg exhumation, transport and deposition.

## 2. Study area

Slaughter Beach is exposed to waves generated within the bay by local winds and waves entering from the Atlantic Ocean. Tides are semi-diurnal with a mean range of 1.40 m and a spring range of 1.68 m. Prevailing winds are from the west and blow offshore, but low-pressure centers bring strong onshore winds from the northeast and southeast. The active foreshore is about 20.0 m wide during spring tides and has a slope of 9.0°. A gently sloping low tide terrace extends bayward of the base of the foreshore. The break in slope between these two beach components is near the elevation of mean low water.

The beach is on an eroding, sandy, former overwash barrier that was, like most of the best spawning sites in Delaware, modified for shore protection through beach nourishment and artificial dune construction. The most recent documented beach nourishment project was in 1986. Sediments are predominantly quartz and feldspar. Mean grain size of sediment is in the range of medium to coarse sand. The study site is not near any longshore obstructions that would interfere with transport of horseshoe crab eggs and sediment alongshore. The closest obstruction is a jetty 3.7 km north of the site. This jetty is too far away to cause conspicuous accumulation or losses of eggs or sediment or changes in beach morphology.

## 3. Methods

All data were collected 1–6 June 2004, the week after the usual peak in shorebird numbers in Delaware Bay (Clark et al., 1993). A wire mesh enclosure fence with openings of

$0.1 \times 0.1$  m was constructed on the foreshore (Fig. 1D) to create a space free of disturbance by crabs to determine whether burrowing had an effect on beach change.

Samples were taken to characterize the number of eggs, embryos and larvae at the following locations: (1) in the litter lines and on the surface of the exposed beach between the litter lines; (2) at depth within the foreshore; and (3) in transport in the swash zone during the rise and fall of the tide. Multiple samples were taken each time data were gathered. These samples (here termed sub-samples) were grouped to reduce the cost of processing and counting eggs. The multiple sub-samples provide a reasonable estimate of mean conditions, but grouping does not allow specification of the variation within the sub-samples, and statistical tests are limited to non-parametric tests. A Mann–Whitney test (two-tail) is used to evaluate differences in the number of eggs at different depths and locations across the foreshore and on different days. This test is used because of its high power efficiency for small samples.

Visual counts of spawning female crabs were made near high tide on the evenings of 1, 3, and 5 June, two days before, the day of, and two days after spring tide, respectively. Counts were made by walking the beach just above the swash for a distance of 0.5 km on each side of the study site and counting crabs 1 m into the water. The 1-m distance captures a high proportion of all spawning crabs at low densities; Brockmann (1990) observed 94% of nesting females within 1 m of the maximum high water line.

### 3.1. Measuring beach changes

Beach elevation changes and depths of sediment activation (depths of disturbance or reworked sediments) were monitored inside and outside the enclosure to determine the potential for buried eggs to be exhumed by waves and swash. Measurements of elevation were made at 2-m intervals along two cross-shore lines (Fig. 1D) during both low tides on 3, 4, and 6 June and during the afternoon low tide on 5 June. Surface elevations were taken from the tops of 10 mm diameter steel rods driven into the sand and tied into a common datum using rod and transit surveys. These elevation rods enable measurement of changes of the sand surface to within 0.5 mm. A loose-fitting washer was placed over the rods to determine depth of sediment activation according to the procedure described in Greenwood and Hale (1980). The distance between the top of the rod and the sand surface is used to measure net change over the monitoring period, whereas the distance between the top of the rod and the washer, which is free to move down the rod as the sediment matrix is reworked, provides a measurement of the lowest level of activation by waves in association with burrowing by horseshoe crabs, if they are present. The depth of activation is always equivalent to or lower than the lowest elevation of the beach surface at the beginning or ending measurement, and it represents the lowest elevation at which eggs can be exhumed or buried. Activation depths where spawning crabs are present are greater than activation depths under waves alone (Jackson et al., 2005), and the depth of activation along the transect outside the enclosure is

used here to describe the maximum potential for release of buried eggs.

### 3.2. Measuring physical processes

Wind speed and direction were monitored to determine the potential for generation of waves and currents and provide insight to conditions during the night when the field team was not on site. These measurements were taken using a Gill 3-cup anemometer and vane mounted 2.65 m above the crest of the dune–dike (Fig. 1D). Water level data used for monitoring tidal rise and fall were collected using a pressure transducer placed 0.10 m above the surface of the low tide terrace, 35 m bayward of the break in slope at the base of the foreshore. Data from this transducer and the wind instruments were sampled continuously throughout the day and night and recorded as 5-min means. Detailed data to determine wave height and period were gathered near time of daytime high water and periodically during trapping using this pressure transducer with wave data recorded at 4 Hz in 17.1-min records. Wave heights reported are significant heights. Wave periods represent the peak energy variance from spectral estimates of transducer data.

Visual observations of the upper limit of swash uprush and the base of the swash, where the breaker meets the backwash of the previous wave, were taken when traps were employed. These locations are used to define the position of mid-swash for trap sampling and to estimate swash width, which provides an estimate of its energy level under the plunging wave conditions occurring during the study.

### 3.3. Sampling eggs visible on the beach surface

Surface samples taken on the exposed beach at low water provide an estimate of the amount of horseshoe crab eggs visible to birds feeding on the foreshore above the limit of swash. The method of sampling was based on a pilot study of egg counts on the beach after high tide on 31 May. Thereafter, samples were taken before and after trapping on 3 and 6 June, after trapping on 5 June, and before trapping on 4 June. Three samples were gathered on each litter line over a longshore distance of 9 m. The number of litter lines across the beach varied between 9 ( $9 \times 3$  sub-samples) and 21 ( $21 \times 3$  sub-samples). An 84-mm wide, 0.5-mm thick card was used to sample the entire width of each litter line and all litter superimposed above the sand surface. The width of each litter line varied. Values per unit area are used to compare concentrations of eggs in litter lines to concentrations on the beach surface between litter lines for data gathered on 31 May and 3 June. Data for those days and subsequent days are reported as mean number of eggs across the entire foreshore  $m^{-1}$  of beach alongshore. The greatest concentration of eggs is in the uppermost litter line. That litter line was sampled separately on 31 May and 3 June to determine the percentage of eggs within it. Data from all other litter lines were grouped, and eggs were counted as one comprehensive sample as an estimate of mean conditions.

Three sub-samples of eggs were taken from the surface of the upper beach in the three zones between each of the upper four litter lines and below the lowest one on 31 May to establish the cross-shore gradient in number of eggs visible on the beach surface but not incorporated into the litter. Once this cross-shore gradient was established using the values from 31 May and visual observations on later days, subsequent monitoring of surface samples consisted of taking three sub-samples at mid-foreshore to represent a mean value for the entire foreshore. Surface samples were gathered over a distance of 0.1 m to a depth of about 3 mm using the 84-mm wide card. The 3-mm depth is the minimum that can be sampled effectively on the surface of the beach and may slightly overestimate the number of eggs visible to birds. Each set of three samples was grouped and reported as number of eggs  $m^{-1}$  alongshore and  $m^{-2}$  of beach surface.

### 3.4. Sampling eggs at depth

Samples taken at depth within the foreshore provide insight to the number of horseshoe crab eggs that can be delivered to shorebirds as a result of exhumation by wave action and digging by spawning crabs. These samples were taken in the zone where greatest spawning intensities normally occur. Sampling was done using a 50-mm diameter core inserted to 200 mm depth along four shore-parallel lines (identified as Lines A–D), spaced 1 m apart (Fig. 1D). Samples on each line were taken at 1-m intervals along a 20-m section of foreshore, resulting in 80 sub-samples. The top line (Line A) was located at mean high water. Cores were taken at times of low water on 1 and 2 June before and after the evening spawning during low energy conditions to provide baseline conditions prior to trapping. Cores also were taken 6 June to identify the effects of relatively high waves occurring on 4 and 5 June. Sub-samples were split into the top 50 mm and 50–200 mm. The top 50 mm has been used to represent the depth at which eggs are available to shorebirds (Botton et al., 1994), and it is a reasonable approximation of the depth frequently reworked by normal bay waves, based on data in Jackson et al. (2005). The 50–200 mm depth represents the location where most horseshoe crab eggs remain undisturbed by non-storm waves but can be reworked during spawning or storm waves. Depths of activation during intensive spawning and low wave heights on beaches in Delaware Bay can be 100 mm (Jackson et al., 2005); depths of activation by storm waves can be 150 mm (Jackson and Nordstrom, 1993). All 20 sub-samples at each of these two depths in each shore-parallel line were then grouped for egg counting, resulting in eight grouped samples per sampling day. These data are presented as number of eggs  $m^{-2}$ .

### 3.5. Sampling eggs in the swash

Estimates of number of eggs in transport were taken in the middle of the swash zone on the upper foreshore using a streamer trap deployed at selected times 3–6 June. Streamer traps are hydraulically efficient and have been used to provide reliable estimates of sediment flux in the surf and swash zones

(Kraus and Dean, 1987; Masselink and Hughes, 1998; Wang et al., 1998). The advantages and limitations of streamer traps relative to alternative techniques for estimating sediment transport are discussed in detail in Wang et al. (1998). The mean error of this kind of trap is calculated as 10%, with a standard deviation of 9%, based on differences in trap weights of side-by-side measurements (Edwards, 1997). The trap used in this study has a 0.1-m wide, 0.8-m high opening and a 1-m long net composed of 0.1-mm nylon mesh. Trap height is higher than the depth of the swash, resulting in a complete sampling of the water column.

The trap was placed facing directly offshore at an estimated mid-swash position based on the amount of beach inundated and exposed during several preceding swash excursions. Each wave within a wave train breaks at a different position, so the relative position within each uprush varied somewhat for each wave sampled, but the mean position is near mid-swash for the time of deployment. The trap was used to sample 5–10 waves per trap deployment during low and moderate energy conditions (3, 4 and 6 June) and for three waves during the relatively high-energy conditions on 5 June. The trap was tilted back and lifted at slack water after each sampled uprush, so sediment and eggs would not be removed by the subsequent backwash, and it was repositioned at the same location on the surface of the beach prior to the next uprush. An additional set of trap samples was obtained within the zone of breaking waves on 4 June to relate the number of eggs in the more turbulent breakers to the number in the swash zone. The total number of eggs, embryos and larvae in each run of 3, 5, or 10 waves was converted to a mean value per wave and multiplied by 10 to represent the number of eggs  $m^{-1}$  of beach length.

Trapping on 3 June began 40 min before high water and lasted until 4 h 35 min after high water. A second set of samples was taken on the subsequent rising tide, from 1 h 30 min after low water to time of mid-tide, when darkness made sampling difficult. Large number of eggs were recovered near mid-tide, so trapping began at least 3 h 40 min before high water on the other days. Trapping ended 55 min after high water on 4 June, 3 h 55 min after high water on 5 June and 2 h 50 min after high water on 6 June.

The beach was occupied by members of the field team during all daylight hours during each trapping experiment, and their presence prevented birds from eating eggs. Negligible spawning occurred during the daytime high tide when trapping occurred, so trap samples represent the amount of eggs made available at that time by wave processes, without addition of newly laid eggs or exhumation of older eggs by crab spawning. Birds feeding at a distance from the site could have reduced the number of eggs delivered by longshore transport, but the number of birds was small.

### 3.6. Egg counts

Samples from the beach surface, the cores and the traps were flushed through a series of screens to separate eggs, embryos and larvae from coarser material and then separate them from the remaining materials by elutriation with running tap

water for large samples and by hand for small samples. Trap samples were sieved to remove as much sediment as possible, but the large amount of vegetation litter in the swash required stirring and decanting samples to separate this debris from eggs, embryos and larvae. Dead (desiccated) eggs were removed and not counted. Eggs were then separated from the other larger stages by sieving (for small quantities) or flotation in a solution of  $MgSO_4$  and tap water. The small eggs sink but embryos and most larvae float or remain in the water column. Damaged embryos and larvae also sink, so they were separated from eggs by sieving. Embryos and larvae were then separated by hand. Direct counts were made for small quantities of eggs. Larger numbers were determined by volume using 212 eggs  $ml^{-1}$  and 60 embryos  $ml^{-1}$ . Seven replicates of volume estimates for egg samples and four replicates of volume estimates for embryo samples were made. Counts of larvae were estimated using damp weights of washed and towel dried samples, using a mean weight per larva of 0.0071 g. Three replicates were used to determine larval weight. Separate counts of eggs, embryos and larvae are presented in the data tables. The interest in this paper is in the availability of eggs for shorebirds rather than evolution of these eggs to mature stages, so all three stages are grouped and referred to as eggs in discussions about the potential for shorebird feeding.

## 4. Results

Onshore wind speeds and wave heights were low on 1–3 June and on 6 June (Table 1). The lack of energetic bay waves caused ocean swell (periodicities  $> 5.0$  s) to be dominant in the wave record at times. Wave period was bimodal on 6 June, with two distinct peaks in the spectral record. Wave heights were greater on 4 and 5 June, due to relatively strong onshore winds. Tidal amplitudes were similar during all trapping experiments (Fig. 2). The strong onshore winds of 5 June caused a slight rise in both the high and low elevations for that day and on 6 June. The greatest swash widths monitored during the study were 9.0 m, occurring at high tide on 5 June.

Net beach profile change was limited during the low energy conditions between 1 June and the morning of 4 June (Fig. 3). The wind events of 4 and 5 June resulted in erosion of the lower beach and deposition on the upper beach, where cores were taken. Erosion occurred on the upper foreshore between 5 and 6 June while the lower foreshore remained stable.

Spawning counts revealed 50 spawning females  $km^{-1}$  alongshore the evening of 1 June and 140 females  $km^{-1}$  the evening of 3 June. No counts were made on 2 June. Spawning could be expected on 2 June, given the spawning that occurred on the evenings of 1 and 3 June and the similar wave conditions on 2 June (Table 1). No spawning was observed on the evening of 5 June, and it is unlikely that spawning occurred during the evening of 4 June, given the high wave heights.

### 4.1. Eggs at depth

Samples from the 12 coring lines for all days (Table 2) reveal that the wave-reworked upper substrate (top 50 mm)

Table 1

Mean wind and wave data gathered during the high tide before cores were taken on 1 and 6 June and during the rise and fall of the tide during trapping. Data for 2 June are for the high tide prior to trapping on 3 June

Day	Time of trapping	Wind speed (m s <sup>-1</sup> )	Wind direction (deg. from shore normal)	Wave height (m)	Wave period (s)
1 June					
Pre-coring	N/A	1.1	65.3	0.10	3.2
During spawn	N/A	0.8	6.3	0.09	9.2
2 June	N/A	1.4	44.5	0.09	10.6
3 June	08:55–15:25	2.8	0.4	0.10	10.1
	17:20–19:10	3.2	26.4	0.08	8.0
4 June	06:45–11:40	6.5	41.9	0.21	3.6
5 June	07:30–15:30	10.4	55.6	0.40	4.2
6 June	09:00–15:30	3.9	2.9	0.13	8.5, 2.8 <sup>a</sup>

<sup>a</sup> Bimodal.

has far fewer eggs than the 50–200 mm deep substrate below it (Mann–Whitney test,  $p = 0.0002$ ). No spawning occurred during the daytime high tide preceding the pre-spawning coring on 1 June. Eggs exhumed by waves prior to coring were not replenished by crabs, and the top 50 mm has the fewest eggs of the three sampling times. Net beach change between 1 and 2 June was  $-30$  mm, and depth of sediment activation was 105 mm lower than the previous surface. The larger number of eggs in the top 50 mm of the cores after spawning appears to reflect the

remobilization of buried eggs supplemented by new eggs made available during spawning.

Fewer eggs occur in the 50–200 mm portion of the four coring lines on 6 June than on 1 and 2 June (Table 2) (Mann–Whitney test,  $p = 0.03$ ). This occurs because eggs near the surface of the pre-storm beach were removed by storm-wave activation and because the accretion on the upper beach resulting from the storms of 4 and 5 June increased the depths to any undisturbed eggs (Fig. 3, detail of core area). No spawning occurred to add eggs to the beach matrix. The

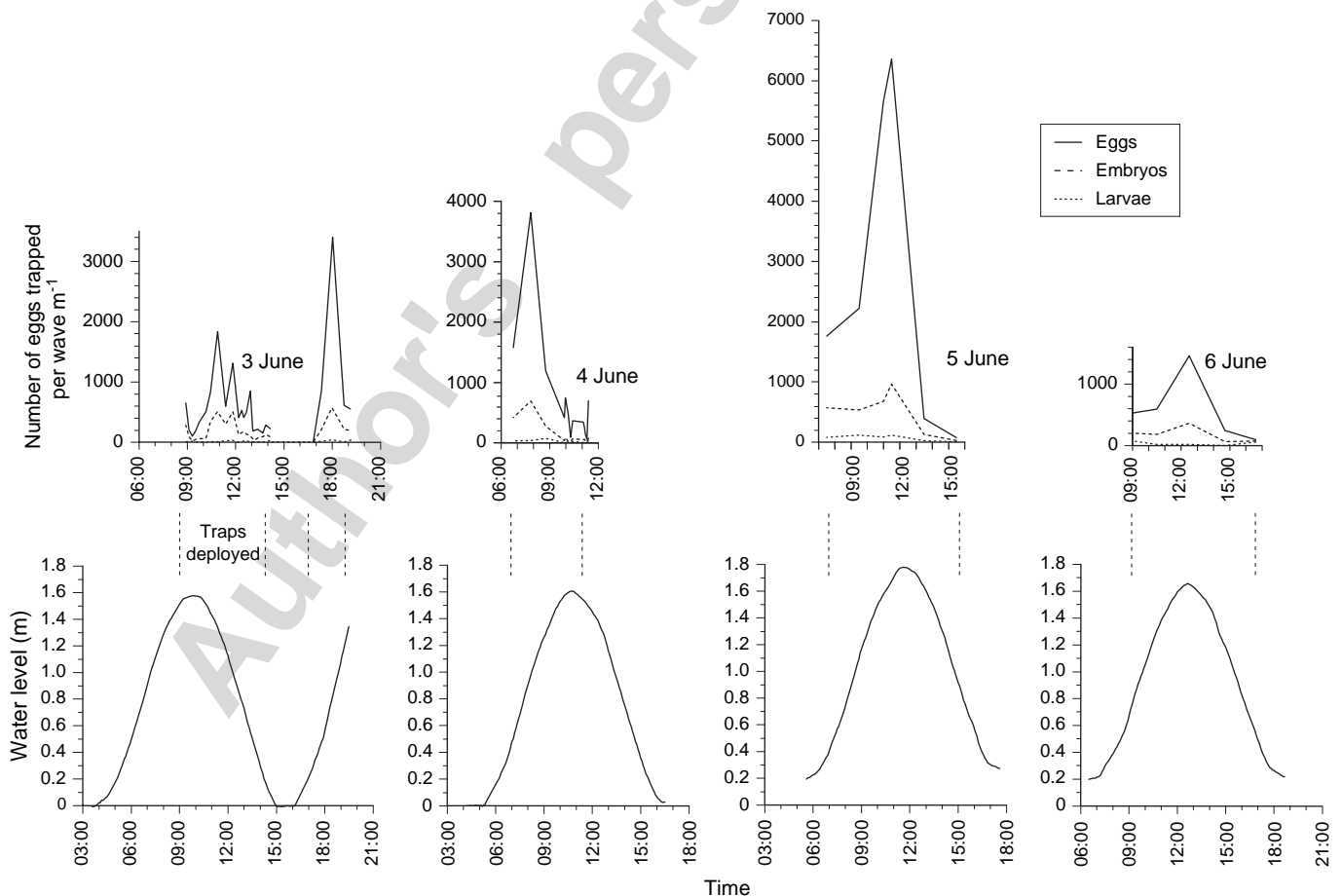


Fig. 2. Water levels and rates of trapping per wave. Trap measurements are discrete points; lines are fitted for ease of interpretation.

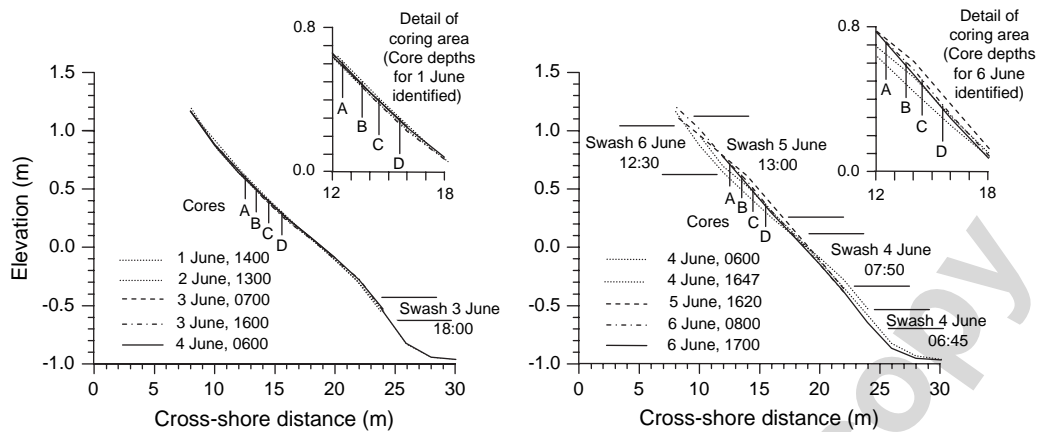


Fig. 3. Beach profiles measured at low tide on elevation rods on south line (Fig. 1D) during trapping period. Swash zone widths are depicted for key times during trapping.

number of eggs between 50 and 200 mm at the two lower coring lines (C and D) is greater because at least a portion of the bottom of the core reached the part of the beach that was not reworked by the higher waves (Fig. 3, detail). The number of eggs in the top 50 mm of the upper two coring lines (A and B) on 6 June is similar to the number of eggs in the top 50 mm of beach in the wave-reworked samples taken prior to spawning on 1 June, but the other two coring lines, which are lower on the beach, have quantities at least as great as the wave-reworked beach after spawning on 2 June.

#### 4.2. Eggs in the swash

Plots of number of eggs, embryos and larvae collected by streamer trap (Fig. 2) reveal similar temporal trends in trapping rates of eggs and embryos although the magnitudes differ each day, and there are short-term fluctuations. The low number of larvae trapped is not surprising since few larvae could be expected to emerge from the beaches and enter the plankton until late June (Botton and Loveland, 2003) and because

larvae tend to emerge during nocturnal high tides (Rudloe, 1979), which were not sampled. The most conspicuous trend in the plots in Fig. 2 is a pronounced peak in number of eggs in the swash during the higher stages of the rising tide and a pronounced decrease in the number of eggs as water levels fall. Data from the traps cannot be correlated with individual wave heights directly because each wave cannot be isolated from the record from the pressure transducer, but correlations of the trap samples with the means of 13 17.1-min records taken during sampling reveal a Pearson coefficient ( $r$ ) of 0.599 ( $p = 0.031$ ). There appears to be little relationship between mean wave height and number of eggs in transport in the swash at some of the times in the tidal cycle, as revealed in the relatively high rate of trapping on the evening of 3 June when mean wave height was  $<0.10$  m. The reasons for differences in trapping rates are best evaluated by examining the way wave conditions and beach changes vary each day.

Maximum depth of sediment activation during the day on 3 June was only 46 mm, so relatively few buried eggs were released by wave activation and incorporated into the swash

Table 2  
Eggs, embryos and larvae in beach cores. Numbers for each coring line represent the grouped counts of the 20 sub-samples adjusted to represent a value  $m^{-2}$

Day/location	Top 50 mm			50–200 mm		
	Eggs	Embryos	Larvae	Eggs	Embryos	Larvae
1 June, after day high tide						
Coring line A (uppermost)	2255	372	353	267,967	105,877	27,450
Coring line B	3373	372	157	400,077	21,979	17,391
Coring line C	6509	745	137	608,499	25,979	7392
Coring line D (lowest)	2863	78	39	307,730	99,995	1196
2 June, after night spawn						
Coring line A (uppermost)	8568	1804	333	499,622	176,462	14,196
Coring line B	8902	1921	10,784	524,895	188,226	41,802
Coring line C	8784	666	412	603,931	76,744	14,862
Coring line D (lowest)	11,038	1235	314	551,933	64,703	6118
6 June, after high waves						
Coring line A (uppermost)	2333	275	20	9489	490	137
Coring line B	3510	471	20	8803	1059	980
Coring line C	14,744	2118	0	29,253	3156	392
Coring line D (lowest)	11,803	1706	137	62,605	11,921	1529

(Fig. 2). As on the other days, the number of eggs decreased as water level fell after high water, but the number of eggs increased dramatically during the subsequent rise. Wave and swash energies were low at that time, seen in the narrow width of the swash zone (Fig. 3).

Maximum depth of sediment activation on the foreshore during high water prior to trapping on 4 June was 83 mm, indicating that relatively high waves occurred. Many more eggs were trapped in the uprush per wave early during the rising tide than near high tide on 4 June (Fig. 2). No wave record was taken early in the rising tide, but the low water levels would have caused wave energy dissipation on the low tide terrace, resulting in low wave energies in the swash, as documented in the narrow swash zone width of 1.5 m at 06:45 (Fig. 3). The amount of eggs in transport peaked at 07:50, when swash energies were greater (Fig. 3). Maximum depth of sediment activation measured after trapping was 81 mm. Beach change on the upper foreshore was greater than on 3 June (Fig. 3) and could have helped mobilize eggs from the beach matrix. Up to 40 mm of erosion occurred low on the foreshore, which would have mobilized additional eggs.

Maximum depth of sediment activation during the night prior to trapping on 5 June was 151 mm, reflecting high wave heights. This depth is only slightly less than the activation depth of 182 mm occurring during the 0.4 m high waves on 5 June when traps were employed. The net result of this storm on the beach profile was accretion on the upper foreshore, but maximum activation depth was 220 mm lower than the surface of the beach on the morning of 4 June, indicating that eggs deposited on the beach prior to the morning of 4 June had been reworked.

The trap sample taken at 07:30 on 5 June is in, approximately, the same location and stage of the tide as the sample taken on 4 June at 06:45, and trapping rates (Fig. 2) are similar (2032 eggs of all stages on 4 June and 2414 on 5 June). Wave heights were greatest from 11:00 to 13:00 (mean of 0.43 m), and swash uprush widths at this time (Fig. 3) were the greatest of all days monitored. The number of eggs trapped in the uprush per wave was greatest of all days under these conditions when water level was high but then was reduced dramatically when water level fell (Fig. 2), although wave heights remained high.

Maximum depth of sediment activation during the night prior to trapping on 6 June was 100 mm, indicating relatively

high waves. In the absence of spawning, these waves were responsible for making eggs available on the beach prior to trapping (Table 3). Wave heights during trapping on 6 June were low and varied little between 10:45 and 14:45, when process data were measured. The number of eggs trapped in the uprush was greatest near high water (Fig. 2) and then decreased, although wave heights remained similar. The width of the swash zone was only 3.6 m during high water (Fig. 3). Maximum depth of activation during the daytime tidal cycle was only 34 mm.

#### 4.3. Eggs on the beach surface

On 31 May, the numbers of eggs of all stages in the top four litter lines proceeding downslope over a distance of 0.7 m were  $172,750 \text{ m}^{-2}$  ( $3,455 \text{ m}^{-1}$ ),  $91,200 \text{ m}^{-2}$  ( $912 \text{ m}^{-1}$ ),  $18,667 \text{ m}^{-2}$  ( $280 \text{ m}^{-1}$ ) and  $15,205 \text{ m}^{-2}$  ( $456 \text{ m}^{-1}$ ). The numbers of eggs of all stages on the surface of the upper foreshore between the upper four litter lines and 0.6 m below the fourth litter line are 4920, 2333, 752 and  $70 \text{ m}^{-2}$  proceeding downslope. These differences in the number of eggs within the four litter lines and at the four sampling locations between the litter lines are significant at the 0.03 level (Mann–Whitney test). Thus, the concentration of eggs in the litter lines and on the surface of the foreshore decreases with distance offshore, and the concentration of eggs in the litter lines is much greater than on the beach surface between them, making foraging by shorebirds in the litter lines more productive.

Surface samples taken prior to trapping on 3 June (Table 3) reveal the most eggs encountered during all inventories of litter lines. The uppermost litter line had 29.9% of eggs of all stages. There were  $134 \text{ eggs m}^{-2}$  on the surface of the foreshore between litter lines. Surface samples taken near the time of low water after trapping on 3 June (15:30) reveal relatively large numbers of eggs, with the uppermost wrack line containing 20.6% of them. The surface of the intertidal beach at that time had  $24 \text{ eggs m}^{-2}$ .

Samples of the 13 litter lines at 06:00 near morning low water on 4 June (Table 3) reveal fewer eggs than the previous day, presumably because there was little vegetative litter to provide an effective trap. Surface samples between the litter lines indicated that there were  $103 \text{ m}^{-2}$  of eggs  $\text{m}^{-1}$  of beach. Samples of all litter lines at low tide after trapping on 5 June reveal the fewest eggs  $\text{m}^{-1}$  of beach, although the trapping rates

Table 3

Grouped total number of eggs, embryos and larvae in beach litter lines and in the largest set of uprush samples, adjusted to represent a value  $\text{m}^{-1}$  alongshore

Day	In all litter lines ( $\text{m}^{-1}$ beach)			In uprush sample (per wave, $\text{m}^{-1}$ beach)				
	Time	Eggs	Embryos	Larvae	Time	Eggs	Embryos	Larvae
3 June	Pre-trap, 06:00 (12 lines)	9973	4782	647	10:54 (10 waves)	1837	507	10
	Post-trap, 15:30 <sup>a</sup> (9 lines)	7095	1172	126	18:00 (10 waves)	3403	580	37
4 June	Pre-trap, 06:00 (13 lines)	2564	1529	169	07:50 (5 waves)	3816	692	36
5 June	Post-trap, 17:30 (uncounted)	686	333	55	11:30 (3 waves)	6360	967	120
6 June	Pre-trap, 08:00 (21 lines)	3387	1646	463	12:30 (5 waves)	1462	362	18
	Post-trap, 18:30 (16 lines)	1247	886	318				

<sup>a</sup> Represents pre-trap sample for trapping period 17:20–19:10.

preceding these recoveries were the greatest of all days (Table 3), indicating that high wave energies can move many eggs in the swash, but these eggs may not be available on the surface of the beach after water level falls. The average number of eggs  $m^{-1}$  alongshore in one swash uprush in the largest sample on 5 June is an order of magnitude greater than the number  $m^{-1}$  alongshore remaining across the entire beach surface (Table 3). The average number of eggs moved in one swash uprush during the best time for egg transport on 4 June is also greater than the number remaining on the beach  $m^{-1}$  (Table 3). Samples of the 16 litter lines after trap sampling in the afternoon of 6 June reveal relatively few eggs  $m^{-1}$  of beach. The lack of eggs on the surface and in the swash zone (Fig. 2) implies that the storm on the previous day had depleted the eggs in the top few centimeters of the beach where the low energy waves could rework them.

## 5. Discussion

Some of the variability in number of eggs in trap samples (Fig. 2) may be due to the interaction of the breaking wave with the backwash of the previous wave at different phases in the breaking cycle and at different locations on the beach. These short-term fluctuations make it impossible to accurately predict where the position of the trap within the swash zone will be on the subsequent uprush, so the trap will not sample the exact midpoint of each swash uprush. Differences in relative position of the trap do not obscure the overall trends in the data that reveal greater quantities of eggs on the rising tide than the falling tide.

The number of eggs transported in the swash and remaining on the beach is not solely a function of wave energy. More eggs are moved in the swash during the rising tide than during the falling tide at similar or higher wave heights, implying that eggs removed from the beach during rising tide are dispersed offshore or remain trapped in the breaker zone after high tide. The low recovery of eggs of all types in all of the litter lines across the beach on 5 June, despite the large numbers in the swash (Table 3) implies that the energetic and turbulent swash keeps vegetative litter and eggs in suspension and disperses them offshore or buries them within the large amount of sand and gravel moved under these conditions. Preferential surface transport and accumulation of the lighter and more readily suspended biogenic particles would occur under low energy conditions, when the sand fraction is less mobile. The inverse relationship between number of eggs in the swash and number of eggs remaining on the surface of the beach on the morning of 3 June and on 5 June indicate that low wave energies facilitate the accumulation of surface eggs, just as low wave energies facilitate the accumulation of surface gravel and vegetative litter (Nordstrom, 1992; Nordstrom and Jackson, 1993).

Whether eggs are available to migratory shorebirds is influenced in part by their foraging behaviors. Shorebirds do not all pick eggs off the surface of the beach. Ruddy Turnstones dig pits up to 50 mm depth, and these pits may be subsequently reworked by other species. Our results are most applicable

to birds feeding in the swash and on the surface within and between the litter lines.

The concentration of eggs in the litter lines is much greater than the concentration of eggs on the beach surface between them. Vegetative litter and other flotsam on the beach provide local traps for eggs, making eggs more available for shorebirds. Vegetative litter has greater potential for retaining moisture than the surrounding sediment (Jansson, 1967) and may keep the eggs fresher and more appealing as food for birds. The accumulation of vegetative litter on days when wave energy is low increases the probability that eggs will remain on the surface. The importance of litter lines in concentrating prey, retaining prey across a range of tide levels, and serving as substrate for litter-associated invertebrates has been observed in studies of shorebird foraging in sandy beach habitat (Dugan et al., 2003; Hubbard and Dugan, 2003). Dugan et al. (2003) reported a direct association between shorebird abundance and the amount of litter on sandy beaches.

The large number of eggs moving in the active swash zone when wave energies are relatively high (4 and 5 June) increases the value of birds foraging there rather than on the beach above it. The number of eggs remaining on the beach above the swash zone is finite and can be rapidly depleted during feeding, so the swash zone may be preferable to the beach. Counts of eggs remaining on the beach at low tide may underestimate the availability of eggs to birds using the active swash zone for foraging.

The tendency for shorebirds to feed along the edge of the water, following the tide line, rather than feeding higher on the beach has been attributed to the softer wetted substrate (Penn and Brockmann, 1994). The large number of eggs in the swash and the lack of appeal of desiccated eggs may be additional factors. It is also possible that eggs moving in the swash zone are easier to see, especially at low flow velocities, when the more buoyant eggs remain in transport after most of the heavier terrigenous sediments settle. Competition for food and feeding space is intense in the swash zone, and birds can exhibit high levels of aggression here (Burger et al., 1977). When gulls are present, they can monopolize the water line, limiting shorebirds to drier sand farther up the beach (Botton et al., 1994). The limited availability of eggs higher on the beach places shorebirds at a disadvantage under these conditions.

Decreasing numbers of eggs in transport in the swash during the falling tide and decreasing numbers of eggs in litter lines with lower elevations on the beach imply that foraging in and above the upper limit of swash becomes less productive as the tide falls. The tendency of shorebirds to feed during times of higher water levels rather than on falling tides or low tides during times when horseshoe crab eggs are available, noted by Burger et al. (1997), could be partially attributed to the greater number of eggs in the swash during rising or high tide than falling or low tide. They note that shorebirds on beaches where horseshoe crabs spawn leave the beach after high tide. Foraging could be successful during a falling tide that occurs right after intensive spawning, but eggs would be limited when little spawning occurs the previous high tide

and wave energies are too low to mobilize buried eggs. Enhanced opportunities for shorebird feeding on incoming tides and high-energy events due to active release of buried prey was also noted by Hubbard and Dugan (2003).

The nutrient stores accumulated by shorebirds during their stopover in Delaware Bay are critical to their survival (Baker et al., 2004; Morrison et al., 2004). The availability of eggs is not only simply related to the numbers laid on the beach but also to the numbers of eggs that are released from the beach matrix by crab digging and wave activation (Jackson et al., 2005) and the numbers delivered by swash. Fewer eggs are available in the swash and on the surface of the beach above the active swash after peak spawning periods, making reworking of eggs already in the beach critical to the survival of shorebirds that are still feeding after peak spawning periods. The inverse relationship between number of eggs moved in the swash and number of eggs remaining on the surface of the beach and the unequal distribution of eggs with distance across the beach and through time within the swash point to the importance of understanding the way eggs are moved and distributed by wave and swash action, which in turn is related to weather conditions.

## 6. Conclusions

- (1) Peaks in the number of eggs in the swash occur during high stages of the rising tide or high tide.
- (2) The number of eggs in the swash decreases considerably after high tide.
- (3) Many eggs may be moved in the swash during high wave energy conditions, but these eggs may not be available on the surface of the beach after water levels fall.
- (4) Eggs remaining on the beach surface are concentrated in litter lines where vegetative flotsam provides a local trap.
- (5) Eggs in litter lines increase in quantity with elevation on the upper beach.
- (6) The concentration of eggs in the litter lines is much greater than the concentration on the beach surface between them, making foraging in the litter lines more productive.
- (7) The large number of eggs in the swash relative to those remaining on the beach above the active swash may increase the success of birds that forage in the active swash zone.
- (8) Counts of eggs remaining on the beach at low tide may underestimate the availability of eggs to birds using the active surf zone for foraging.

## Acknowledgements

We are grateful to Bill and Shawna McSpadden for access to their property and for logistical support and to Dipanjali Chavan, Eric Crawford, Jim Julian, Mike Kirkland and Ronnachai Tiyyarattanachai for assistance in the field and lab. This publication was supported by the National Sea Grant Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant No. R/CZM-

2004-1. NJSJG-06-634. The views expressed herein do not necessarily reflect the views of any of those organizations.

## References

- Baker, A.J., González, P.M., Piersma, T., Niles, L.J., de Lima, I., do Nascimento, S., Atkinson, P.W., Clark, N.A., Minton, C.D.T., Peck, M.K., Aarts, G., 2004. Rapid population decline in red knots: fitness consequences of decreased refueling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B* 271, 875–882.
- Botton, M.L., Loveland, R.E., 2003. Abundance and dispersal potential of horseshoe crab (*Limulus polyphemus*) larvae in the Delaware Estuary. *Estuaries* 26, 1472–1479.
- Botton, M.L., Loveland, R.E., Jacobsen, T.R., 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. *Auk* 111, 605–616.
- Brockmann, H.J., 1990. Mating behavior of horseshoe crabs, *Limulus polyphemus*. *Behaviour* 114, 206–220.
- Brown, C.A., Holt, S.A., Jackson, G.A., Brooks, D.A., Holt, G.J., 2004. Simulating larval supply to estuarine nursery areas: how important are physical processes to the supply of larvae to the Aransas Pass inlet? *Fisheries Oceanography* 13, 181–196.
- Burger, J., Howe, M.A., Hahn, C., Chase, J., 1977. Effects of tidal cycles on habitat selection and habitat partitioning by migrating shorebirds. *Auk* 94, 743–758.
- Burger, J., Niles, L., Clark, K.E., 1997. Importance of beach, mudflat and marsh habitats to migrant shorebirds on Delaware Bay. *Biological Conservation* 79, 283–292.
- Castro, G., Myers, J.P., 1993. Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. *Auk* 110, 927–930.
- Clark, K.E., Niles, L.J., Burger, J., 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95, 694–705.
- Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science* 58S, 25–40.
- Edwards, T., 1997. Sediment transport in the swash zone of a sandy beach. Unpublished honors thesis, Department of Environmental Engineering, University of Western Australia, Nedlands.
- Garvine, R.W., Epifanio, C.E., Epifanio, C.C., Wong, K.-C., 1997. Transport and recruitment of blue crab larvae: a model with advection and mortality. *Estuarine, Coastal and Shelf Science* 45, 99–111.
- Greenwood, B., Hale, P.B., 1980. Depth of activity, sediment flux and morphological changes in a barred nearshore environment. In: McCann, S.B. (Ed.), *The Coastline of Canada*. Geological Survey of Canada, Ottawa, pp. 89–109 (Paper 80-10).
- Hubbard, D.M., Dugan, J.E., 2003. Shorebird use of an exposed sandy beach in southern California. *Estuarine, Coastal and Shelf Science* 58S, 41–54.
- Jackson, N.L., Nordstrom, K.F., 1993. Depth of activation of sediment by plunging breakers on a steep sand beach. *Marine Geology* 115, 143–151.
- Jackson, N.L., Nordstrom, K.F., Smith, D.R., 2005. Influence of waves and horseshoe crab spawning on beach morphology and sediment grain size characteristics on a sandy estuarine beach. *Sedimentology* 52, 1097–1108.
- Jansson, B.-O., 1967. The significance of grain size and pore water content for the interstitial fauna on sandy beaches. *Oikos* 18, 311–322.
- Kraus, N.C., Dean, J.L., 1987. Longshore sediment transport rate distributions measured by trap. In: *Proceedings of Coastal Sediments '87*. American Society of Civil Engineers, New York, pp. 818–896.
- Masselink, G., Hughes, M., 1998. Field investigation of sediment transport in the swash zone. *Continental Shelf Research* 18, 1179–1199.
- Morrison, R.I.G., Ross, R.K., Niles, L.J., 2004. Declines in wintering populations of Red Knots in southern South America. *Condor* 106, 60–70.

- Myers, J.P., 1986. Sex and gluttony on Delaware Bay. *Natural History* 95, 68–77.
- Nordstrom, K.F., 1992. *Estuarine Beaches*. Elsevier Science Publishers, London.
- Nordstrom, K.F., Jackson, N.L., 1993. Changes in cross shore location of surface pebbles on a sandy estuarine beach. *Journal of Sedimentary Petrology* 63, 1152–1159.
- Penn, D., Brockmann, H.J., 1994. Nest-site selection in the horseshoe crab *Limulus polyphemus*. *Biological Bulletin* 187, 373–384.
- Puleo, J.A., Beach, R.A., Holman, R.A., Allen, J.S., 2000. Swash zone sediment suspension and transport and the importance of bore-generated turbulence. *Journal of Geophysical Research* 105, 17021–17044.
- Roman, M.R., Boicourt, W.C., 1999. Dispersal and recruitment of crab larvae in the Chesapeake Bay plume: physical and biological controls. *Estuaries* 22, 563–574.
- Rudloe, A., 1979. Locomotor and light responses of larvae of the horseshoe crab, *Limulus polyphemus* (L.). *Biological Bulletin* 157, 494–505.
- Smith, D.R., Pooler, P.S., Loveland, R.E., Botton, M.L., Michels, S.F., Weber, R.G., Carter, D.B., 2002. Indices of horseshoe crab (*Limulus polyphemus*) reproductive activity on Delaware Bay beaches: interactions with beach characteristics. *Journal of Coastal Research* 18, 730–740.
- Wang, P., Kraus, N.C., Davis Jr., R.A., 1998. Total longshore sediment transport rate in the surf zone: field measurements and empirical predictions. *Journal of Coastal Research* 14, 269–282.

Author's personal copy