Physical and chemical changes in the foreshore of an estuarine beach: implications for viability and development of horseshoe crab *Limulus polyphemus* eggs

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ABSTRACT: Knowledge of conditions that favor development of eggs is important for management of species whose population growth is sensitive to early life history survival. Viability and development of the eggs of horseshoe crabs *Limulus polyphemus* on a sand and gravel beach were evaluated using data gathered on Delaware Bay, USA, from 18 May to 19 June 2004. Eggs were transplanted to pouches and buried in the foreshore for up to 6 wk. Viability and developmental stage were estimated as a function of oxygen and temperature gradients across the foreshore. These gradients were related to the characteristics of the intertidal foreshore sediments, beach water table changes, and frequency of inundation due to tide and swash/backwash processes. Results demonstrate the importance of interstitial temperature for development to larvae and the passive role of sediment characteristics on moisture retention and temperature. Percentage of eggs remaining in egg stage was similar across the foreshore, but more eggs developed to embryos at 0.45 of foreshore width, where moisture and gravel content were greater and interstitial temperature was lower. More eggs developed to larvae at 0.60 and 0.75 of foreshore width, where moisture and gravel content were less but interstitial temperature was higher. The beach above 0.75 of foreshore width came under the influence of wave action or full tidal inundation only during high wave heights or spring tides, and pouches at 0.75 of foreshore width were inundated only 19% of the time. Periodic wetting at this elevation did not reduce overall viability of the eggs. High wave energy events resulted in sediment activation depths to pouches at 0.30 of foreshore width, where loss of eggs due to wave activation was the most important control on the development of eggs.

KEY WORDS: Delaware Bay · Estuarine foreshore · Horseshoe crab · Egg development · Sediment activation

INTRODUCTION

Knowledge of changes in chemical and physical parameters in the interstitial foreshore is important to understanding zonation patterns of fauna, including nest site selection and subsequent success of eggs laid in the sediment matrix (Brown & McLachlan 1990, Penn & Brockmann 1994, Wood & Bjorndal 2000). Marine species that live in the aquatic environment but spawn on the intertidal foreshore of beaches include capelin *Mallotus villosus* (Nakashima & Taggart 2002), grunion *Leuresthes tenuis* (Smyder & Marin 2002), horseshoe crab *Limulus polyphemus* (Shuster et al. 2004), surf smelt *Hypomesus pretiosus* (Rice 2006) and sand lance *Ammodytes hexapterus* (Robards et al. 1999). These species bury their eggs within the upper decimeters of the foreshore, where they are subject to wave shoaling and breaking, wave-induced currents,

and periodic wetting and drying from tide and swash excursions. Oxygen, temperature and moisture in the foreshore influence the rate that eggs develop and hatch. Less than optimal conditions for egg development in the interstitial foreshore environment can lead to higher risk of mortality.

Spawning and subsequent development success is important to population viability for species under population stress, due to commercial and ecological demands. Recent declines in the American horseshoe crab population from past harvest and foreshore modification for shore protection have raised concerns for long-term viability of the species and dependent species including migratory shorebirds (Odell et al. 2005). Early life history survival, including egg development, is an important link to population growth for the American horseshoe crab (Sweka et al. 2007). Thus, conditions that favor faster development from egg to larvae may enhance survival.

The horseshoe crab spawns on the intertidal foreshore of beaches in estuaries on the mid-Atlantic coast of the United States. Females lay their eggs at depths up to 0.20 m in the sediment matrix during high water (Shuster & Botton 1985) mostly in May and June. Eggs incubate and develop to embryos and then to larvae in the interstitial environment below the active foreshore. Controlled laboratory studies reveal that embryonic development of horseshoe crab eggs is arrested under hypoxic conditions (Palumbi & Johnson 1982) and temperatures less than 15°C (French 1979, Brown & Clapper 1981). In natural beach systems these parameters change over time during incubation based on tidal amplitude, pore water chemistry, and the ability of the beach matrix to store or transmit water.

The textural properties of foreshore sediments influence horseshoe crab egg viability and development by controlling moisture retention and rate of movement of water through the beach over the tidal cycle. Permeability of the foreshore increases with grain size and, to a lesser extent, with improved sediment sorting (Krumbein & Monk 1943). Residual moisture in coarse, poorly sorted sediment is lower than in finer better-sorted sediment over depths of decimeters (Jansson 1967). Oxygen content increases with increasing drainage rates, but decreases with increasing percentage of fine sands that decrease interstitial flow (Brafield 1964). Decoupling of the beach water table from the tide elevation can occur during tidal fall (Nielsen 1990). Saturation of sediment may persist low on the foreshore during low water, but oxygen levels may be sustained by water moving through the sediment. Temperature within the top decimeters will change over the tidal cycle when the beach is exposed (Pollock & Hummon 1971). The elevation of the beach water table will influence the heating effect of solar radiation (and thus temperature) within the upper decimeters, but local moisture content may not be directly related to the beach water table elevation (Li et al. 2006), particularly for finer sediments where a capillary fringe may develop and persist during low water (Atherton et al. 2001).

Erosion, deposition or activation of the beach matrix by waves and bioturbation by horseshoe crab spawning later in the season may cause buried eggs to be exhumed or repositioned relative to the surface of the foreshore during incubation (Jackson et al. 2005). Exhumation of eggs by wave activation can be enhanced when the surface is lowered during erosive conditions. Moisture and oxygen regimes can vary with depth from the surface, while eggs activated and moved in the swash may be removed from the beach entirely. Thus, foreshore response to wave energy may alter egg development by activating eggs, relocating them higher or lower in the sediment column and exposing them to different moisture or oxygen regimes.

The purpose of this study was to assess horseshoe crab egg viability and development on a sand and gravel estuarine beach during a spawning season. Previous studies of horseshoe crab egg viability and development show that viability can be threatened on the upper foreshore, where recharge by swash runup is infrequent and ability of sediments to hold moisture is low, causing egg desiccation (Penn & Brockmann 1994) and also low on the foreshore, where dissolved oxygen levels are low and moisture content is high below the beach water table outcrop during low tide. This study built on Penn & Brockmann (1994), who found that moisture content was the most important factor influencing horseshoe crab egg development in high micro-tidal environments such as Delaware Bay. Moisture content, oxygen and temperature of interstitial sediments are responses to hydrodynamic processes associated with tides, waves and swash uprush/backwash, which are, in turn, influenced by foreshore morphology and sediment characteristics. We examined changes in beach morphology, wave activation, tide and beach water table elevation to account for the cross-shore gradient in interstitial moisture and pore water conditions that influence viability and development of horseshoe crab eggs. Regression analysis was used to predict egg development stage across the foreshore after 44 d of incubation.

MATERIALS AND METHODS

Study area. Slaughter Beach (Fig. 1A,B) is an eroding sandy former overwash barrier modified by artificial beach nourishment and construction of a dune dike 2.3 m above backshore elevation. The most recent
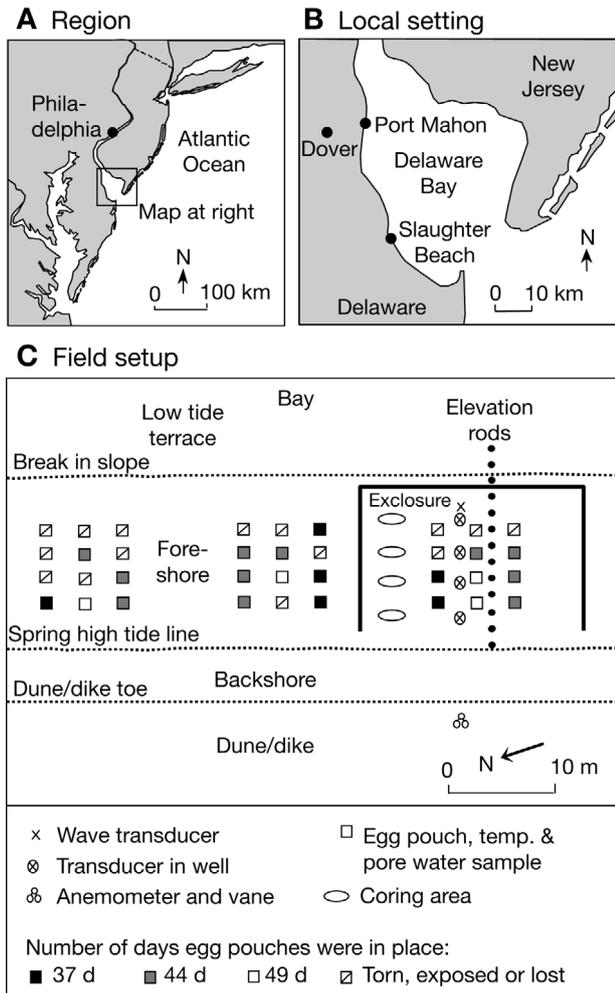
Fig. 1. (A) Study region and (B) local area of the study site and (C) diagram of the field deployment

The 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 1.4 m and a spring range of 1.7 m (NOAA 2005). Prevailing winds are from the west and blow offshore, but low-pressure centers bring strong onshore winds from the northeast and southeast.

Data collection. The field study was conducted from 18 May to 19 June 2004. Data on water levels during tidal rise and fall were collected using a pressure transducer placed 35 m bayward of the break in slope. Elevation of the beach water table was obtained from pressure transducers installed in four 41.0 mm internal diameter commercial well points at 0.25, 0.45, 0.65 and 0.85 of foreshore width measured from the break in slope to the spring swash limit. Data from these instruments were gathered at 1 Hz over the tidal cycle and recorded as 5 min averages. Data to determine wave height and period were gathered near times of daytime high water using a pressure transducer placed on the lower foreshore (Fig. 1C). These wave data were recorded at 8 Hz in 17.1 min bursts. A wire mesh exclosure fence with openings of 0.1×0.1 m was constructed on the foreshore (Fig. 1C) to prevent disturbance of sampling instruments by horseshoe crabs. Visual observations of wave height revealed no conspicuous differences within and outside the fence, implying that wave energies were not dampened by the fence. Wave heights reported are significant heights.

Beach elevation changes were monitored at 2 m intervals along a cross-shore transect (Fig. 1C) during each daytime low tide. Surface elevations were measured from the tops of 10 mm diameter steel rods driven into the sand and tied to a common datum using rod and transit surveys. These rods enable measurement of elevation changes to within 0.5 mm. A loose-fitting washer was placed over the rods to determine depth of sediment activation according to the procedure in Greenwood & Hale (1980).

Moisture content of interstitial sediment was determined from core samples, 0.20 m long and 0.05 m in diameter, gathered across the intertidal foreshore (Fig. 1C). Cores were taken every 2 h over complete tidal cycles twice a week for 6 consecutive weeks. Samples were partitioned into four 0.05 m slices. Sediments were weighed, air-dried and reweighed to determine gravimetric moisture content. The moisture held by unsaturated quartz gravel is not considered significant (Coile 1953), so moisture was determined from the sand and granule fraction, where particle sizes are <4 mm (-2ϕ). Dry weight gravimetric moisture content, in percent (Gardner 1982) was calculated. Coring was not possible when sampling locations were inundated, so representative samples were saturated, weighed and compared to their dry weights.

beach nourishment project was in 1985, and the beach has had ample time to be reworked. Beach sediments are moderately to moderately-well sorted medium to coarse sands, and grain size generally increases with distance offshore. Sediments are generally finer and better sorted on the upper foreshore than on the lower foreshore. There is little variation in size or sorting with depth on the upper foreshore, and the gravel subfraction is less than 15% by weight. Gravel content increases offshore and at depth below the sand surface (reaching a maximum of 70%), as expected on estuarine beaches reworked by low energy waves (Nordstrom & Jackson 1993). Pits dug across the foreshore revealed that sediments were well oxidized down to depths reached by burrowing crabs. The active foreshore has a slope of about 9.0° and is 20 m wide during spring tides. A gently sloping low tide terrace (tidal flat) extends bayward of the foreshore. The break in slope between the foreshore and low tide terrace is near the elevation of mean low water.

Continuous measurements of temperature of the interstitial foreshore were taken using submersible loggers buried adjacent to the egg pouches along one transect. We calculated degree days to measure the cumulative effect of temperature on incubation (Sweeney 1984). Degree days represent the summation of degrees in excess of 15°C based on daily averages. This threshold was chosen because egg development at temperatures below 15°C is expected to be minimal or suspended (French 1979, Brown & Clapper 1981). A multi-level piezometer was used to collect pore water from sediments adjacent to the egg pouches along 2 transects inside the exclosure and one transect outside the exclosure (Martin et al. 2003). A YSI 556 multi-probe system was used to measure dissolved oxygen, oxidation reduction potential, pH and salinity. Pore water measurements were gathered once each on the rise and the fall of the tide when the beach water table was at the egg pouches. An average of the readings by elevation from the transects inside the exclosure was used in the analysis.

Survival and development of eggs to embryo or larvae stage were evaluated by burying eggs in the beach (Penn & Brockmann 1994). Newly laid eggs were extracted from the beach at Port Mahon (Fig. 1B) and buried at Slaughter Beach. Port Mahon was chosen because the relatively high density of horseshoe crab spawning there early in the season enabled easy location and extraction of the required volume of eggs. Transplanted eggs had well-defined and firm clusters, no swelling, and a coloration of light green or light blue. Egg clusters weighing a median of 21 g (14 to 42 g) were placed in thirty-six $150 \times 150 \times 35$ mm mesh pouches and buried flat at 0.15 to 0.20 m depths along 9 cross-shore transects arranged in 3 blocks (Fig. 1C). Adjacent blocks were 10 m apart; transects within each block were 3 m apart. Cross-shore locations represented 0.30, 0.45, 0.60 and 0.75 of foreshore width, measured from the break in slope at the base of the foreshore to the spring tide swash limit. Pouches were not buried at the highest and lowest elevation across the foreshore because these locations are not optimal for egg viability or development (Penn & Brockmann 1994).

Pouches were excavated in stages (37, 44, and 49 d after initial burial) (Fig. 1C). Only one egg pouch remained at 0.30 of foreshore width after a storm on 5 June. Egg pouches buried at 0.45 of foreshore width were not recoverable along 3 transects because the pouches were torn (two) or removed (one) during the storm of 5 June. All pouches remaining and recoverable at this location were excavated at 44 d to prevent further loss of data. One pouch at 0.65 of foreshore width was exposed and not recovered and one pouch

at 0.75 of foreshore width was not found. Pouch contents were preserved in 10% buffered formalin and separated from sand in the lab, where eggs that survived or developed to embryo or larvae stage were identified under magnification. All stages lacking jointed legs were considered eggs (cf. Sekiguchi 1988). Stages that had jointed legs, but retained the surrounding membranous tissue (chorion or inner membrane) were classified as embryos (cf. Sekiguchi 1988, Stages 18 to 21). Stages that developed beyond embryo stage and shed their chorion and inner membrane were classified as larvae (cf. Sekiguchi 1988, Stage 21b and older).

Statistical analysis. General linear models, including analysis of variance and regression techniques, were used to assess differences in physical and chemical characteristics across the foreshore, to assess differences in stage of egg development across the foreshore and to relate stage of egg development to physical and chemical characteristics. Analysis of variance (ANOVA) was used to contrast interstitial pore water conditions (temperature, dissolved oxygen, oxidation reduction potential, pH, salinity) and moisture content at the 4 monitoring locations across the foreshore. In a separate analysis, degree days (as a measure of interstitial temperature) were regressed against time separately for each foreshore width. Regression slope estimates and confidence intervals were compared across the foreshore width.

ANOVA was used to assess differences in stage of egg development for the 3 excavation times (37, 44, and 49 d) and the 3 foreshore widths (0.45, 0.60, and 0.75 of foreshore width). Because pouches at 0.45 of foreshore width were excavated only at 44 d, we used a 1-way ANOVA to assess changes in stage of egg development across the foreshore (0.45, 0.60 and 0.75 of foreshore width). Since pouches at 0.60 and 0.75 of foreshore width were excavated at 37, 44, and 49 d, we used a 2-way ANOVA to assess changes in stage of development across the upper foreshore (0.60 and 0.75 of foreshore width) and excavation time (37, 44, and 49 d). When making multiple comparisons, a Tukey adjustment was applied to account for experiment-wise error. Data from the egg pouch recovered from 0.30 of foreshore width were excluded from the statistical analysis because of the lack of replication, but were used to provide qualitative insight into conditions on the lower foreshore.

Multiple regression was used to relate stage of egg development across the foreshore to oxygen and temperature. Pouches excavated at 44 d for 0.45, 0.60, and 0.75 of foreshore width were used to determine the effect of oxygen and temperature on egg development with location on the foreshore. Statistical analyses were conducted in SAS ver. 9 (SAS Institute).

RESULTS

Foreshore conditions

Interstitial mean temperature at the egg pouches varied little by cross-shore location, ranging from 23.3°C at 0.45 of foreshore width to 24.3°C at 0.75. The temperature logger at 0.30 of foreshore width was lost during the storm, but had recorded a mean of 22.9°C until then. Cumulative temperature (degree days > 15°C), was markedly higher in the upper foreshore compared to 0.45 of foreshore width, and the difference increased over time (Fig. 2). Rates of accumulation of degree days were similar at 0.60 and 0.75 of foreshore width, being 8.5 degrees per day (95% CI: 8.2, 8.8) and 8.4 degrees per day (95% CI: 8.2, 8.7), respectively. The rate of accumulation of degree days at 0.45 of foreshore width was only 7.6 degrees per day (95% CI: 7.4, 7.8).

The pore water pH at each foreshore location varied little, ranging from a mean of 6.4 to 6.6. Salinity ranged from a mean of 23.0 to 24.6 ppt. Pore water in the upper foreshore (at 0.75 of foreshore width) had a higher mean dissolved oxygen level than the other locations, where dissolved oxygen levels were similar ($F_{1,152}$ = 66.6, p < 0.001; Fig. 3A). A Tukey-method multiple comparison supports the observation that dissolved oxygen levels at 0.75 of foreshore width are different from other elevations and that the other dissolved oxygen levels are similar. Oxidation reduction potential levels are significantly higher at 0.30 and 0.45 of foreshore width than at 0.60 and 0.75 of foreshore width ($F_{1,152}$ = 4.52, p = 0.04; Fig. 3B).

Mean daily moisture differed across the foreshore ($F_{3,153}$ = 265, p < 0.0001) and with sediment depth ($F_{3,153}$ = 6.42, p = 0.0004). Gravimetric moisture content of the sand and granule fraction over tidal cycles (Table 1) increases with distance bayward and with sediment depth. The coefficients of variation (Table 1) at 0.85 and 0.25 of foreshore width are lower than at
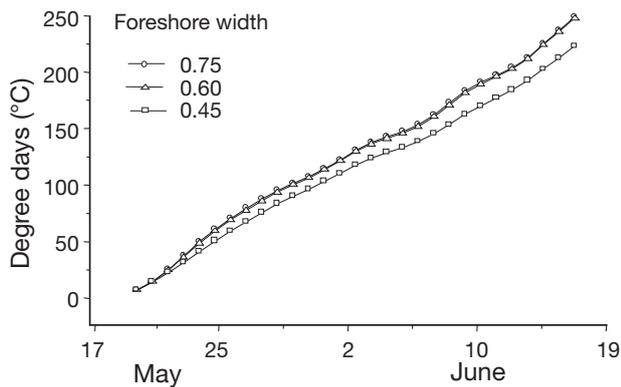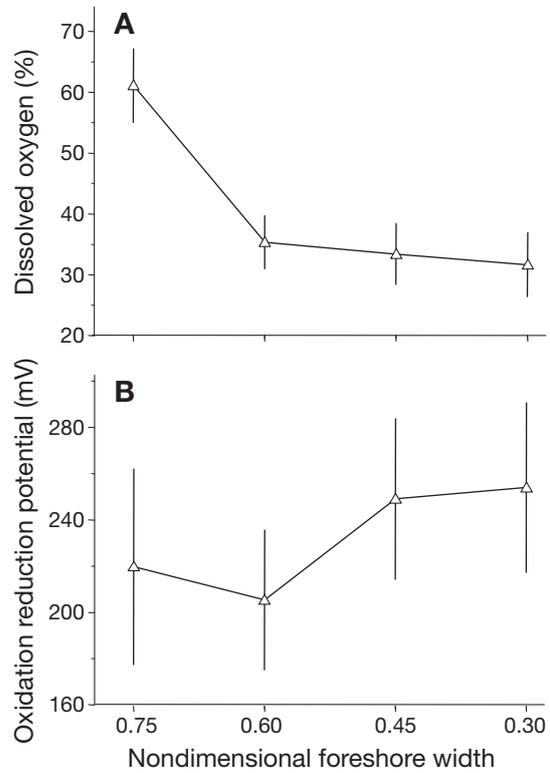
Fig. 3. (A) Dissolved oxygen and (B) oxidation reduction potential. Error bars: upper and lower 95% confidence limits

Table 1. Gravimetric water content (%) of the sand and granule fraction of foreshore sediments from cores taken every 2 h over tidal cycles twice a week for 6 wk. SD: standard deviation; CV: coefficient of variation

Cross shore location Sediment depth	Min.	Max.	Mean	SD	CV
0.85 foreshore width					
0–0.05 m	1.1	10.9	3.9	2.0	0.52
0.05–0.10 m	2.1	8.2	5.0	1.5	0.30
0.10–0.15 m	2.4	8.7	4.5	1.3	0.29
0.15–0.20 m	3.0	8.8	4.7	1.3	0.26
0.65 foreshore width					
0–0.05 m	2.7	27.6	9.4	9.0	0.96
0.05–0.10 m	2.9	29.9	10.0	9.2	0.92
0.10–0.15 m	2.8	27.6	10.5	9.1	0.87
0.15–0.20 m	2.9	27.6	11.4	9.2	0.81
0.45 foreshore width					
0–0.05 m	2.9	26.1	14.4	10.0	0.70
0.05–0.10 m	3.8	26.1	14.9	9.6	0.64
0.10–0.15 m	2.4	26.1	15.6	9.3	0.60
0.15–0.20 m	5.0	48.9	18.9	8.7	0.46
0.25 foreshore width					
0–0.05 m	4.5	23.5	18.6	7.2	0.39
0.05–0.10 m	5.0	27.4	19.7	6.3	0.32
0.10–0.15 m	5.1	23.5	20.5	5.3	0.26
0.15–0.20 m	2.8	33.8	21.7	4.8	0.22

Fig. 2. Pore water temperature (°C) as a function of degree days

0.45 and 0.65, where moisture content fluctuates more in response to tidal excursion and beach water table elevation. The zone above 0.75 of foreshore width is where swash/backwash dominates only at high tide. The upper limit of swash uprush at high tide (identified by the location of the wrack line after 35 events) ranged from 1.0 to 0.60 of foreshore width during non-storm conditions. The upper limit of swash was located above 0.75 of foreshore width 74% of the time. The location at 0.75 of foreshore width came under the influence of breaking wave action or full tidal inundation only during high wave heights or spring tides (n = 6). The well site at 0.85 of foreshore width was inundated 1.9% of the time, and the pouch site at 0.75 was inundated 5.9% of the time. Changes in moisture content at sediment depths of 0.15–0.20 m were influenced by the elevation of the beach water table at 0.85 of foreshore width where tidal inundation and infiltration from swash was at a minimum. Moisture contents at this location decreased with increased distance from the water table over the tidal cycle (r^2 = 0.45, n = 44). The pouches at 0.60 of foreshore width experienced inundation by tidal excursion 28% of the time, but there were additional occasions when periodic wetting by swash/backwash occurred (19%).

Topographic profiles taken at low tide (Fig. 4) indicate that the subaerial beach surface did not erode to the depth that egg pouches were initially buried (0.15–0.20 m). Differences in the depth from the surface to egg pouches relative to their initial position did not exceed ±0.05 m during non-storm conditions. The largest differences occurred during a storm on 4–5 June, when significant wave heights of 0.48 m resulted in sediment deposition between 0.30 and 1.0 of foreshore width, burying the pouches by 0.09 to 0.18 m at 0.45, 0.60 and 0.75 of foreshore width. Accretion on this region of the profile lasted for 4 tidal cycles; non-storm profile conditions were re-established by the fifth tidal cycle and egg pouches were at approximately the same depth below the surface as their initial burial. Net surface change at 0.30 of foreshore width was minor during the storm, but the activation depth was 0.23 m, which exceeded the depth of pouch burial and resulted in loss of 7 of 9 pouches. Maximum depth of activation relative to the initial beach profile (Fig. 4) was less than 0.12 m on the upper foreshore and did not reach pouches buried at 0.60 and 0.75 of foreshore width. Maximum depth of activation at 0.45 of foreshore width was 0.19 m. Only 6 of 27 pouches in other locations were exhumed by natural processes.
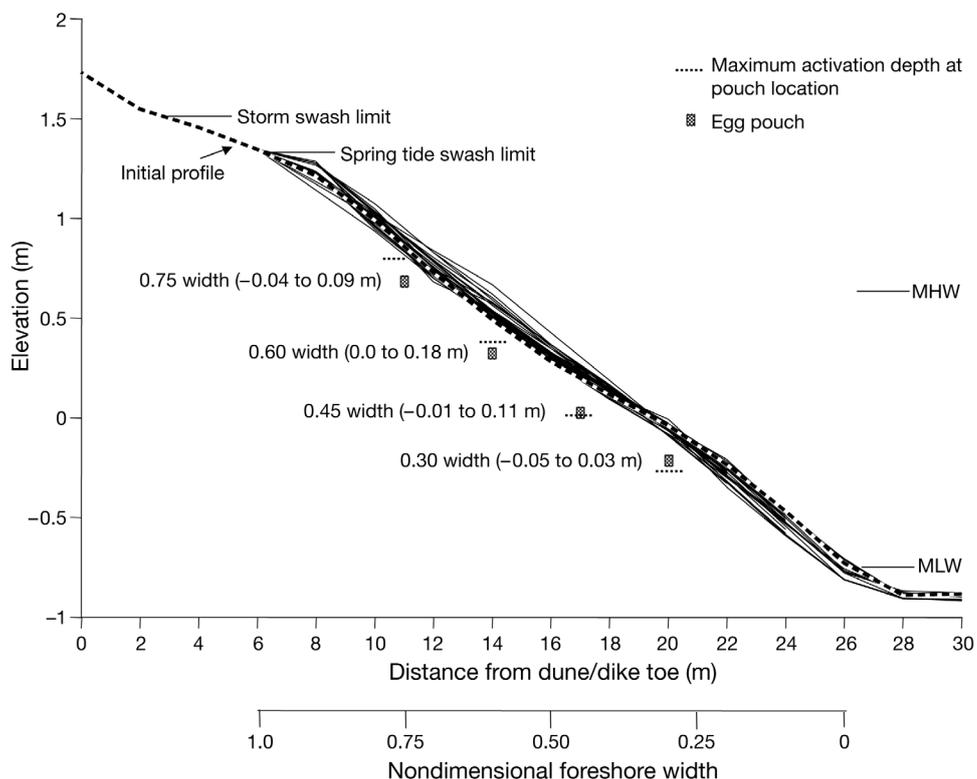

Fig. 4. Profiles taken at low tides when *Limulus polyphemus* eggs were buried. Initial depth of egg burial is shown along with the maximum depth of activation and change in depth from the eggs to the sand surface due to erosion or accretion of the profile. Numbers in parentheses represent change in depth of egg pouches relative to initial position at burial due to profile change. Positive numbers represent burial after initial placement. MHW: mean high water; MLW: mean low water

Horseshoe crab egg viability and development

Fig. 5 presents the percentage of eggs in pouches that were live, developed to embryo or developed to larvae for the 3 time periods. The percentage remaining in the egg stage after 44 d did not differ across the foreshore ($F_{2,8} = 0.38$, p = 0.70). The percentage of eggs that had reached embryo stage after 44 d did vary across the foreshore width ($F_{2,8} = 9.21$, p = 0.008) with a larger percentage reaching embryo stage at 0.45 of foreshore width than in the upper foreshore. The difference in the mean percentage of embryos between 0.45 and 0.60 of foreshore width was 52.5% (90% CI:
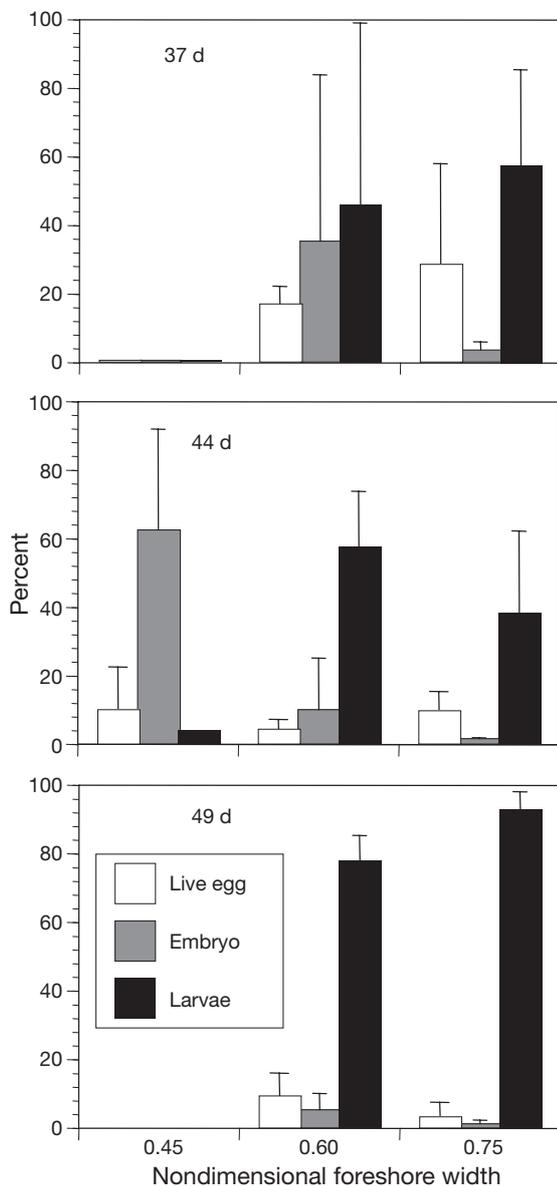

Fig. 5. *Limulus polyphemus*. Percentage of live eggs, embryos and larvae across the foreshore after 37, 44 and 49 d of incubation

13.9, 91.1) and between 0.45 and 0.75 of foreshore width was 61.7% (90% CI: 23.1, 100.2). The percentage of eggs that had reached larval stage after 44 d also varied across the foreshore ($F_{2,8} = 13.96$, p = 0.003) with a larger percentage reaching larval stage on the upper foreshore than at 0.45 of foreshore width. The difference in mean percentage of larvae between 0.60 and 0.45 of foreshore width was 53.8% (90% CI: 28.6, 79.1) and between 0.75 and 0.45 of foreshore width was 34.4% (90% CI: 9.1, 59.7). Pair-wise multiple comparisons with Tukey adjustment revealed no differences across the upper foreshore in the percentage of eggs reaching embryo stage ($t = 0.51$, 8 df, p = 0.87) or larval stage ($t = 1.64$, 8 df, p = 0.28). No egg pouches were recovered at 0.30 of foreshore width after 44 d, but one pouch recovered earlier revealed that 46% of the eggs had reached embryo stage and there were no larvae.

Comparison of egg development on the upper foreshore over time revealed a mix of embryos and larvae in the upper foreshore, especially after 37 and 44 d. Development had progressed predominantly to larval stage by 49 d. The percentage of larvae in the upper foreshore after 49 d had increased to over 78% ($F_{1,9} = 5.46$, p = 0.04). Thus, the rate of development in the upper foreshore seemed to level off by 49 d, but there had been significant larval development prior to that time.

Comparison of the percentage of larvae at 0.45 of foreshore width after 44 d with development after 37 d in the upper foreshore reveals that egg development in the lower foreshore was slower ($t = 3.66$, 16 df, p = 0.01). The difference in mean percentage of larvae between the upper foreshore after 37 d and 0.45 of foreshore width after 44 d was 48.8% (90% CI: 15.6, 82.0), indicating that development progressed faster in the upper foreshore.

The multiple regression model used to predict stage of development does not include salinity and pH because of lack of variation in these parameters through time. Oxidation reduction potential was not included because that parameter has an inverse relationship with dissolved oxygen. Initial analyses for each response variable (live eggs, embryos and larvae) with average moisture content, dissolved oxygen and temperature revealed a weak correlation between moisture content and stage of development and this parameter was excluded in subsequent analyses.

Fig. 6 presents stage of egg development after 44 d as a function of oxygen and temperature measured in the field and predicted from the regression model. Development to larval stage is positively associated with temperature and negatively associated with percentage of dissolved oxygen (Fig. 6A, Table 2). A greater percentage of eggs reached larval stage in the
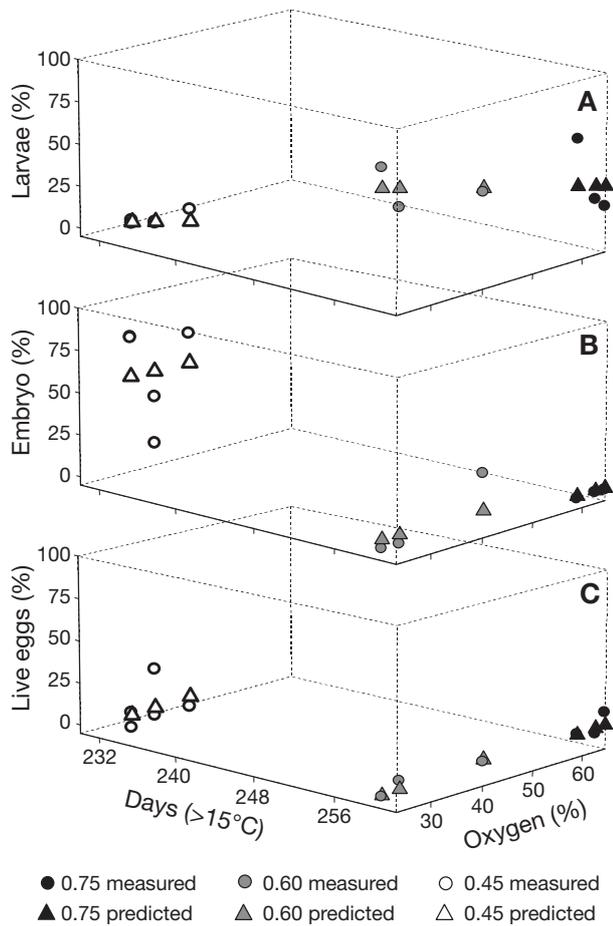
Fig. 6. *Limulus polyphemus*. Percentage of egg development to (A) larvae, (B) embryos, and (C) live eggs as a function of measured dissolved oxygen and interstitial temperature (expressed as degree days greater than 15°C) after 44 d across the foreshore. Circles represent measured egg development stage and triangles represent predicted egg development stage from multiple regression analysis. Fewer predicted versus measured values appear where there are multiple observations for the same level of the dependent variable

Table 2. Regression coefficients, standard errors (SE), and p-values based on analyses of *Limulus polyphemus* egg development at 0.45, 0.60, and 0.75 of the foreshore width after 44 d of incubation as a function of average dissolved oxygen (%) and degree days above 15°C

Stage	Dissolved oxygen	SE	p	Degree days	SE	p
Larvae	−0.82	0.3044	0.028	2.08	0.3323	<0.001
Embryo	−0.04	0.5422	0.945	−2.05	0.5918	0.008
Live egg	0.17	0.2297	0.489	−0.20	0.2507	0.442

The percentage of live eggs after 44 d incubation is similar across the foreshore (Fig. 6C), and there is no strong correlation with either temperature or dissolved oxygen (Table 2), suggesting that the most extreme condition for each of these parameters did not affect viability.

DISCUSSION

Comparing development rates of horseshoe crab eggs on beaches in different geographic regions is complicated due to differences in tidal range, wave energy, sediment characteristics, beach morphology, and water quality. The cross-shore distribution of eggs that develops on a high micro-tidal beach generally reveals a higher percentage development near mean high water and lower percentage higher and lower on the foreshore (Penn & Brockmann 1994). Penn & Brockmann (1994) found higher percentage development at 0.50 and 0.67 of foreshore width at a site closer to the mouth of Delaware Bay, but for at least one of their 2 years, development was similar between 0.34 and 0.80 of foreshore width. Our results support their findings that development beyond egg stage is similar across the foreshore but the rate of egg development varies. More eggs in the pouches buried at 0.30 and 0.45 of foreshore width developed to embryos in the 6 wk incubation period, whereas more eggs buried in the pouches at 0.60 and 0.75 of foreshore width developed to larvae.

Our findings reveal that conditions within 0.15–0.20 m of the foreshore surface are favorable for egg development but that the different hydrodynamic conditions may lead to variations in the rate of development. Periods of wetting that are intermittent due to swash uprush/backwash, or continuous during tidal inundation, do not reduce egg development by increasing egg mortality. The location at 0.75 of foreshore width is where moisture values are dominated by swash infiltration but eggs remain viable. Egg viability there indicates that moisture provided by intermittent swash infiltration is sufficient, given the moisture-holding

upper foreshore (0.60 and 0.75 of foreshore width), where the number of degree days greater than 15°C was higher than at 0.45 of foreshore width. The inverse relationship between development to larvae and oxygen is revealed in the upper foreshore (Fig. 6A), where the percentage of eggs developed to larvae increases with decreases in dissolved oxygen.

Temperature is the best predictor of development to embryo stage across the foreshore (Fig. 6B), revealing an inverse relationship between embryos and number of degree days greater than 15°C (Table 2). Fig. 6B shows the highest percentage of embryos in the lower foreshore (0.45 of foreshore width) compared to the upper foreshore (0.60 and 0.75 of foreshore width), where a larger percentage of eggs had advanced to larval stage.

capability of the sediments. Moisture content is a factor in egg development (Penn & Brockmann 1994) by threatening viability at the highest and lowest elevations of the active foreshore. Our results did not find a direct relationship between moisture and viability or development but moisture is a broad spatial control on temperature in the beach matrix.

Changes in temperature will be greatest at low tide when there is greater likelihood of exposure to solar radiation (Pollock & Hummon 1971), but moisture retention and frequency of inundation will also have an influence on interstitial temperature (Li et al. 2006). Significant differences in number of degree days above 15°C suggest that the differences in frequency of inundation and moisture retention capacity of the sediments influence interstitial temperature and in turn influence egg development. The higher frequency of inundation by tides and the elevation of the beach water table on the lower foreshore likely contributed to the lower number of degree days and could account for the temporal lag in egg development between the upper and lower regions of the foreshore.

Observations under laboratory conditions have demonstrated that temperature affects egg development (French 1979, Jegla & Costlow 1982, Ehlinger & Tankersley 2004). For example, Jegla & Costlow (1982) found that time to hatch decreased by 2 d with an average temperature increase of 5°C. Our results show development effects at smaller increases in average daily temperature. Daily temperature differed by only 1°C on average between 0.45 and the upper foreshore, but percentage of eggs developing to larvae stage was higher in the upper foreshore. Cumulative interstitial temperature as measured by degree days differed significantly across the foreshore. Thus, *in situ* egg development appears sensitive to variation in cumulative interstitial temperatures. Whether earlier hatching in the upper foreshore translates into a selective advantage due to earlier emergence is unknown.

Sediment activation is greatest just landward of wave breaking at high water on an estuarine beach (Jackson & Nordstrom 1993, Sherman et al. 1994). Depth of activation increases with both beach slope and breaking wave height (Ciavola et al. 1997) and may be sufficiently deep to exhume buried eggs (Nordstrom et al. 2006). In the present study, wave heights were sufficiently high to re-suspend sediments near the depths of the buried egg pouches in the lower foreshore. Eggs that were not exhumed at 0.30 and 0.45 of foreshore width reached embryo stage, but wave activation and changes to the beach profile were sufficient to remove most eggs buried at 0.15–0.20 m depth. Thus, depending on storm characteristics, loss of eggs due to wave breaking and beach profile change can be an important factor controlling the quantity of eggs that remain in the beach and develop beyond the egg stage.

Plunging breakers, the dominant wave type on beaches in Delaware Bay, can increase aeration of water at depth (Chanson & Cummings 1994). The high gravel content and coarse sands on the lower foreshore that facilitate beach draining, but not complete drying, may contribute to the relatively high dissolved oxygen levels at these locations. Although dissolved oxygen levels were highest in the upper foreshore, our results suggest that development will occur when dissolved oxygen is much less. Dissolved oxygen levels at 0.30 of foreshore width were similar to levels at 0.45 of foreshore width. The lower levels may have reduced, but not arrested, egg development on the lower foreshore.

Under conditions monitored at the field site, results of this study reveal that

• Egg development can occur over approximately half of the active foreshore on a mixed sand and gravel beach in a high micro-tidal environment.

• Conditions for development exist at approximately 0.30 to 0.45 of foreshore width, but egg loss due to wave activation can prevent this zone from being high quality habitat.

• Egg development below the median foreshore width is slower than development above the median foreshore width because of a slower accumulation of degree days.

• The lower foreshore can have high activation depths relative to the depths that horseshoe crab eggs are found.

• Presence of appreciable quantities of gravel below mean tide elevation and dominance of plunging breakers may be an influence on the relatively high levels of dissolved oxygen there.

Faster egg development and subsequent emergence from the foreshore may provide an advantage to the early life history of horseshoe crabs. The results of this study demonstrate the importance of interstitial temperature to reducing time to development of larvae. The passive role of sediment characteristics on moisture retention and interstitial temperature suggests beach nourishment can artificially influence the rate of development. Comprehensive planning for horseshoe crab populations should be integrated with shoreline planning to ensure optimal conditions for egg development.

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