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AN EVALUATION OF MISSISSIPPI BARRIER ISLANDS AS SPAWNING AND NESTING HABITAT FOR THE AMERICAN HORSESHOE CRAB, *LIMULUS POLYPHEMUS,* WITH IMPLICATIONS FOR ISLAND RESTORATION

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Abstract: The American horseshoe crab (HSC), *Limulus polyphemus*, is an economically and ecologically important species in the coastal ecosystem. Horseshoe crabs inhabit the continental shelf and estuaries from Maine to the central Gulf Coast and the Yucatán Peninsula. Although the presence of horseshoe crabs in southern Mississippi is known locally, there are limited data specific to the area and population, particularly regarding spawning and nesting habitat. Surveys of HSC presence, habitat use, and behavior on Mississippi barrier islands were conducted between March and November 2007 to 2009. These data, combined with habitat surveys of the barrier islands, were used to characterize HSC use of these islands. Horseshoe crabs were present on barrier island beaches from March to November, but active spawning and nesting occurred primarily in April and May. Peak abundance varied by year but not between islands surveyed. Nesting activity was only observed on the north side of both islands and was generally clustered in areas with a mild elevation profile. In comparison to other studied populations both in the Gulf of Mexico (GOM) and along the U.S. Atlantic coast, HSC nesting on Mississippi barrier islands followed generally similar patterns, but did display some important differences. Nesting was highest in low energy, well oxygenated habitat, which included the sub–tidal sand flats that are common along these islands. In addition, HSC are smaller than the range–wide mean reported in the literature, but that may be related to these islands being close to the edge of the reported HSC range in the GOM. The continued existence of HSC in Mississippi appears tied to their preference for barrier island beaches as spawning and nursery habitat. More research is needed, but this study documents that the distribution of HSC nesting habitat includes Mississippi beaches and this should be considered as a part of restoration plans being evaluated for these barrier islands.

Key Words: *Limulus*, habitat, nesting, restoration

Introduction

The American horseshoe crab, *Limulus polyphemus*, is an economically and ecologically important invertebrate in United States coastal waters. American horseshoe crabs (HSC) are harvested for bait in the eel and conch fisheries (Shuster et al. 2003), extraction of *Limulus* amoebocyte lysate (LAL) to screen for endotoxins is a multi–million dollar biomedical industry (Berkson and Shuster 1999), and research focusing on the crab's compound eyes has resulted in many medical advances in the structure and physiology of vision (Battelle 2006). Horseshoe crab eggs are also managed as a valuable nutrient–rich food source for a variety of migrating sea birds (Castro and Meyers 1993, Shuster et al. 2003) and the threatened loggerhead turtle, *Caretta caretta* (Keinath et al. 1987).

American horseshoe crabs are distributed along the U.S. Atlantic coast and in the Gulf of Mexico (GOM) (Shuster 1982, Anderson and Shuster 2003). In the Gulf, they have been documented from the Florida Keys north to Mobile Bay, AL and on the coast of the Yucatan Peninsula (Sekiguchi and Shuster 2009). American horseshoe crab populations and their impacts on the Atlantic ecosystem have been extensively researched; however, populations in the northern GOM have not. In particular, although the presence of HSC has been acknowledged in Mississippi (Richmond 1962, Shuster and Sekiguchi 2009), this is not a formally recognized portion of the species' range, and there is a deficit of information specific to this region.

A key component of population distribution for HSC is the availability of beach nesting habitat (Brockmann 2003, Shuster and Sekiguchi 2009). In the spring, mature HSC begin moving from deeper water toward sandy beaches where spawning occurs and females deposit their eggs to be fertilized and develop buried in the sand (Brockmann 2003). The larvae and juveniles then recruit to nearshore benthic habitat (e.g., sand flats, seagrass beds) for much of their first year of life (Gilbert and Clark 1981, Carmichael et al. 2004). Adult HSC habitat is in deeper water, so the existence of quality spawning and nursery habitat has been suggested as a key limiting factor for their distributional range in coastal ecosystems (Sekiguchi and Shuster 2009).

In areas of the northern GOM west of Mobile Bay, particularly Mississippi Sound (Sound), intertidal sandy beach habitat is highly limited in spatial extent. Excepting artificially maintained beach, intertidal sandy beach habitat is almost exclusively found on the four barrier islands forming the southern boundary of the Sound. Artificially maintained beach has been used as nesting habitat by HSC in other regions (Jackson et al. 2005), however artificial beach in our study area is closer to shore and subject to much lower salinities and much higher human traffic than the barrier islands. The barrier islands may therefore be critical habitat for HSC at the previously undocumented western boundary of their range in the northern GOM. Mississippi barrier islands are composed of four outer islands, 15—20 km offshore, and two inner islands about 10 km off the coast. In particular, West Ship Island and Horn Island form most of the southern boundary of the Sound and are of interest with regards to HSC habitat, as these islands are a part of the Gulf Islands National Seashore and therefore protected from major human—induced changes. If these islands contain critical HSC spawning habitat then this would be one of the ecosystem services of these federally protected islands and would have to be considered as a part of any alteration plans for these islands.

Horseshoe crabs show a significant level of plasticity in spawning/nesting habitat choice. The seasonal patterns of activity differ between geographically separate populations of HSC, and physical and behavioral characteristics of multiple populations are not identical (Shuster 1982, Brockmann 2003, Mattei et al. 2010). Spawning/nesting behavior is best documented along the U.S. Atlantic coast and the coast of Florida in areas with semi—diurnal tides (Rudloe 1985, Shuster and Botton 1985, Penn and Brockmann 1994). Nesting by HSC has been documented in microtidal systems (Ehlinger et al. 2003), but both Brockmann (2003) and Sekiguchi and Shuster (2009) suggest that tidal amplitude and period is a primary determinant of HSC distributional range through its effects on nesting behavior. Yet, if HSC use the Mississippi barrier islands as nesting habitat, then the reduced tidal range, high wind influence of tides, and the general lack of sandy shoreline along the Mississippi coast may result in key regional differences in spawning and nesting behavior for HSC that need to be accounted for in protecting habitat.

The purpose of this study was to: 1) document HSC spawning and nesting activity on Mississippi coastal islands; 2) Investigate seasonal changes in relative population abundance of adult spawning using catch per unit effort (CPUE) analysis; and 3) identify preferred habitat characteristics of spawning adult horseshoe crabs along the Mississippi coast and compare these results to reports on HSC nesting habitat from other regions. To facilitate objective three, habitat data were collected using commonly cited habitat characteristics from other areas including environmental conditions, sediment characteristics, and beach topography. These outcomes will allow for a better understanding of local habitat dependencies of this species.

MATERIALS AND METHODS

Sampling Location and Period

All sampling occurred on Horn (lat 30°13'57.0"N, long 88°40'21.7"W) and West Ship (lat 30°12'29.1"N, long 88°57'45.6"W) Islands, which together form most of the principal southern boundary of the Sound (Figure 1a). Sampling was conducted between March and November in 2007—2010, and occurred bi—monthly within 48 hours of the new and full moon at or near high tide. The islands were divided into north and south sites (Figure 1). Samples collected on Horn Island were limited to the western half of the island due to limited accessibility. All sampled sandy beach areas met generally—cited requirements for suitable HSC spawning habitat, (e.g., sandy sloping shoreline; Shuster and Sekiguchi 2009).

Biological Data Collection

Data on spawning activity was gathered by counting HSC on both islands along a randomly selected 1km transect of shoreline on each date. All HSC encountered between the Mean High Water Line (MHWL) and a water depth of 100 cm were counted and measured. Parameters collected for each animal included sex, prosomal width (mm), state (paired, unpaired, dead, or exuviae), water depth (cm), and distance from shore (m). Sex was determined by presence or absence of modified pedipalps. Sex ratio was estimated for each survey based on all crabs examined and was summarized based on the mean by island and year. Catch per unit effort (CPUE/km) was used as an index of HSC abundance for comparisons between and within islands.

Beach Sediment Composition

Sediment composition analysis was based on sediment cores taken with a 5 cm diameter PVC pipe to a 30 cm depth. Cores were taken every 2 km on the north side of West Ship Island (~10 km, n=5) and at 3 randomly located sites on the south side of West Ship Island (Figure 1b). Horn Island has an approximate perimeter length of 40 km; therefore, sites at Horn Island were selected on both the northern and southern shores, but they were concentrated along the western end of the island (Figure 1c). Core sites were characterized based on the HSC abundance data collected in 2007—2009 as sites of high (> 50/km), low (1—49/km), and no presence of HSC. At each site, 4 cores were taken in each of 2 strata; just below the high tide line on the beach, and 10 m seaward of the tide line. The 4 cores from each site were thoroughly mixed by sifting them together.

Particle size was determined from a 60 g (dry weight) subsample taken from the composite cores and disaggregated using a mortar and pestle. Particle size distribution was estimated by mechanically sifting the samples for 15 min through a series of graduated sieves ranging from 63 μm (4ϕ, #230) to 1600 μm (—1 ϕ, #5) at 1.0 ϕ intervals (Boggs 1987). Particle sizes are defined according to Boggs (1987) as 1 ϕ = $-\log_2(S)$ where S is the particle size (mm). The particles that were retained on the sieve screens were weighed (g) and converted to a percentage in each size class for each composite sample.

Non—sand composition of sediment samples was estimated in 2 categories representing calcium—based material such

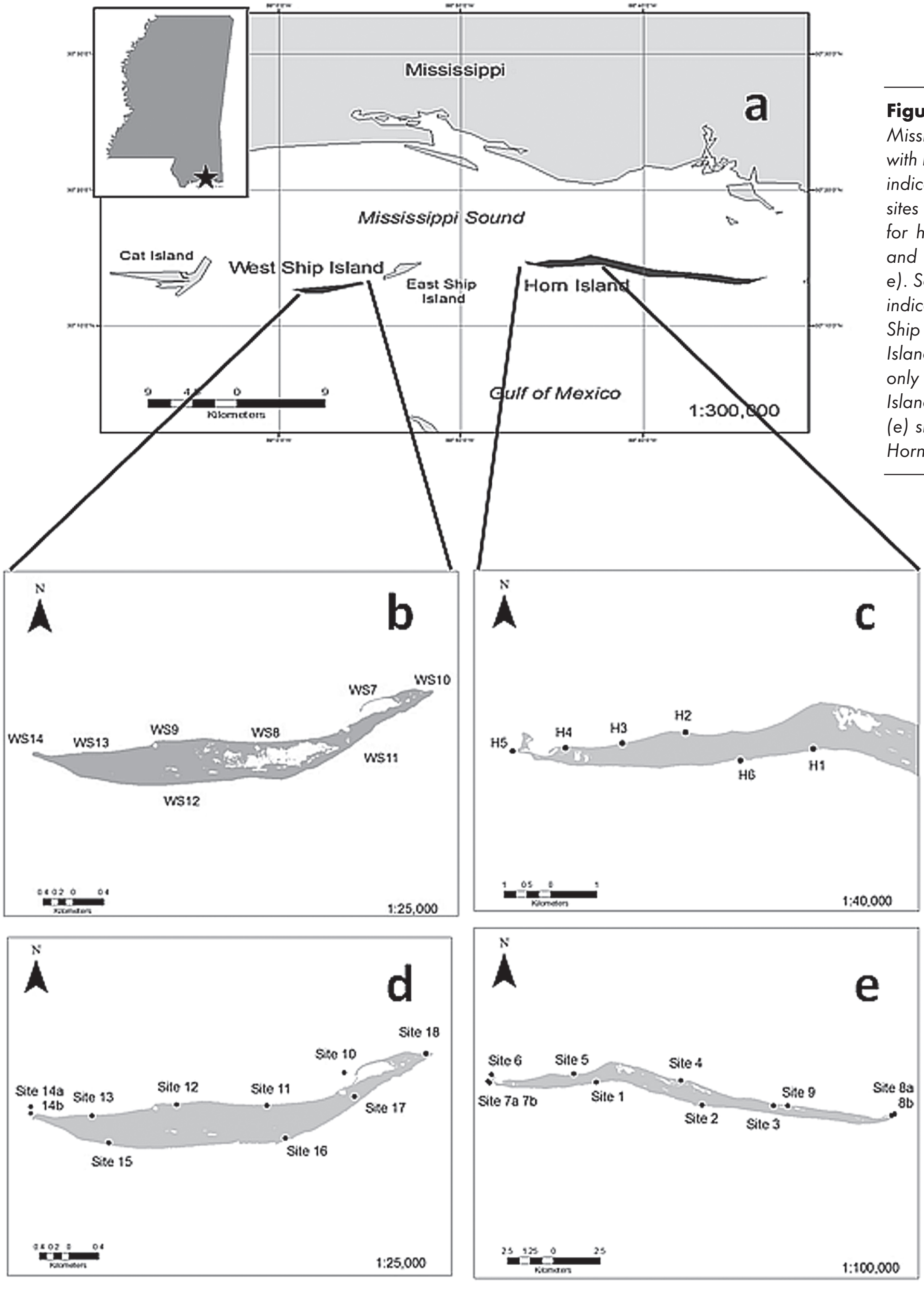

Figure 1. *Map of coastal Mississippi study area (a) with islands used for this study indicated in black. Collection sites on each island are given for habitat sampling (b & c) and beach topography (d & e). Sample collection sites are indicated separately for West Ship Island (b & d) and Horn Island (c & e). Panel (c) shows only the western end of Horn Island for clarity while panel (e) shows the entire length of Horn Island.*

as shell or gravel (shell hash) and organic content. Percentage composition of shell hash was determined by the addition of 10% HCl to a second 60 g (dry weight) disaggregated sample until the reaction (off—gassing) ended. The reacted samples were then rinsed with tap water and dried at 95°C to a constant weight (0.01 g). The difference between initial dry weight and acid—washed dry weight was classified as shell hash weight. Percentage organic composition (e.g., detritus, living organisms) of the sediment was determined from a separate 3 g (dry weight) sub—sample taken from each stratum composite core. The sub—sample was dried at 95°C and weighed to the nearest 0.01g. The samples were then placed in a muffle furnace at 550°C for two hours and cooled in a desiccator. The cooled samples were weighed (g), and the percent difference between sample dry weight (g) and post—muffle weight (g) was recorded as the organic content (%).

Beach Topography

Depth to Reducing Layer (DRE) measures the vertical height of the oxygenated sediment suitable for nesting (Thompson 1999). The transition from normoxic to anoxic sediment is clearly visible as a change from light to dark coloration. This can be compared to direct estimates of sediment oxygen levels re—parameterized to a normoxic/anoxic delineation, and was chosen as it is simpler and does not require an oxygen meter. Beach DRE samples were collected in May 2010 by taking core samples along multiple 100 m transects running seaward perpendicular to the high tide line. The sites selected on Horn and West Ship Island corresponded with the sites sampled for sediment analysis (Figure 1b, c). A single core was taken every 10 m along the 100 m transect using a clear acylic tube. The depth from the core surface to the beginning of the visible reducing zone, indicated by a transition to dark grey sediment, was measured (cm). A profile was composed showing the location of the reducing zones.

Beach slope was measured perpendicular to the Extreme High Tide Line (EHTL) every 2 km on West Ship Island (Figure 1d) and every 10 km on Horn Island (Figure 1e) out to 100 m or until water depth interfered with measurement. Two poles (1.5 m height) marked in 1cm increments were placed perpendicular to the beach 1.5 m apart. The landward observer's eye was aligned with the top of the seaward rod and horizon. The distance *a* (cm) down from the top of the observer's pole where the top of the seaward pole and horizon line intersect with the observer's pole was recorded. Measurements were continued seaward by moving the landward pole 1.5 m past the seaward pole (modified from Emery 1961). This measurement of beach slope was then converted to a measure of foreshore width and standardized to a 100 cm decline in elevation from EHTL that is equivalent to the 'beach distance' measurement given by Penn and Brockmann (1994) based on their reported tidal range and is labeled Equivalent Foreshore Width (EFW).

Environmental Factors

At each sampling site and time, physical conditions were measured. These included water temperature (°C), salinity, wind speed (knots) and direction, wave height (m, observed), and cloud cover (%). Proximity of observed seagrasses or other structure within sampled transects was also recorded.

Statistical analysis

Statistical comparisons of HSC CPUE and prosomal width, as well as comparisons of beach characteristics, were conducted between islands, years, and sites within island with an ANOVA or t—test as appropriate unless data failed to meet assumptions of normality or equal variance. If assumptions were not met, then an analogous non—parametric test was used. Comparisons of observed sex ratio to an expected value of 1:1 were conducted for each island with a Chi—square analysis. All statistical tests were conducted at an experimentwise type I error rate of 5%.

RESULTS

Spawning Surveys

A total of 14 spawning surveys were completed on the western end of Horn Island (2007 = 3, 2008 = 8, and 2009 = 3) and West Ship Island had 13 surveyed transects (2007 = 5, 2008 = 5, and 2009 = 3). No evidence of HSC spawning was ever found on the southern GOM side of either island, so biological data are presented for the north side only. Evidence of HSC presence in the form of exuviae was found on the north side of both islands as early as March 5th (Figure 2). The earliest live unpaired HSC were observed on the beach on 7 April 2008. The earliest date spawning activity was observed was 21 April 2008 on West Ship Island, with salinity of 13.4 and water temperature of 20.9°C. Mated pairs were not observed in 2007 until 16 May; the salinity was 27.5 on this date but had decreased from 30 on 17 April, and the temperature increased to 26.6°C from 16.7°C. The earliest sampling date in 2009 was 23 April; the water temperature was 22.8°C, and the salinity was 18. The peak of the spawning season on both islands occurred during late April and early May in 2008. During this period, temperature increased from 17.3°C (5 March) to 19.3°C, and salinity increased from 24.0 to 26.3. Unpaired crabs and exuviae were found through 27 September in 2007 and 13 November in 2008. The temperature was 29.9°C and the salinity was 30.8. During the time of peak spawning activity in April/May active nesting was concentrated on the near subtidal flats rather than in the intertidal zone, likely due to the extremely narrow and steep nature of the intertidal beach.

Overall, the highest total CPUE of live animals was in 2009 (Figure 2). The CPUE was only slightly different between years on Horn Island, but was an order of magnitude higher in 2009 on West Ship compared to 2007 and 2008.

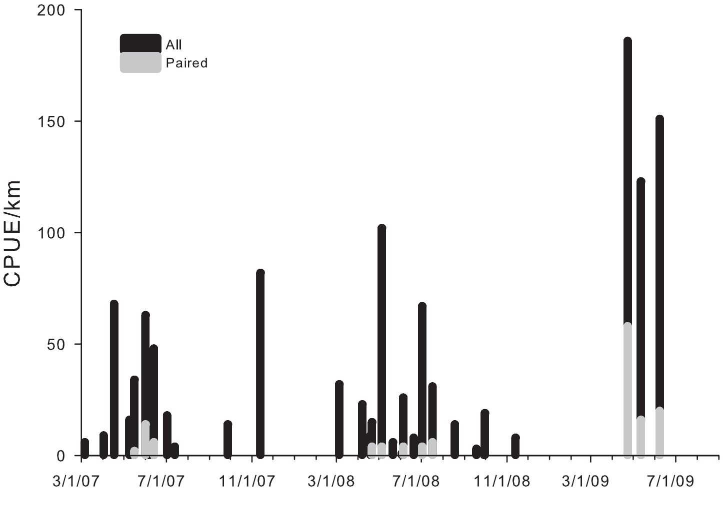

Figure 2. *Horseshoe crab CPUE/km (excluding exuviae) from random beach surveys conducted within 4 hrs of the new or full moon between March 2007 and June 2009. Data for all crabs counted and those found in mating pairs are given separately. Lack of a bar outside the sampling period each year does not indicate zero CPUE.*

Overall, differences in CPUE among years were significant (Kruskal—Wallis test, $p< 0.01$), but there was no significant difference in total CPUE between islands ($p> 0.05$). Spatially, all HSC spawning was observed on the north side of both islands and was most abundant on West Ship Island near Sites 10 and 18 (Figures 1d and 3) and on Horn Island near Site 5 (Figures 1e and 3).

The overall ratio of males to females was higher on the western area of Horn Island than on West Ship Island (Table 1). Both islands had proportions found to be significantly different then 1:1 based on Pearson's Chi—square test (West ship, $\chi^2_{13} = 266.737$, $p < 0.01$ and Horn, $\chi^2_{11} = 326.282$, $p < 0.001$). Mean prosomal width was not found to be significantly different between islands. The mean sizes of males and females were found to be significantly different on both West ship ($t_{(38.235)} = 13.498$, $p < 0.001$) and Horn ($t_{(59.665)} = 12.053$, $p < 0.001$) islands with an independent sample t—test, which is consistent with observed differences along the U.S. Atlantic coast and in Florida (Table 2) although mean size of both males and females were small compared to data from the middle of the species range in Delaware and the Carolinas and more similar to sex—specific mean size for the northern edge of the range and other sites in Florida.

Physical Habitat Characteristics

Differences in substrate particle size distribution were not present among sites located at the middle/ends or with distance from shore (0 m/10 m) on Horn Island and West Ship Island (Figure 4). There were significant differences in the particle size categories —1 ϕ and 3 ϕ between Horn and West Ship Islands ($t_{(15)} = -2.907$, $p < 0.05$ and $t_{(17.005)} = -3.677$, $p < 0.01$, respectively) with an increase in smaller (3 ϕ) particles at the 3 sites on the southern side of West Ship island (Sites WS10,WS11,WS12; Figure 1b). Overall, the north and south shores had significant differences in the 0 ϕ, 1 ϕ and 3 ϕ particle size categories ($t_{(20.609)} = 4.450$, $p < 0.001$, $t_{(23.337)} = 5.372$, $p < 0.001$ and $t_{(11.763)} = -3.464$, $p < 0.01$, respectively).

With the exception of Site WS13 on West Ship Island, all sites had an organic content of < 1%. The percent organic content was higher on West Ship Island in all categories (north and south, middle and end, 0 m and 10 m). The middle of both islands had higher percent organic content than the ends of the islands; and organic content was higher at 10 m depth than on the beach (Table 3). No clear pattern was observed for % shell hash ($CaCO_3$) between the

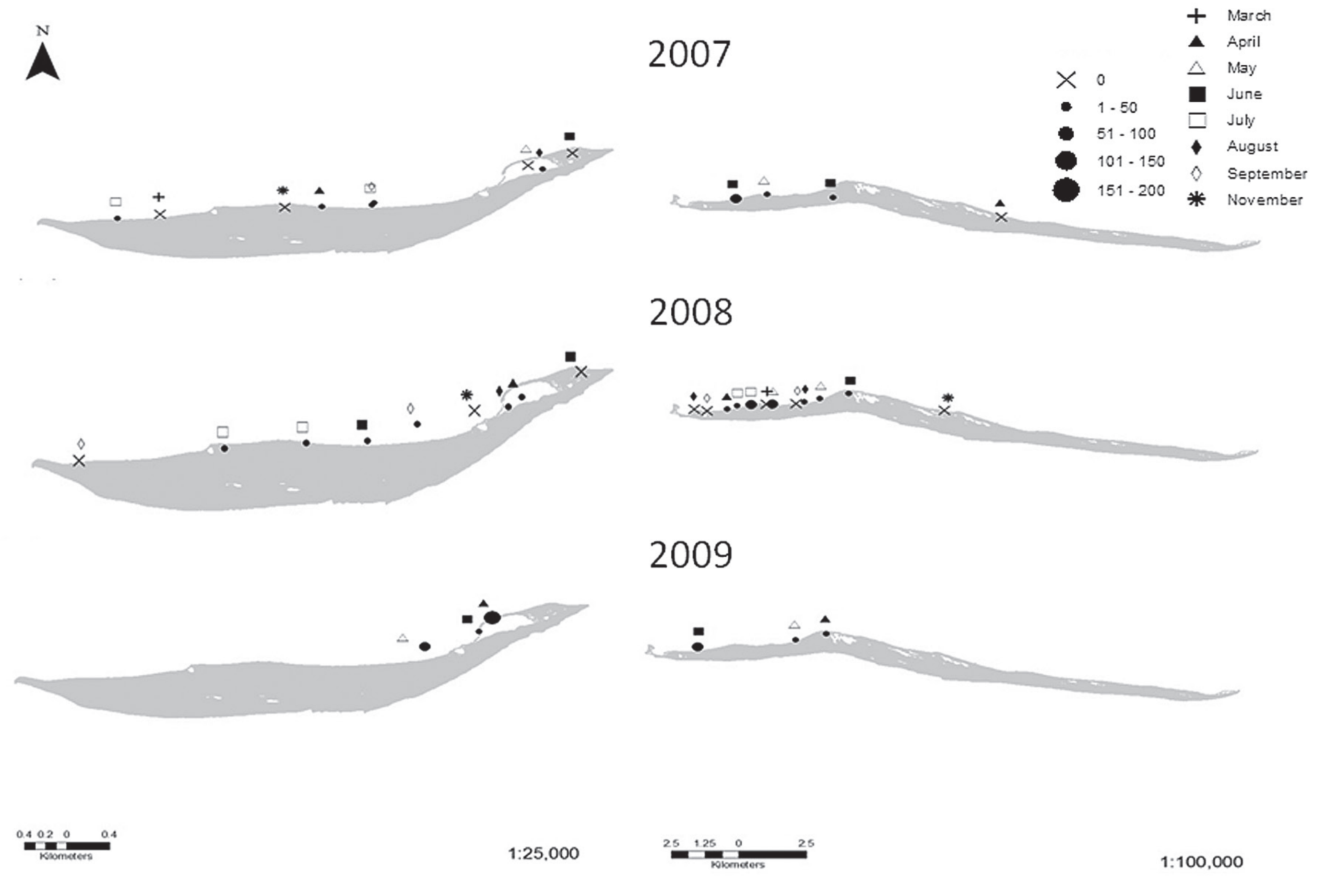

Figure 3. *Spatial distribution of horseshoe crabs CPUE/km on Horn island (right) and West Ship island (left) for 2007–2009. Symbols indicating collection month within year are offset for clarity.*

TABLE 1. *Summary of demographic data for horseshoe crabs,* Limulus polyphemus, *observed on Horn and West Ship Islands during 2007–2009. Size metric reported is prosomal width (mm). Value in parenthesis for CPUE and size is the standard deviation.*

	Horn Island	West Ship Island
Number of surveys	14	13
Mean CPUE/km	28(25)	28(23)
Female size range	149– 304	152– 286
Female mean size	214(36)	211(35)
Male size range	143– 255	144– 217
Male mean size	179(14)	179(13)
F:M ratio	1:9.76	1:5.30

islands' middle and ends or distance from shore (0 m or 10 m). However, the north shore of both islands had a greater percentage of shell hash than the south shore (Table 3). The percent organic matter and percent shell hash had no significant differences between Horn and West Ship Island, north and south sides, middle and ends, or distance from shore (0 m or 10 m).

The DRE was beyond sample maximum depth (300 mm) close to shore but decreased away from shore. All transects 70 m or less were well drained as indicated by the absence of an anaerobic layer shallower than 300 mm deep (Horn Island: 3 sites, West Ship Island: 5 sites). The transect at Site H4 on Horn Island was 80 m in total length, and a DRE was found at 50 m from shore at 111 mm depth. The DRE was found within 300 mm of the surface in all samples > 50 m from shore at this site. Sites WS7 and WS8 on West Ship Island were composed of aerobic sediment out to 90 m from shore. Sites H2 and H3 on Horn Island and Site WS9 on West Ship Island had a maximum distance from shore of 100 m. Site H3 was well–mixed throughout, whereas at Site H2 the DRE was located at 100 m from shore at 55 mm depth. The DRE was at 44 mm depth 90 m from shore and at 40 mm depth 100 m from shore at Site H9.

The length of elevation transects for both islands were standardized to a standard decline in elevation (equivalent foreshore width; EFW) from the EHTL line of 100 cm that ranged from 20–600 m on both Horn Island (Figure 5) and West Ship Island (Figure 6). Mean tidal amplitude for West ship Island in May is 0.24 m above sea level and EHTL is 0.52 m (NOAA *unpublished data*) making the actual maximum foreshore width about half this distance at any given site. The shortest elevation profile is Site 18 on the east end of West Ship Island at 22.86 m. A significant difference in elevation was found between end (Sites 6–8) and middle (Sites 1–5, 9) sites on Horn Island ($t_{(10)} = –2.982$, $p < 0.05$). No other t–tests were found to be significant. On the north side of both islands, transects collected near areas of high HSC CPUE (Sites 11,12, and 18 on West Ship; Site 5 on Horn) were the longest overall at > 500 m. The elevation distance in areas of high HSC CPUE on both islands was consistently > 200 m.

DISCUSSION

Horseshoe crabs show a large degree of plasticity in spawning behavior throughout their range. This is evident in both the timing (Penn and Brockmann 1994, Sekiguchi and Shuster 2009) and the location (Badgerow and Sydlik 1989, Penn and Brockmann 1994, Brockmann 2003) of spawning activity, as well as the dominant behavioral cues (Rudloe 1985, Barlow et al. 1986, Brockmann 2003, Ehlinger et al. 2003). Typically this type of plasticity is highly localized and more pronounced at the extreme edges of a species' distribution (Fraser 1999, Haak et al. 2010), so in examining HSC spawning patterns on Mississippi barrier islands we expected to find some differences, particularly in comparison to well studied populations along the U.S. Atlantic coast and in Florida.

In some ways HSC spawning in Mississippi is predictably similar to well–studied HSC populations along the Florida Gulf coast. The spawning season in Mississippi is highly similar to HSC populations in Florida (Penn and Brockmann 1994, Ehlinger et al. 2003, Brockmann and Johnson 2011), but somewhat earlier than reported peaks in Delaware and Massachusetts (Penn and Brockmann 1994, Smith et al. 2002, Carmichael et al. 2003). This was expected as

TABLE 2. *Summary of mean prosomal width (mm; ± sd for present study only) by sex reported for horseshoe crabs,* Limulus polyphemus, *at sites along the US Atlantic coast and in Florida. Florida sites are separated by those on the Atlantic (ATL) and Gulf (GUL) coasts.*

	Female	Male	Source
Maine	180	154	Moore and Perrin (2007)
New Hampshire	189	144	Watson and Chabot (2010)
Rhode Island	220	168	Shuster (1982)
Massachusetts	238	188	James–Pirri et al. (2005), James–Pirri (2010)
New Jersey	243	204	Swan (2005)
Delaware	271	210	Smith (2010)
Maryland	256	206	Swan (2005)
South Carolina	313	239	Shuster (1982)
Indian River, FL (ATL)	189	136	Ehlinger et al. (2003)
Appalchee Bay, FL (GUL)	229	171	Rudloe (1985)
Seahorse Key, FL (GUL)	227	165	Penn (1992)
Mississippi barrier island	214 (27)	179 (14)	Present study

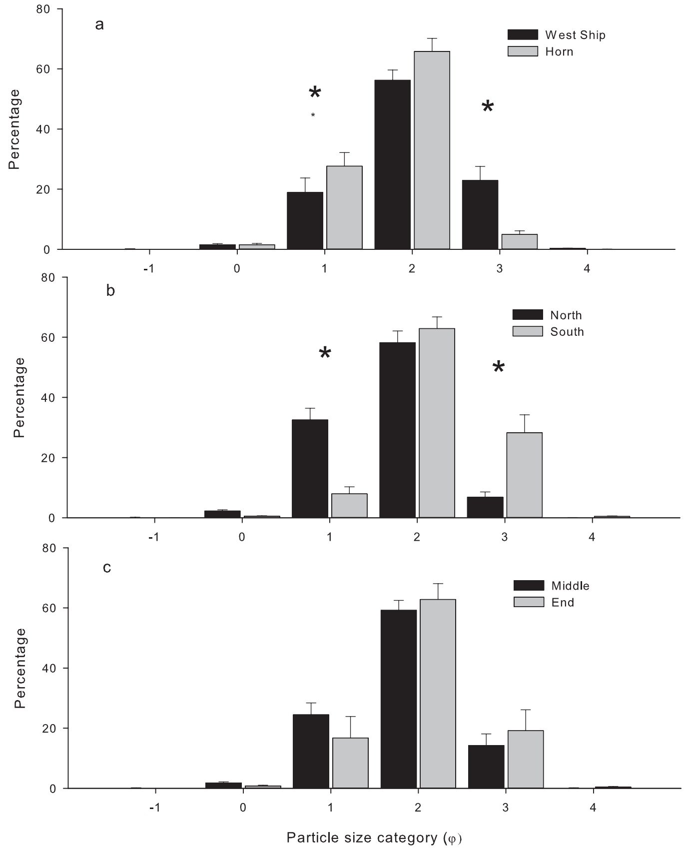

Figure 4. *Particle size distribution of sediment.* ***a.*** *Comparison between islands.* ***b.*** *North and South side of islands.* ***c.*** *Middle and end of the islands. Units for grain size are 1 ϕ = –log2(S) where S = particle diameter (mm). Asterisk (*) indicates a significant different between groups. Categories –1 and 4 ϕ were consistently less than 0.1%.*

temperature is a significant driver for the onset of spawning and nesting activity (Penn and Brockmann 1994, Jackson et al. 2008, Brockmann and Johnson 2011). Both male and female HSC in Mississippi were small in comparison to reported prosomal width in Maryland, New Jersey, and Delaware, but similar to other populations in Florida, as well as at the northern edge of their range in New Hampshire and Maine. This trend is in line with the observations of Shuster (1982) that both male and female size is highest in the middle of their range and smaller on the edges. The ratio of males to females in Mississippi was within the overall range reported for other populations along the U.S. Atlantic coast and the Florida Gulf coast, but was higher than the mean for all except for heavily harvested populations (Carmichael et al. 2003, James–Pirri et al. 2005, Mattei et al. 2010). The lower abundance of females relative to males in this population cannot be attributed to harvest, as it might be elsewhere, so the cause for this is unclear.

In terms of where HSC choose to spawn and nest, Mississippi barrier islands seem to have some unique characteristics. No spawning was ever observed on the south side of the two islands used for this study. The only overt differences observed between the north and south side of these two islands were a higher proportion of small sediment sizes on the southern (i.e., Gulf) side, and a higher amount of wave energy. Percent shell hash across both islands was consistent with reports of percent gravel at nesting beach sites in Florida, but much lower than similar values for nesting beach sites in Delaware (Penn and Brockmann 1994). Sediment size is also related to wave energy (Malvarez et al. 2001), but typically larger particle sizes are associated with high wave action. In the case of Mississippi barrier islands this relationship was somewhat reversed and this suggests that other factors such as longshore currents or depth may affect particle size on these islands.

Based on research into *Limulus* nesting habitat conducted elsewhere, it seems that higher wave action might be the more important determinant of HSC nesting activity. Beaches with moderate wave activity in Delaware have higher HSC abundance (Smith et al. 2002) and spawning activity in a similar population near Seahorse Key along the Florida Gulf coast was concentrated on the south side where wave energy was higher (Brockmann and Johnson 2011). However, higher wave energy has been found to inhibit nesting activity and beaches in Delaware Bay sheltered from wave action by orientation or topography were identified as an important focal point for HSC conservation by Smith et al. (2011), which is consistent with our observations in Mississippi. These studies reported that wave energy probably increases the total beach area available for nesting and improves sand aeration, but that wave energy can be too high, possibly disrupting nests (Jackson et al. 2008). Quantifying total wave energy is difficult and as a result this factor is often qualitatively reported in the literature, yet wave energy can potentially be too high and probably interacts with other factors to create locally optimal conditions.

One of the more interesting observations in this study was that HSC along the Mississippi barrier islands exhibited significant amounts of sub–tidal nesting behavior. Location of spawning activity on beaches has been examined for populations in Delaware and Florida and key differences existed

TABLE 3. *Summary of index elements (% organic content and % CaCO3) of nesting beach sediment on Horn and West Ship Islands. Data summarized across sites based on location on island (end/middle; north/south) or water depth (0 m/10 m).*

% organic content	end	middle	north	south	0 m	10 m
Horn Island	0.17	0.21	0.21	0.22	0.17	0.27
West Ship Island	0.33	0.36	0.38	0.33	0.27	0.38
% CaCO3						
Horn Island	2.63	3.22	3.40	2.36	2.42	3.95
West Ship Island	3.02	2.44	2.27	2.05	2.77	2.17

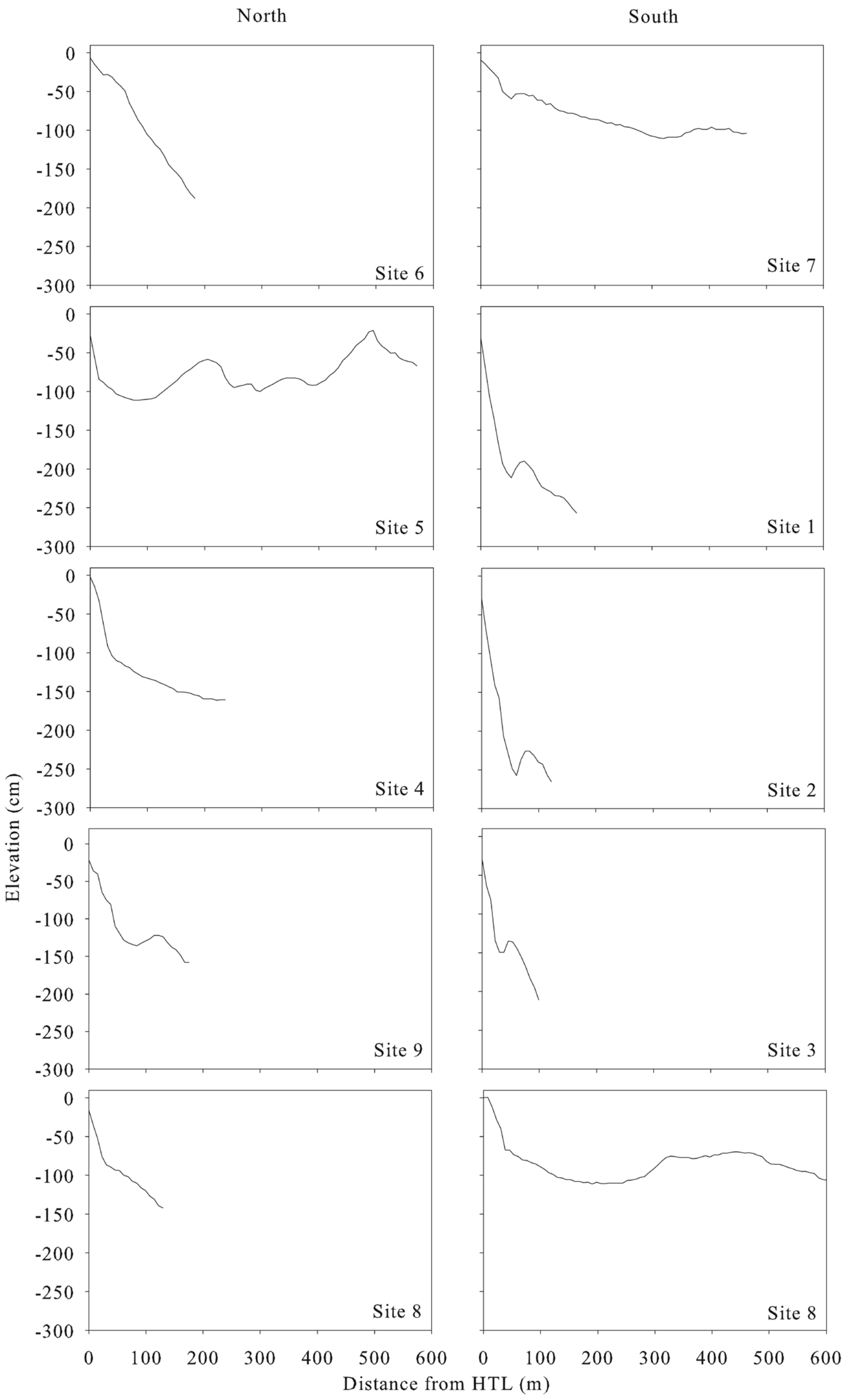

Figure 5. *Elevation profiles for Horn Island from the High Tide Line (HTL). Site labels are as given in Figure 1e and are ordered with southern sites to the right and northern sites to the left with western sites at the top and eastern sites at the bottom. Sites that appear in both columns are near the end of the island; north and south samples were collected within 100 m of each other but on opposite sides of the island. See Figure 1 for details.*

that were related to beach slope, beach grain size, and interstitial dissolved oxygen concentration (Penn and Brockmann 1994). Horseshoe crab nests in Delaware were found spread over a wider area including the lower beach, while nests in the Florida population were concentrated farther from the low tide line. In addition, egg survival was found to be directly related to nest height in Florida, but not in Delaware (Penn and Brockmann 1994, Jackson et al. 2008). This was thought to be largely driven by differences in sand drainage as the smaller—sized grains on the beach in Florida were not well drained, and largely anoxic close to the low tide line, resulting in high mortality for nests in this region. In contrast, small differences in drainage were evident on the Delaware beach and nests located lower where the risk of desiccation was lower did as well as those higher on the beach. However, subtidal nesting was not reported as common on either site and it is rarely mentioned in the HSC literature although it has been reported for HSC populations in Connecticut (J. Mattei, Sacred Heart University, *pers. comm.*) and references in the grey literature suggest that sub—tidal nesting may have been observed in Florida HSC populations (A. Rudloe, *unpublished comment*).

Nesting behavior on Mississippi barrier islands was consistently observed on the sub—tidal sand flats just off the beach. These areas had a high DRE suggesting the sediment is well—oxygenated and a grain size more consistent with Delaware beaches than those in Florida (Penn and Brockmann 1994). Sub—tidal nesting behavior is not commonly reported in Delaware, but the key difference may be the lower tidal amplitude and gentle beach slope found in Mississippi. Penn and Brockmann (1994) reported a distance to a 1m decline in elevation from the extreme high tide line of approximately 12 m in Delaware, and based on their reported tidal amplitude this is a foreshore width available for inter—tidal nesting. Penn and Brockmann (1994) also reported a significant decline in egg development in the lower 2 m of the foreshore based on experimental observation that they attributed to a decline in oxygen concentration in the sediment. Similar results were reported by Jackson et al. (2008) for beaches in Delaware where egg development was significantly lower on the lower foreshore where sediment oxygen levels fell below 3 ppm. The EFW in Mississippi was consistently over 100 m and could be as high as 500 m particularly in areas with consistent HSC presence. However the tidal range at spring tide in Mississippi is half that reported for both Florida and Delaware populations. An examination of beach pro-

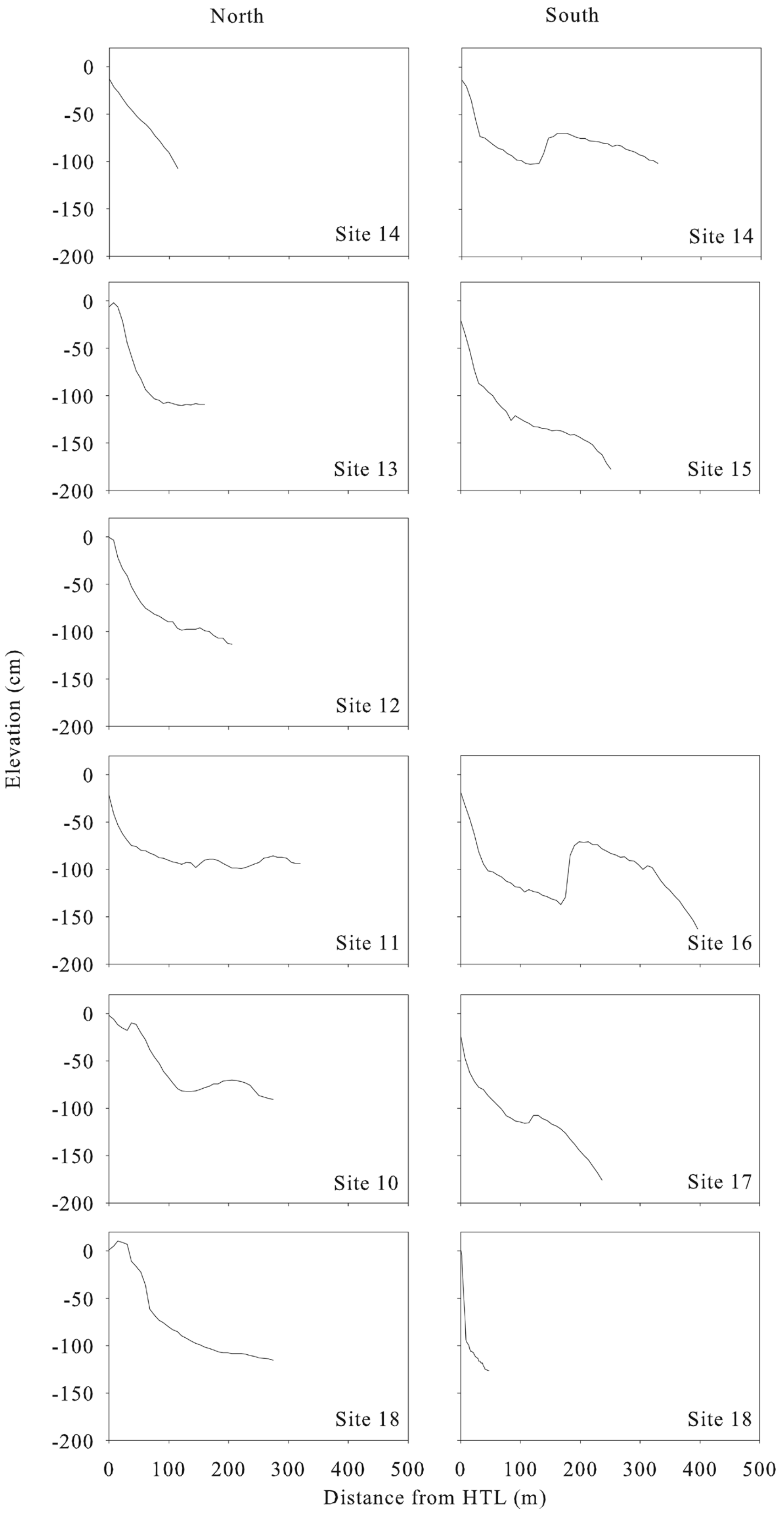

Figure 6. *Elevation profiles for West Ship Island from the High Tide Line (HTL). Sites labels are as given in Figure 1d and are ordered with southern sites to the right and northern sites to the left with western sites at the top and eastern sites at the bottom. Sites that appear in both columns are near the end of the island and north and south samples were collected within 100 m of each other but on opposite sides of the island. See Figure 1 for details.*

files for both islands in this study show a consistent decline from the EHTL of 0.5 m within the first 10—20 m suggesting actual foreshore width is about the same in Mississippi as in Florida and Delaware, but it is bordered on the seaward side by a much wider sub—tidal sand flat that is consistently well—oxygenated to a depth below the depth commonly reported for HSC nests (11—18 cm; Kraeuter and Fegley 1994). The well—oxygenated sediment combined with wide flat sub—tidal areas may provide unique habitat for HSC nesting in that it is not prone to desiccation, and is also well—protected from nest predation by shorebirds. Smith et al. (2002) reported that nests in Delaware were most dense within 3—5 m of EHTL and Penn and Brockmann (1994) found that nests higher on the beach showed higher percent egg development due to warmer temperatures and higher oxygen levels, so it is important to examine whether egg development and survival in subtidal nests is sufficient for them to contribute to the population. Presence of diurnal tidal cues has been provided as an important limiting factor on the range of HSC (Brockmann 2003), but evidence in Mississippi and elsewhere suggests this may not be the case (also see Ehlinger et al. 2003). Preference for intertidal nesting in HSC is generally attributed to protecting eggs and larvae from fish and invertebrate predators (Brockmann 2003). An interesting area of future study would be to examine the importance of egg and larval survivorship in areas where tidal cues for nesting are weak and well—oxygenated nest habitat is available below the low—tide line. The contribution of nesting on these islands, be it intertidal or subtidal, can only be indirectly inferred from anecdotal historical reports of HSC nesting on these islands going back over 20 years and the observed abundance of juvenile HSC in the adjacent sea grass beds in the summer (R. Heard, University of Southern Mississippi, *unpublished data*). Nonetheless, Mississippi barrier islands may represent microtidal habitat for horseshoe crab nesting similar to that reported by Ehlinger (2003) in Florida, but on a federally protected series of barrier islands which should be accounted for in management plans for the islands.

Mississippi barrier islands are subject to both natural and anthropogenic change that may alter HSC nesting habitat. Previous studies of long—term and historical characteristics of sediment transport on West Ship Island and Horn

Island indicate that these islands will continue to reduce in size (Schmid 2001). This is partially attributed to the dredged channels adjacent to the western edge of the islands that disrupt normal barrier island migration by intercepting the sediments brought by long shore transport that would build up creating elevated area on the western edge. These sediments would fill a naturally occurring or undredged area resulting in an increase in island size, as well as contribute to westward land extension and migration (Morton 2007). Barrier island restoration along the Mississippi Gulf Coast has also been a critical topic for the U.S. Army Corps of Engineers since 2005. The damage done, principally by Hurricane Katrina, fostered a study into island re—nourishment of West Ship Island and Horn Island for storm protection (USACE United States Army Corps of Engineers, 2011). Yet, the islands are managed by the National Park Service, whose mission includes habitat protection for vulnerable populations such as nesting horseshoe crabs. From this perspective it will be vital that the characteristics of the islands, particularly the lower beach and sand flats, be maintained if they are found to be critical to local HSC nesting success (Jackson et al. 2010). More research is needed, but this study has demonstrated that HSC do commonly use Mississippi barrier island beaches for nesting, they appear to do so in a unique way that demonstrates the behavioral plasticity of this species, and these factors need to be better understood in order to properly manage the barrier island ecosystem.

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