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SITE SELECTION BY MIGRATORY SHOREBIRDS IN DELAWARE BAY, AND ITS RELATIONSHIP TO BEACH CHARACTERISTICS AND ABUNDANCE OF HORSESHOE CRAB (*LIMULUS POLYPHEMUS*) EGGS

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ABSTRACT.—The distribution of migratory shorebirds within Delaware Bay, New Jersey, was examined relative to prey abundance and the physical characteristics of the intertidal beaches. Red Knots (*Calidris canutus*), Sanderlings (*C. alba*), Ruddy Turnstones (*Arenaria interpres*), and "peeps" comprised nearly 100% of the shorebirds on seven study beaches from mid-May to early June in both 1990 and 1991. The most abundant food item on these beaches was horseshoe crab (*Limulus polyphemus*) eggs, and there were few other available macroinvertebrates. Beaches preferred by shorebirds had higher numbers of crab eggs; the density of eggs in some surface (0–5 cm) sediments exceeded $10^5/m^2$. In general, both horseshoe crab eggs and shorebirds increased along the bay shore from Higbee's Beach (near Cape May Point) to Moore's Beach, 32 km up-bay. However, shorebirds were widely distributed within the bay, possibly because eggs were sufficiently abundant on most beaches to support foraging by at least four birds per meter of shoreline. Shorebirds aggregated near shoreline discontinuities, such as salt-marsh creeks and jetties, that acted as concentrating mechanisms for passively drifting eggs. Sediment grain size and heterogeneity were probably not a primary determinant of shorebird distribution within Delaware Bay. Intertidal sand flats were not extensively used by foraging shorebirds, but the potential importance of nearby salt marshes as foraging sites requires further investigation. *Received 20 January 1993, accepted 27 March 1993.*

WESTERN HEMISPHERE SHOREBIRDS undertake lengthy migrations from coastal beaches and wetlands in South America, to arctic and subarctic breeding areas (Myers 1981, Morrison 1984, Myers et al. 1987). "Staging areas" are intermediate stopover points along the migration route, where shorebirds feed en masse before continuing their journey. The Delaware Bay estuary in New Jersey and Delaware (38°47′ to 39°20′N, 74°50′ to 75°30′W) is a staging area for an estimated 425,000 to 1,000,000 shorebirds during May and June (Wander and Dunne 1981, Myers 1981, 1986, Burger 1986, Myers et al. 1987, Clark et al. 1993). The Delaware estuary is particularly important to Ruddy Turnstones (*Arenaria interpres*), Semipalmated Sandpipers (*Calidris pusilla*), Red Knot (*C. canutus*) and Sanderlings (*C. alba*), which collectively comprise about 95% of the feeding shorebirds (Wander and Dunne 1981, Clark et al. 1993). Dense flocks of Laughing Gulls (*Larus atricilla*) populate these beaches throughout the spring and summer (Botton 1984), often feeding along with shorebirds on a common food resource: horseshoe crab (*Limulus polyphemus*) eggs.

Staging areas provide abundant food, which enables shorebirds to gain mass rapidly and continue the migration (Morrison 1984, Myers et al. 1987). The spring migration in Delaware Bay coincides with the spawning of horseshoe crabs on sandy beaches (Shuster and Botton 1985, Botton et al. 1988). It has been presumed (Wander and Dunne 1981, Myers 1986) that the abundance of horseshoe crab eggs during the spring shorebird migration contributes to the importance of the Delaware estuary as a feeding ground. An enormous quantity of eggs is potentially available to shorebirds, as each female

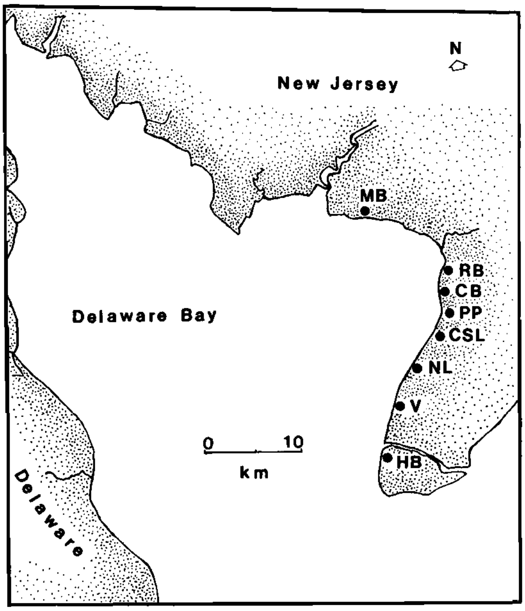

Fig. 1. New Jersey shoreline of lower Delaware Bay. (HB) Higbee's Beach; (V) Villas; (NL) Norbury's Landing; (CSL) Cape Shore Laboratory; (PP) Pierce's Point; (CB) Cook's Beach; (RB) Reed's Beach; and (MB) Moore's Beach.

horseshoe crab may lay up to 20 egg clusters, each with an average of 3,650 eggs (Shuster and Botton 1985), and the population within Delaware Bay is about two to three million adults (Botton and Loveland 1989). Castro et al. (1989) concluded that a high rate of consumption was required to compensate for the low assimilation efficiency of Sanderlings feeding on *Limulus* eggs.

We examined the environmental factors that influence the distribution and abundance of shorebirds around Delaware Bay. Previous authors have found that shorebirds concentrate in areas of maximal food abundance (e.g. Goss-Custard 1979, Bryant 1979, Puttick 1984). Wander and Dunne (1981) suggested that Red Knots, Ruddy Turnstones, Semipalmated Sandpipers, and to a lesser extent Sanderlings concentrated along those Delaware Bay beaches with the most horseshoe crabs. Horseshoe crabs are not evenly distributed along the bay shore; they respond to habitat type and prefer to spawn on undisturbed beaches, free from reducing sediments which generate H_2S (Botton et al. 1988).

The variety of habitat types within Delaware Bay (e.g. sandy beaches, salt marshes, and bulkheaded areas) could also influence shorebird distributions. For instance, foraging shorebirds may select a habitat based on degree of vegetation or algal cover (Burger et al. 1977, Davidson and Evans 1986), sediment wetness and/or penetrability (Kelsey and Hassall 1989, Mouritsen and Jensen 1992), or sediment grain size (Quammen 1982, Hicklin and Smith 1984, Grant 1984). In addition, since shorebirds may use different habitats over the tidal cycle (Burger et al. 1977, Puttick 1984), the relationship of habitat diversity to bird abundance needs to be considered. Intertidal sand flats and salt marshes are found at some Delaware Bay beaches. These could be important to shorebirds as supplementary feeding and/or roosting areas (Wander and Dunne 1981, Botton 1984).

STUDY AREA AND METHODS

Sampling sites.—We observed shorebirds and horseshoe crabs during May and June of 1990 and 1991. Seven primary study beaches in New Jersey (Fig. 1) provided representative habitat types. Higbee's Beach is a State Wildlife Management Area located near the mouth of Delaware Bay. Except for a jetty at the north end, this beach is undisturbed. At Villas, there are numerous houses, but all are located well behind stable sand dunes; thus, the beach is relatively natural and wide. The study area at Norbury's Landing is bulkheaded adjacent to a small parking area, with a few houses behind low sand dunes to either side of the observation site. Pierce's Point was located on an undeveloped beach approximately 0.25 km north of the town; several decades of bulkheading within the town has virtually removed the sand dunes and much of the beach south of our study site. Cook's Beach is a sandy beach with adjacent salt marsh dominated by *Spartina alterniflora*; eroded peat banks are prevalent to the north and south, in the vicinity of tidal marsh creeks. The study area at Reed's Beach was at the northernmost extent of the town, near a long jetty stabilizing the entrance to Bidwell's Ditch. Most of the beachfront houses in the town are on elevated pilings, since high tide routinely comes under these houses. Moore's Beach is a severely disturbed habitat. Unsuccessful attempts were made in past years to protect dwellings from beach erosion by dumping various kinds of fill (cinderblocks, bricks, chunks of asphalt and concrete, etc.) on the beach. The observation site was near the confluence of a salt-marsh creek and the bay, at the northwest end of the town. Additional information is presented from a long-term horseshoe crab study site referred to as the North Beach (Botton et al. 1988), which is located by the Rutgers "Cape Shore" Laboratory near Green Creek.

Shorebird surveys.—At each beach, we counted shorebirds 5 to 11 times during the peak of the migration period (mid-May to early June) in 1990 and 1991, with the exception of Pierce's Point, which was surveyed 4 times in 1990 only. All beaches were surveyed during low tide (predicted low tide from NOAA [National Oceanic and Atmospheric Administration] tide tables ± 1 h), high tide (± 1 h), and midtide periods. Observations generally lasted 30 min. We did not conduct shorebird censuses after dark, because we have not seen shorebirds on these beaches during many years of nighttime observations of horseshoe crabs.

Shorebirds were observed through binoculars by a team of two or more individuals from an inconspicuous location above the high-tide line. We counted birds that were on the beach as well as those flying parallel to the shoreline. Visual and/or verbal communication enabled us to avoid duplicate recording of the same flock of birds by two different observers. When flock movements were rapid, we estimated flock sizes on a scale of 1, 2, 3, or 4, corresponding to a median of 5, 25, 100, and 200 birds, respectively. For statistical purposes, and to compensate for differences in observation duration or number of observers, we normalized shorebird abundance to: number of birds $\cdot$ observer$^{-1}\cdot$h^{-1}. Species composition of the flock was also noted; small sandpipers (mostly *Calidris pusilla*) were categorized only as "peeps." All statistical comparisons among beaches in this paper were made using the PROC ANOVA routine in SAS, followed by the LSD multiple comparison procedure (SAS Institute 1985).

Horseshoe crab abundance.—We estimated the abundance of adult horseshoe crabs in three ways, because we did not know which variables might be important to shorebirds in their choice of foraging sites. At high tide, horseshoe crabs are spawning and would be easily visible to passing flocks of birds. We counted the number of spawning crabs along five or six consecutive 15-m transects parallel to the water's edge. After the tide receded, we counted the number of "nests," bowl-shaped depressions in the sand corresponding to the places where female crabs had deposited their eggs. We did this because shorebirds, especially Ruddy Turnstones, seemed to be attracted to these sediment disturbances (or even to fresh footprints of similar depth). At low tide, we also counted the number of "stranded" crabs (i.e. animals overturned by wave action during spawning, or disoriented during their return to the water; Botton and Loveland 1987, 1989). Further discussion of these methods is found in Botton and Loveland (1989); estimates of nests and stranded crabs provide only a measure of relative abundance among beaches.

Sampling of beach sediments.—Sediment samples were taken during "early" (late April to early May) and "peak" (mid-May to early June) periods of shorebird abundance in 1990 and 1991. Two replicate transects were established 1 m apart from the spring high-tide mark to the mean low water mark. Stations on the transect were at 3-m intervals; plots within a station along the transect were 35 cm on a side (= 0.1225 m^2). We sampled surface (0 to 5 cm) sediments on all dates to estimate the abundance of eggs available to shorebirds. We also sampled at a depth of 15 to 20 cm during the peak period in 1990 to estimate egg abundance; most egg clusters are initially deposited at this depth (Botton et al. 1992). Approximately 6.1 L of sand from each horizon were thoroughly mixed in a plastic bucket; then, a 1-L sediment subsample was removed and refrigerated (5°C) for laboratory analysis, which commenced within a few days.

Three separate aliquots of sand (usually 80 ml, but occasionally less with samples containing large numbers of eggs) were washed through a 1-mm wire mesh sieve. All horseshoe crab developmental stages (eggs, embryos, and "trilobite" larvae), and any other invertebrates retained on the screen, were enumerated.

Sediment grain-size analysis was performed by sieving approximately 200 g of oven-dried sediment through a standard sieve series, with mesh openings of 4 mm, 2 mm, 1 mm, 500 μ, 250 μ, 125 μ, and 62 μ (-2 ϕ through 4 ϕ). The trace amount of sediment comprising the silt-clay (< 62 μ) fraction was not further fractionated. Graphic mean and inclusive graphic standard deviation (a measure of "sorting" or sediment heterogeneity) were calculated following Folk (1974).

Beach width and slope were measured on 5 and 6 July 1990. Beach width was defined as the distance from the highest spring tide to the mean low-water mark. However, on those beaches where adjacent intertidal flats occurred, we measured to the break between the beach and intertidal flats. Beach slope was determined by dropping a plumb line at 3-m intervals along a level line on the transect. Other attributes of the study sites, such as the presence of sand dunes, proximity to salt marsh systems, or degree of human disturbance, were directly observed throughout the study.

RESULTS

Physical characteristics of beaches.—A synopsis of the characteristics of the study areas is presented in Table 1. Beach sediments varied from medium sand on lower Delaware Bay beaches (Higbee's Beach, Villas) to coarse sand further up-bay, particularly at Moore's Beach (Fig. 2A, B). In general, beach sediments were characterized as moderately well sorted (Fig. 2C), with the exception of Moore's Beach, where the samples contained large stones and fragments of brick, concrete, shell, etc., derived from beach fill.

Shorebird patterns of abundance and behavior.—

TABLE 1. Physical features of study areas on Delaware Bay, New Jersey.

Beach	Distance from Cape May Point (km)	Beach Width (m)	Beach Slope (degrees)	Presence of Salt marshes	Presence of Tidal flats	Major shoreline features
Higbee's Beach	2.0	20.6	6.0	No	No	Uninhabited and protected; extensive dunes
Villas	9.0	21.0	5.5	No	Yes	Houses behind sand dunes
Norbury's Landing	11.9	15.5	6.6	No	Yes	Houses behind sand dunes
Pierce's Point	16.8	15.5	6.5	Limited	Yes	Houses with bulkheaded areas and jetties 0.5 km south of study site
Cook's Beach	19.3	24.0	6.8	Extensive	No	Uninhabited; small boat ramp; salt marsh creeks entering bay
Reed's Beach	21.6	25.0	4.8	Extensive	No	Center of town has bulkheads and pilings; long jetty trapping sand at study site
Moore's Beach	32.4	24.0	6.1	Extensive	No	Severely disturbed: rubble, ruins; salt marsh creek entering bay

Pooling all beaches, shorebird abundance (birds$\cdot$observer$^{-1}\cdot$h^{-1}) was not significantly different for high tide ($\bar{x}$ = 1,146.1), midtide ($\bar{x}$ = 1,260.5), and low tide ($\bar{x}$ = 797.2; ANOVA, F = 0.96, df = 2 and 53, $P > 0.39$). Median flock size, however, was significantly influenced by tidal stage (F = 4.16, df = 2 and 53, $P < 0.02$), such that significantly larger ($P < 0.05$, LSD tests) flocks were seen at high tide ($\bar{x}$ = 38.6) than at midtide (x = 11.2) or low tide ($\bar{x}$ = 8.1).

During the peak of the bird migration (mid-May to early June) in 1990 and 1991, shorebird abundance differed among beaches (F = 2.57, df = 6 and 49, $P < 0.03$), with Norbury's Landing, Moore's Beach, and Reed's Beach having significantly more birds than Cook's Beach, Pierce's Point, and Higbee's Beach (LSD tests, $P < 0.05$; Table 2). Villas occupied an intermediate position. Large numbers of shorebirds (>2,000/h) were seen at least once on all beaches except Pierce's Point and Higbee's Beach, but even the more active beaches had surveys in which very few birds were seen.

Most bird activity we tabulated involved flights parallel to the shoreline, or takeoffs or landings following or preceding feeding activity. We did not observe any feeding activity at Pierce's Point. At Moore's Beach, 33.2% of the 343 records of shorebird flight direction involved movements into or out of the tidal creek.

At high or midtides, shorebirds were generally concentrated at the water's edge, and appeared to be foraging on *Limulus* eggs in the swash zone. Ruddy Turnstones frequently dug for eggs above the water line, especially in areas where horseshoe crab nests were visible. Shorebirds were distributed differently at low tide. At Norbury's Landing and Villas, shorebirds were often dispersed in loose aggregations over the exposed tidal flats, typically feeding at the edges of shallow rivulets and pools. At Cook's Beach and Moore's Beach, breaks in shoreline topography, particularly sand spits at the mouths of tidal creeks, were important feeding sites at low tide.

To further investigate the role of shoreline discontinuities in attracting shorebirds, we repeatedly surveyed a 2.9-km stretch of beach between the North Beach and Norbury's Landing. This uninhabited region lacks any jetties or bulkheads, and broad intertidal sand flats occur offshore of the beach. However, there are two prominent marsh-drainage pipes that jut out onto the flats for about 30 m beyond the beach break. Very few shorebirds were seen along this beach during high or midtide periods. At low tide, scattered, widely spaced shorebirds were seen on sand bars and shallow pools, but larger, more compact flocks of 20 to 200 shorebirds were only seen in the vicinities of the pipe outlets. The birds were actively feeding on aggregations of horseshoe crab eggs mixed with plant

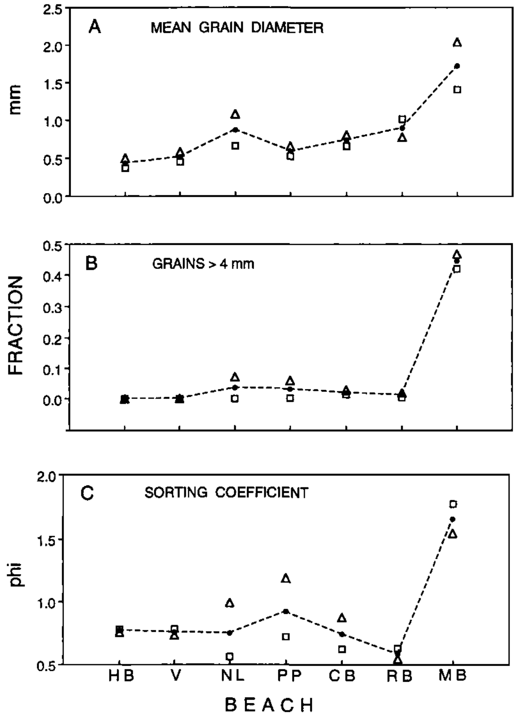

Fig. 2. Characteristics of midbeach sediments on study beaches in Delaware Bay, spring 1990. (A) Mean grain diameter; (B) percentage of particles >4 mm; (C) sorting coefficient (heterogeneity). Stations 6 (squares) and 9 (triangles) were located at 6 and 9 m down a transect line beginning at spring high-water line; dashed line represents average. Beaches arrayed left to right in up-bay direction (see Fig. 1).

TABLE 2. Abundance of migratory shorebirds on Delaware Bay beaches during peak of spring migration.

Beach	No. surveys	Mean no. birds·h^{-1}·observer^{-1}	Minimum	Maximum
Norbury's Landing	11	1,748.1[a]	164	5,260
Moore's Beach	8	1,285.3[ab]	352	2,733
Reed's Beach	10	1,230.0[ab]	0	2,796
Villas	8	1,142.8[b]	103	2,494
Cook's Beach	10	740.0[bc]	203	2,000
Pierce's Point	4	373.0[bc]	20	958
Higbee's Beach	5	70.0[c]	16	118

[a,b,c] Means with same superscript letter are not statistically different (ANOVA; means compared by LSD tests; $P < 0.05$).

detritus that were trapped in the vicinity of the pipes.

When both shorebirds and gulls were present, there were predictable interactions. Approaching flocks of shorebirds seemed to be deterred from landing on a stretch of beach if a dense flock of gulls was already present at the water's edge. Dense, mixed flocks of gulls and shorebirds were observed on several occasions at Norbury's Landing, Cook's Beach, and Reed's Beach, and when this occurred, gulls monopolized the waterline, limiting shorebirds to drier sand further up the beach.

Red Knots, Ruddy Turnstones, Sanderlings, and peeps comprised 98 to 99% of all shorebirds counted on each beach in both years (Table 3). Peeps were especially numerous at Moore's Beach on a sand spit during low tide. Sanderlings, Ruddy Turnstones, and Red Knots were distributed throughout Delaware Bay. Sanderlings comprised the greatest percentage of birds seen at Higbee's Beach and Villas, in lower Delaware Bay. Ruddy Turnstones dominated at Reed's Beach, and Red Knots were the most common shorebird at Cook's Beach. Smaller numbers of Dunlins (*Calidris alpina*), Willets (*Catoptrophorus palmatus*), Black-bellied Plovers (*Pluvialis squatarola*), Spotted Sandpipers (*Actitis macularia*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Short-billed Dowitchers (*L. griseus*), and American Oystercatchers (*Haematopus palliatus*) were recorded, but their frequencies were too low to discern possible site preferences.

Abundance of horseshoe crabs and crab eggs.—The number of spawning crabs on late-day high tides (after 1500 EST; $\bar{x} = 56.2/15$ m) was not significantly greater than the number spawning on high tides before 1500 ($\bar{x} = 48.6$; $F = 0.21$, df = 1 and 139, $P > 0.65$), so all census data were pooled in subsequent analyses. The abundance of spawning crabs on high-tide censuses was significantly higher at Moore's Beach and Reed's Beach than at the two lower-bay beaches (Higbee's Beach and Villas; Fig. 3A). The number of stranded crabs also differed significantly among sites ($F = 5.83$, df = 6 and 94, $P < 0.0001$); stranded crabs were more than twice as numerous at Reed's Beach than at any other site, with the fewest occurring at Higbee's Beach and Villas (Fig. 3B). Numbers of horseshoe crab "nests" also differed significantly among beaches ($F = 17.25$, df = 4 and 25, $P < 0.0001$; Fig. 3C).

Surface sediment samples (0–5 cm) collected from beaches during late April and the first three days in May showed that low numbers of horseshoe crab eggs were present just prior to

TABLE 3. Species composition (proportion of total birds identified) of shorebirds observed on study beaches in Delaware Bay, New Jersey, spring 1990 and 1991. Beaches arranged in an up-bay direction.

Beach	Red Knot	Ruddy Turnstone	Sanderling	"Peeps"	Others
Higbee's Beach	0.023	0.485	0.489	0.000	0.004
Villas	0.109	0.270	0.620	0.000	0.001
Norbury's Landing	0.309	0.452	0.238	0.000	0.001
Pierce's Point	0.196	0.412	0.351	0.029	0.012
Cook's Beach	0.873	0.106	0.006	0.009	0.006
Reed's Beach	0.176	0.757	0.061	0.002	0.004
Moore's Beach	0.322	0.221	0.277	0.165	0.015

the arrival of shorebirds (Fig. 4A). However, even by early May, many more surface eggs were present at Reed's Beach than at any other site.

During the peak of the bird migration in 1990 (Fig. 4B, C) and 1991 (Fig. 4D), the abundance of crab eggs in surface sediments was lowest at Higbee's Beach and Villas, but similar along beaches between Norbury's Landing and Moore's Beach. At least 10^4 to 10^5 crab eggs/m^2 were found in the midbeach region at all sites, except Higbee's Beach, in both years. Midbeach densities of 3×10^5 to 5×10^5 eggs/m^2 were found at Reed's Beach and Moore's Beach.

The abundance of eggs at a depth of 15 to 20 cm (Fig. 5) is indicative of the effects of repetitive horseshoe crab spawning activity on these beaches; that is, eggs accumulated below 15 cm on the beach while the number of surface eggs on the same beaches appeared to reach an equilibrium between the input of fresh eggs and their removal by predators (Fig. 4B, C). Large numbers of horseshoe crab eggs were deposited everywhere except at Higbee's Beach. In general, the number of eggs available at the surface for foraging shorebirds was about an order of magnitude less than the number of eggs at 15 to 20 cm.

In late April and early May, live crab eggs comprised nearly 100% of the total horseshoe crab stages in surface sediments on all beaches. Although the number of live eggs increased over the next two weeks, as noted above, the proportion of live eggs to the total number of stages decreased slightly. During the peak of the bird migration, live eggs comprised between 90% (Cook's Beach, 1990) and 99% (Moore's Beach, 1991) of the total stages. As the season progressed, there was a relative increase in dead eggs (either desiccated or decayed), while live eggs developed into embryos or trilobite larvae.

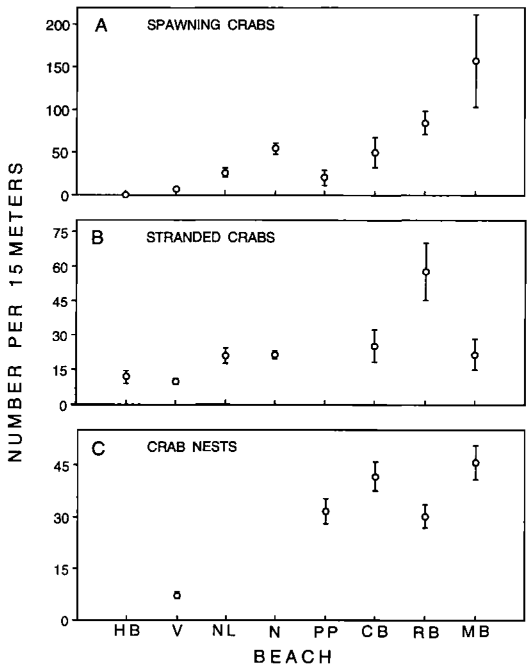

Fig. 3. Mean number (±SE) of horseshoe crabs per 15 m segment of beach in Delaware Bay, spring 1990 and 1991. (A) Spawning adult crabs at high tide; (B) stranded crabs; (C) crab nests. Beaches arrayed left to right in up-bay direction (see Fig. 1).

There were very few surface macroinvertebrates (>1 mm) on any beach. Small worms (oligochaetes and nematodes) and insect larvae were present in the mid- to lower beach, as were a few blue mussel (*Mytilus edulis*) juveniles in 1991. The latter are common epibionts on adult horseshoe crabs, and were probably dislodged from their hosts during burrowing or mating activity. Other macroinvertebrates included beetles, occasionally found in samples from the upper intertidal, and juvenile beach fleas (talitrid amphipods). A few mole crabs (*Emerita talpoida*) and ghost crabs (*Ocypode quadrata*) were seen at the highest salinity beaches. Macroinvertebrates seldom exceeded 200/m^2 in any plot; there were no detectable differences in macrofaunal abundance between beaches.

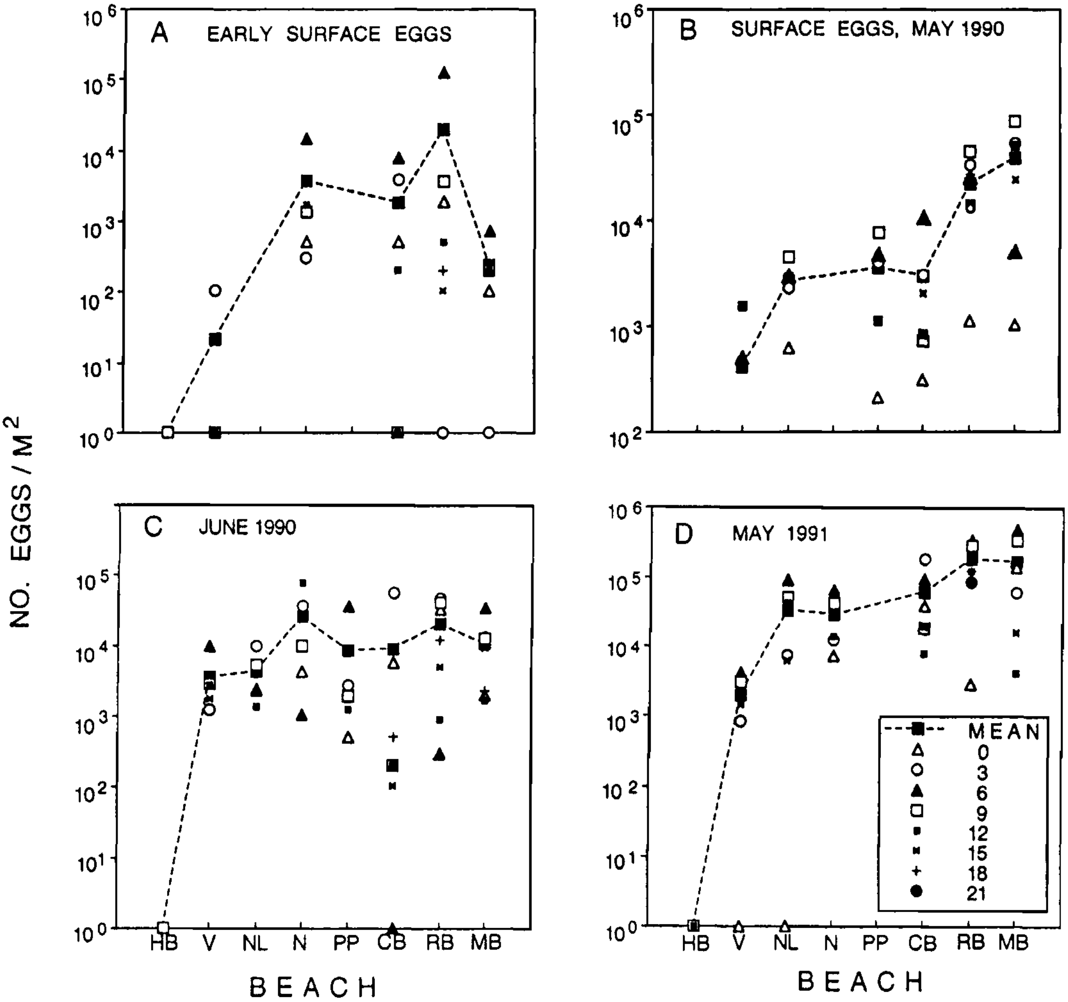

Fig. 4. Surface (0–5 cm) horseshoe crab eggs in Delaware Bay, 1990 and 1991. (A) Late April–early May 1990; (B) mid-May 1990; (C) early June 1990; (D) mid-May 1991. Mean number of eggs/m^2 in entire beach transect shown by dashed line. Data at stations along transect indicated with: (0) spring high-tide line; (3) 3 m down-beach, etc. Note log scale. Beaches arrayed left to right in up-bay direction (see Fig. 1).

DISCUSSION

Shorebird abundance is spatially variable within the Delaware Bay estuary. The importance of two disturbed habitats—Reed's Beach and Moore's Beach—as stopover sites for migrating shorebirds is evidenced by our censuses and previous aerial surveys (Wander and Dunne 1981, Clark 1991). Substantial populations of shorebirds occur further up-bay than Moore's Beach (Clark et al. 1993), even though horseshoe crab spawning areas occur mainly along the extensive sandy beaches of the lower bay, particularly between Villas and Reed's Beach (Shuster and Botton 1985, Botton et al. 1988). Further up-bay, the shoreline is dominated by salt marsh and eroding peat banks, and horseshoe crab spawning is limited to patches of sandy substrate (Botton et al. 1988). A site such as Moore's Beach may attract large numbers of horseshoe crabs and shorebirds by virtue of the fact that it is the only sandy beach for many kilometers in either direction.

Previous authors have found that the spatial

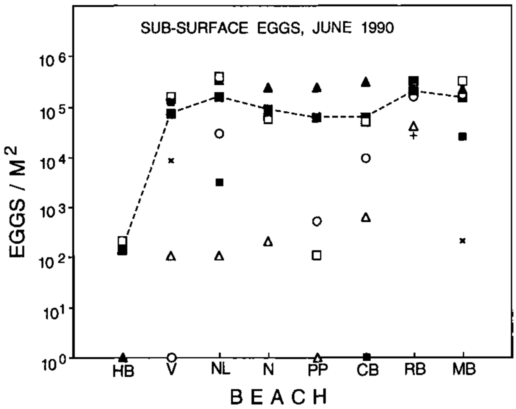

Fig. 5. Subsurface (15–20 cm) horseshoe crab eggs in Delaware Bay in early June, 1990. Mean number of eggs/m² along entire beach transect shown by dashed line. Data at stations along transect indicated with: (0) spring high-tide line; (3) 3 m down-beach, etc. Note log scale. Beaches arrayed left to right in up-bay direction (see Fig. 1).

distribution of foraging shorebirds may be related to sediment characteristics (Hicklin and Smith 1984, Grant 1984, Kelsey and Hassall 1989). Fresh horseshoe crab eggs are approximately 1.6 to 1.9 mm in diameter (Brown and Clapper 1981, Shuster 1982, Sekiguchi 1988). Following Quammen (1982), who found that shorebird foraging success was reduced by the presence of sand grains of comparable size to the prey, one might predict that shorebirds in Delaware Bay would find it easier to pick out eggs from finer sediments. However, birds were most abundant up-bay, at Reed's Beach and Moore's Beach, which have the coarsest sediments (Fig. 2). Fresh green horseshoe crab eggs strongly contrast with the pale sand. Much of the shorebird foraging occurs on eggs in the swash zone, or on distinct windrows of eggs directly on the sediment surface. Under these conditions, sediment texture is probably far less important than when shorebirds probe beaches or mudflats for worms or other infaunal invertebrates. Therefore, we believe it is unlikely that shorebird site preferences within Delaware Bay are determined by sediment grain size or heterogeneity.

Castro and Myers (1993) calculated the total energy requirements of shorebirds, and projected that 539 metric tons of horseshoe crab eggs would be needed to sustain the spring migration through Delaware Bay, assuming that shorebirds ate only horseshoe crab eggs. Given some 160 km of shoreline along Delaware Bay (Clark et al. 1993), this is equivalent to an average of 3.37 kg/m of shoreline. If the average beach is 20.8 m wide (Table 1), then there would need to be an average of 0.16 kg of eggs/m². Assuming an average wet mass of 3.71 mg/egg (Castro et al. 1989), these data suggest that an average of 44,000 eggs/m² are needed to sustain the entire shorebird population. Densities of this order of magnitude were found at most of our study sites during the peak of the migration, with the exception of Higbee's Beach. However, egg densities are probably lower along shorelines with salt-marshes or eroding peat banks, which are known to have minimal horseshoe crab spawning activity (Botton et al. 1988).

It is not possible to predict shorebird abundance within Delaware Bay based solely on the abundance of horseshoe crab eggs. Although Higbee's Beach consistently had the fewest eggs and the fewest shorebirds, elsewhere in the bay there was a large within-site variance component in shorebird abundance. For example, Villas, which had comparatively few eggs, occasionally had large flocks of Sanderlings and Ruddy Turnstones. Reed's Beach, despite the presence of many eggs, had no shorebirds at all during one survey in 1991, which may have been related to the large numbers of gulls on the beach that day.

The wide distribution of foraging shorebirds within Delaware Bay might occur because the number of horseshoe crab eggs exceeds a threshold value, even in the lower bay. This hypothesis follows Wilson (1990), who found no significant relationship between the abundance of Semipalmated Sandpipers and their preferred prey, the amphipod *Corophium volutator*, within the Bay of Fundy. He suggested that once prey density exceeded a threshold, birds found an area to be adequate.

To evaluate this possibility, we estimated the number of shorebirds that could be sustained along a beach by dividing the number of surface horseshoe crab eggs (summed across the intertidal transect) by the daily ration per shorebird. We assumed that each shorebird consumes 8,300 eggs per day, based on a study on Sanderlings by Castro et al. (1989). We neglected the impact of prey depletion by shorebirds, because horseshoe crabs continue to lay eggs throughout the duration of the shorebird migration (Shuster and Botton 1985, Botton and Loveland 1989).

TABLE 4. Estimated number of shorebirds supportable per m of shoreline in 1990, assuming consumption of 8,300 horseshoe crab eggs·bird^{-1}·day^{-1} (based on Castro et al. 1989). For comparison, estimated number of shorebirds per meter, derived from aerial surveys, is given. All beaches sampled at 3-m stations from the spring high-water mark to low-water mark; unsampled regions on transect were assumed to have egg abundances comparable to station above it on tidal gradient.

	Surface horseshoe crab eggs per m shoreline		Estimated no. birds supportable		Actual birds/m based on Clark (1991)	
Beach	24–25 May	1–7 June	24–25 May	1–7 June	1990	5-year average
Higbee's Beach	—	0	—	0.0	—	—
Villas	3,125	62,083	0.4	7.5	6.6	3.4
Norbury's Landing	34,167	61,354	4.1	7.4	0.3	1.0
Pierce's Point	51,771	126,250	6.2	15.2	0.0	0.9
Cook's Beach	49,583	194,271	6.0	23.4	0.0	1.1
Reed's Beach	499,375	406,165	60.2	48.9	24.8	7.6
Moore's Beach	721,354	230,104	86.9	27.7	2.7	4.1

All study beaches, except Higbee's Beach, were capable of supporting at least four birds per meter of shoreline in late May-early June (Table 4). Data from aerial surveys of shorebirds on these same beaches (Clark 1991) supports the hypothesis that the supply of eggs was sufficient to accommodate the number of birds that used these beaches.

The local movements of shorebirds within Delaware Bay may be influenced by competition between shorebirds, or between shorebirds and gulls. In previous studies, shorebirds have aggressively defended patches of horseshoe crab eggs against conspecifics (Recher and Recher 1969, Mallory and Schneider 1979, Sullivan 1986). Aggressive interactions among shorebirds are usually more frequent at higher densities (Recher and Recher 1969, Burger et al. 1979, Puttick 1984). Thus, it could be advantageous for shorebirds to bypass or even disperse from beaches such as Moore's Beach or Reed's Beach, if their net energy gain would be greater on a less crowded beach with fewer eggs, such as Villas or Cook's Beach.

Relative to horseshoe crab eggs, few alternative food items (>1 mm) are available to shorebirds along Delaware Bay beaches, particularly in comparison to nearby Atlantic Ocean beaches (McDermott 1983). The density of horseshoe crab eggs on the bay beaches (10^4–$10^5/\text{m}^2$) is overwhelming compared to the various worms and other macroinvertebrates (0–$10^2/\text{m}^2$). Moreover, during the peak of the shorebird migration, there are relatively few dead crab eggs to potentially interfere with the capture of live eggs. The sandy intertidal flats between Villas and Pierce's Point did not attract large numbers of shorebirds. These flats are dominated by a small (<4 mm) bivalve, *Gemma gemma;* a previous study (Botton 1984) found that predation by shorebirds and gulls did not significantly diminish infaunal prey abundance.

Reed's Beach and Moore's Beach are situated near mature salt marshes, and shorebirds may favor these beaches because they are close to roosting and/or supplementary feeding areas. We observed a large number of birds moving between the sandy beach and salt-marsh habitats, especially at Moore's Beach. Movements of shorebirds from bay beaches to bay marshes, as well as to Atlantic coast marshes and beaches, has been previously reported (Clark et al. 1993). The extent to which shorebirds feed in these marshes has not yet been determined. It is not clear what motivates shorebirds to disperse from Delaware Bay beaches at night, since crab eggs are equally available throughout the night. Nocturnal feeding by shorebird species in other coastal habitats is common, regardless of whether they use visual or tactile cues to locate prey (Evans 1981, Robert et al. 1989, Burger and Gochfeld 1991, McNeil et al. 1992).

Shorebirds in the Delaware estuary must consume horseshoe crab eggs rapidly to meet their energetic needs (Castro et al. 1989, Castro and Myers 1993), but their predatory activities probably have little impact on the horseshoe crab population. Wilson (1991) hypothesized that intense episodic predation by migratory shorebirds could drastically reduce prey densities, perhaps, over time, leading to evolutionary responses by the prey (e.g. in the timing of reproduction). He found evidence for this in the upper Bay of Fundy, but not for Gray's Harbor (Washington), Plymouth Bay (Massachusetts), or Delaware Bay based on data for invertebrates on the intertidal flats (Botton 1984). The placement of most horseshoe crab egg clusters at sediment depths greater than 10 cm affords a degree of protection from the predominantly short-billed shorebird species. Moreover, horseshoe crabs continue to spawn in large numbers for more than a month after the departure of most of the shorebirds. We have routinely found more than 100,000 live *Limulus* trilobite larvae/m^2 in the midbeach sediments during July and August (Botton et al. 1992). The surface eggs consumed by birds might otherwise die from other causes, such as heat stress or desiccation. For these reasons, shorebird predation has probably not been a major factor limiting the reproductive success of horseshoe crabs in Delaware Bay.

Shoreline discontinuities are important in trapping horseshoe crab eggs and in attracting shorebirds. Natural features, such as the sand spits formed at the mouths of salt marsh creeks (e.g. Cook's Beach, Moore's Beach) and manmade obstructions such as the long jetty at Reed's Beach, act as concentrating mechanisms for horseshoe crab eggs. In surveys of the tidal flats between Norbury's Landing and North Beach, we noted concentrations of shorebirds only in the vicinity of marsh drainage systems, which probably function as traps for drifting crab eggs.

Although female horseshoe crabs deposit most of their eggs 10 to 20 cm beneath the surface of the sand (Botton et al. 1992), wave action and burrowing by other horseshoe crabs reworks beach sediments, forcing many eggs to the surface. Once suspended in the water column, eggs act as passive, negatively buoyant particles. Nearshore circulation patterns in lower Delaware Bay are strongly influenced by wind direction (Pape and Garvine 1982, Galperin and Mellor 1990), which is predominantly from the southwest during the late spring. Southwest winds, coupled with the strong flood tide, set up longshore currents moving particles along the Cape May peninsula in the eastern portion of the bay. Eggs will tend to accumulate in the vicinity of any obstruction to the longshore drift. It is possible that birds have learned to associate shoreline discontinuities with high egg abundance and, if so, these geographic features could serve as orientation landmarks for shorebirds within the Delaware Bay staging area.

On a hemispheric scale, there seems little doubt that the spring shorebird migration through Delaware Bay is related to the enormous seasonal abundance of horseshoe crab eggs (Myers 1986, Myers et al. 1987, Clark et al. 1993). Extremely high densities of preferred food items, such as horseshoe crab eggs in Delaware Bay, *Corophium volutator* in the Bay of Fundy (Wilson 1990), *Littorina* spp. in Iceland (Alerstam et al. 1992), or Pacific herring eggs (*Clupea harengus pallasi*) in Prince William Sound, Alaska (Norton et al. 1990), may prove to be general attributes of many shorebird staging areas. Within a staging area, finer-scale patterns of shorebird abundance during the migration season may result from patchiness in physical characteristics, as well as from gradients in prey availability (e.g. Colwell and Landrum 1993).

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