detecting buried bivalve prey. On the breeding grounds, the diet of Red Knots consists mostly of terrestrial invertebrates, though they will also eat plant material especially early in the season. During the rest of the year, at stopover sites and on their wintering grounds in Tierra del Fuego, Chile, Maranhão, Brazil, and the southeastern U.S., they feed almost exclusively in intertidal habitats, particularly on mudflats and beaches and, on the coast of Argentina, on restingas (broad, wave-cut platforms extending across the intertidal zone) where they specialize on bivalves which are swallowed whole. Common bivalves consumed include *Mytilus*, *Mulinea*, *Donax*, *Macoma*, *Tellina*, *Myadora*, *Nucula*, and possibly *Gemma*. They will also take gastropods, such as *Hydrobia*, *Littorina*, and *Heleobia*, amphipods, and occasionally polychaetes.

When stopping over in Delaware Bay, they feed almost exclusively on the eggs of horseshoe crabs. Feeding on horseshoe crab eggs on Delaware Bay, however, is a major departure from the prey usually taken.

HABITAT

Red Knots use very different habitats for breeding and wintering and migration. Breeding habitats are located inland, but close to arctic coasts. Wintering and migration habitats are similar—generally coastal with large areas of intertidal sediments.

PREFERRED MICROHABITATS

Selection of preferred microhabitats on breeding grounds may vary depending on the amount of snow cover individuals encounter when they arrive. Nests are usually located on sparsely vegetated, dry, sunny, elevated, windswept ridges or slopes. Nest locations are also usually located near wetlands and lake edges, which then become the preferred microhabitat after hatching.

Preferred wintering and migration microhabitats are muddy or sandy coastal areas, more specifically, the mouths of bays and estuaries, unimproved tidal inlets and tidal flats (Table 6; Fig. 12).

BREEDING HABITAT

As described above, Red Knot breeding habitat is principally at elevations of <150 m and includes small wetlands where the chicks can feed. At the landscape scale, a model of potential breeding habitat was developed by New Jersey Department of Environmental Protection Division of Fish and Wildlife Endangered and Nongame Species Program (NJENSP) and Rutgers University using remotely-sensed land-cover characteristics. The model showed that Red Knot breeding habitat is generally found at elevations <150 m above sea level, <50 km from the coast and where vegetation cover is <5%. Red Knots and their chicks and fledglings forage in shallow sedge meadows and on sparsely vegetated lake edges proximate to nest sites.

MIGRATION AND STOPOVER HABITAT—CANADA

The critical staging areas for Red Knots during spring and fall migration in Canada are along sandy beaches and tidal mudflats in James Bay and tidal mudflats and salt marshes in the northern Bay of Fundy (R. I. G. Morrison, unpubl. data; M. Peck, unpubl. data; K. Ross, pers. comm.). In the Bay of Fundy, Red Knot migrants are rare in spring, but relatively common in the fall (Hicklin 1987).

MIGRATION AND STOPOVER HABITAT—NORTHEASTERN U.S.

It is not believed that large numbers of Red Knots occur during migration in Maine (L. Tudor, pers. comm.), New Hampshire (C. Raithel, pers. comm.), Connecticut, and Rhode Island (J. Dickson, pers. comm.; D. Varza, pers. comm.). In the northeastern U.S. (New Jersey–Maine), the principal Red Knot staging areas are along the New Jersey, New York, and Massachusetts coastlines. In Massachusetts, Red Knots use sandy beaches and tidal mudflats during fall migration near Scituate, Duxbury, and Plymouth Beach, and along the shoreline in Cape Cod south to Monomoy (B. A. Harrington, unpubl. data). New York's Jamaica Bay Wildlife Refuge has a concentration of migratory Red Knots during spring and fall along sandy beaches and most commonly within the impoundment (K. Tripp, pers. comm.). Along the Atlantic coast of New Jersey, Red Knots utilize sandy beaches during spring and fall migration for foraging (K. Clark, unpubl. data; D. Hernández, unpubl. data; L. J. Niles, unpubl. data; H. P. Sitters, unpubl. data).

MIGRATION AND STOPOVER HABITAT—DELAWARE BAY, U.S.

Delaware Bay is the most important staging area during northbound migration and is normally used by the whole or a large proportion of the *C. c. rufa* population which spends 2–3 wk staging there in the latter half of May. Beaches typical of the Delaware Bay shore are a mixture of sand and smooth gravel, and shorebirds

TABLE 6. HABITAT TYPES UTILIZED BY FORAGING RED KNOTS ON BREEDING GROUNDS (B), SPRING MIGRATION (S), FALL MIGRATION (F), AND WINTERING GROUNDS (W).

#[a]	Location	Sandy beach	Tidal mud-flat	Peat bank	Restinga/ inter-tidal rocky flat	Salt marsh	Man-grove	Brackish lagoon/ impound-ment	Rocky barrens	Source
1	King William Island, Canada								B	R. I. G. Morrison (unpubl. data) M. Peck (unpubl. data) R. K. Ross (pers. comm.)
2	Southampton Island, Canada								B	R. I. G. Morrison (unpubl. data) M. Peck (unpubl. data); R. K. Ross (pers. comm.)
3	James Bay, Canada	S, F								R. I. G. Morrison (unpubl. data) R. K. Ross (pers. comm.)
4	Mingan Archipelago, Canada				F					Y. Aubry (pers. comm.)
5	Northern Bay of Fundy, Canada		S, F			S, F				Hicklin (1987), R.I.G. Morrison and M. Peck (unpubl. data)
6	Massachusetts, U.S.	F	F							B. A. Harrington (unpubl. data)
7	New York, U.S.	S, F						S, F		B. A. Harrington (unpubl. data) K. Tripp (pers. comm.)
8	Atlantic coast New Jersey, U.S.	S, F								K. Clark (unpubl. data) D. Hernández (unpubl. data) L. J. Niles, (unpubl. data) H. P. Sitters (unpubl. data)
9	Delaware Bay, U.S.	S, F				S				K. Bennett (unpubl. data), K. Clark (unpubl. data) K. Kalasz (unpubl. data) H. P. Sitters (unpubl. data)
10	Maryland, U.S.	S, F	S, F							G. Therres (pers. comm.)
11	Virginia, U.S.	S, F		S, F						S. Rice (pers. comm.) B. Truitt (pers. comm.) B. Watts (pers. comm.)
12	North Carolina, U.S.	S, F	S, F							S. Cameron (pers. comm.)
13	South Carolina, U.S.	S, F W?								F. Sanders (pers. comm.)
14	Georgia, U.S.	S, F W?		S, F W?						B. Winn (pers. comm.)
15	North Florida, U.S.	S, F, W	S, F, W			S, F, W		S, F, W		N. Douglass (pers. comm.) P. Leary (pers. comm.) Sprandel et al. (1997)
16	South Florida, U.S.	S, F W	S, F W			S, F W	S, F W	S, F W		N. Douglass (pers. comm.) P. Leary (pers. comm.) Sprandel et al. (1997)

TABLE 6. CONTINUED.

#[a]	Location	Sandy beach	Tidal mud-flat	Peat bank	Restinga/ inter-tidal rocky flat	Salt marsh	Man-grove	Brackish lagoon/ impound-ment	Rocky barrens	Source
17	Texas, U.S.	S, F W	S, F W			S, F W				J. Arvin (pers. comm.) W. Burkett (pers. comm.) B. Ortego (pers. comm.)
18	Panama Bay, Panama	S	S, W				S			Buehler (2002)
19	Maranhão, Brazil	S, F W	S, F W				S, F W			I. Serrano (unpubl. data)
20	Lagoa do Peixe, Brazil	S, F W						S, F W		I. Serrano (unpubl. data)
21	Punta Rasa, Argentina	S, F								P. M. González (unpubl. data)
22	San Antonio Oeste, Argentina	S, F	S, F		S, F					P. M. González (unpubl. data)
23	Chiloe Island, Chile	S								L. A. Espinosa (pers. comm.)
24	Río Gallegos, Argentina	S, F	S, F		S, F					P. M. González (unpubl. data)
25	Bahía Lomas, Chile		W							C. Espoz (unpubl. data) R. Matus (unpubl. data)
26	Bahía San Sebastián, Argentina		W							P. M. González (unpubl. data)
27	Río Grande, Argentina	W	W		W					P. M. González (unpubl. data)

[a] The numbers correspond to those on Fig. 12.

are distributed on Delaware Bay relative to availability of horseshoe crab eggs. One of the most critical issues for the conservation of the Red Knot population is its dependence on huge quantities of eggs produced by the mass spawning of the largest known population of Atlantic horseshoe crabs (Shuster and Botton 1985). Crab eggs are especially important to Red Knots because of time constraints in completing their 15,000 km trans-hemispheric migration from Tierra del Fuego to the Canadian Arctic (Morrison and Harrington 1992, Harrington 2001). To stay on schedule and ensure breeding opportunities, Red Knots must increase body mass in Delaware Bay by 50–100% in 2–3 wk (Baker et al. 2004), one of the most rapid fattening events in birds. Some Red Knots may arrive at or below normal lean body mass of 110 g and depart at 180–220 g. Food quality, quantity and availability as well as the time constraints associated with nutrient acquisition (foraging, food processing, and assimilation) are critically linked in achieving this unique anabolic event.

Habitats important for Red Knots in Delaware Bay

Most horseshoe crabs spawn on sandy beaches around high tide, burying their eggs close to the high-tide line. Spawning activity usually peaks during the latter half of May to early June, which coincides with the main Red Knot stopover (Botton et al. 1994). The most important habitats in Delaware Bay for spawning crabs are the sandy beaches along the New Jersey shore mainly from Town Bank to Gandys Beach and along the Delaware shore mainly from Slaughter Beach to Port Mahon (Fig. 15). In New Jersey, Red Knots also make extensive use of the Atlantic coast, particularly the sand-spits and sandbanks around Stone Harbor Point and Hereford Inlet for roosting and occasionally for foraging on surf clams. They also forage on spat of the blue mussel in the protected intertidal marshes behind the Atlantic coast. In Delaware, Red Knots sometimes roost day and night in an area of relatively unvegetated marsh about 1.7 km inland from the bayshore and 500 m north of the Mispillion River. So far as we can determine, this is the only place in the world where Red Knots have been recorded roosting inland at night. In 2004 and 2005, this site became flooded and many Red Knots regularly commuted from the Delaware shore, where they fed by day, to roost at Hereford Inlet on the Atlantic coast of New Jersey at night, a round trip of 94 km (H. P. Sitters, unpubl. data).

Extensive coastal marshes and mudflats that are typically fronted by a sandy barrier beach fringe Delaware Bay. These sandy beaches mainly overlay marsh sediments (generally a fibrous peat formed by the root mat of the marsh plants) and vary in thickness from a thin veneer to about 2 m (Phillips 1986a). The back beaches, above normal high tide, form a low dune and are often colonized by common reed (*Phragmites australis*; Phillips 1987). The intertidal portions of the sandy beaches are of special significance as these are the focus of horseshoe crab spawning activity and of Red Knots' foraging. Horseshoe crabs prefer beaches dominated by coarse sandy sediments and avoid beaches that have a high amount of peaty sediments or are adjacent to exposed peat banks (Botton et al. 1988). These factors were used by Botton et al. (1988) to develop a classification scheme that ranked beaches as either preferred or avoided habitat for horseshoe crab spawning. Horseshoe crabs deposit most of their eggs 10–20 cm deep in sandy beach sediments (Botton et al. 1992); eggs are then redistributed to shallower depths or the surface and become available to foraging shorebirds by subsequent spawning and wave action. Although it is widely thought that the major process that brings eggs to the surface is the action of female crabs digging up earlier nests as they spawn, the way this works is poorly understood. Possibly there is some critical density of spawning crabs below which few eggs come to the surface and above which many do. If so, it would be valuable to determine what that density is as an aid to establishing the size of the crab population that is needed to support the shorebird stopover.

Starting in 1999, systematic surveys were conducted to count intertidal (i.e., spawning) horseshoe crabs throughout Delaware Bay (Smith et al. 2002a, 2002b). Various short-term studies of egg density preceded systematic surveys that were started on the New Jersey shore in 1996 and on the Delaware shore in 1997 (M. L. Botton, pers. comm.; R. E. Loveland, pers. comm.; NJDFW, unpubl. data; Weber 2003). These used different methods making it difficult to determine how egg densities varied between the two states and it was not until 2005 that the two projects were combined into a single bay-wide survey using the same methodology. All these surveys show that egg densities vary by several orders of magnitude, sometimes exceeding 10^6/m of shoreline (Smith et al., 2002b). Smith et al. (2002b) found that beach morphology and wave energy interact with the density of spawning females to explain much of the variation in the density and distribution of eggs and larvae between the study beaches. Horseshoe crabs showed a preference for spawning on low-energy (i.e., wave-protected) sandy beaches. While the surveys

FIGURE 15. Map of the Delaware Bay (New Jersey and Delaware) showing some of the most important refueling sites for Red Knots.

only sampled bay-front beaches, beaches along tidal creeks were also noted as being potential hotspots for crab spawning and shorebird foraging. At a broader, bay-wide scale, the use of intertidal beaches as horseshoe crab spawning habitat is limited in the north by low salinity (Sea Breeze in New Jersey and Woodland Beach in Delaware) and by ocean-generated energy in the south (North Cape May, New Jersey and Broadkill, Delaware).

Not surprisingly, migratory shorebird abundance is spatially variable within the Delaware Bay estuary as a consequence of these larger bay-wide patterns of horseshoe crab abundance and spawning activity. Migratory shorebirds in Delaware Bay showed a strong preference for beaches with higher numbers of crab eggs although shorebird abundance also depends on other factors such as competition, disturbance, and risk of predation (Botton et al. (1994). Shorebirds were recorded to aggregate near shoreline discontinuities, such as salt marsh creek deltas and jetties, which acted as concentration mechanisms for passively drifting eggs. Human disturbance can greatly reduce the value of foraging habitat for Red Knots. The various studies outlined above show that a complex array of factors determine the value of Delaware Bay beaches as horseshoe crab spawning and shorebird foraging habitat.

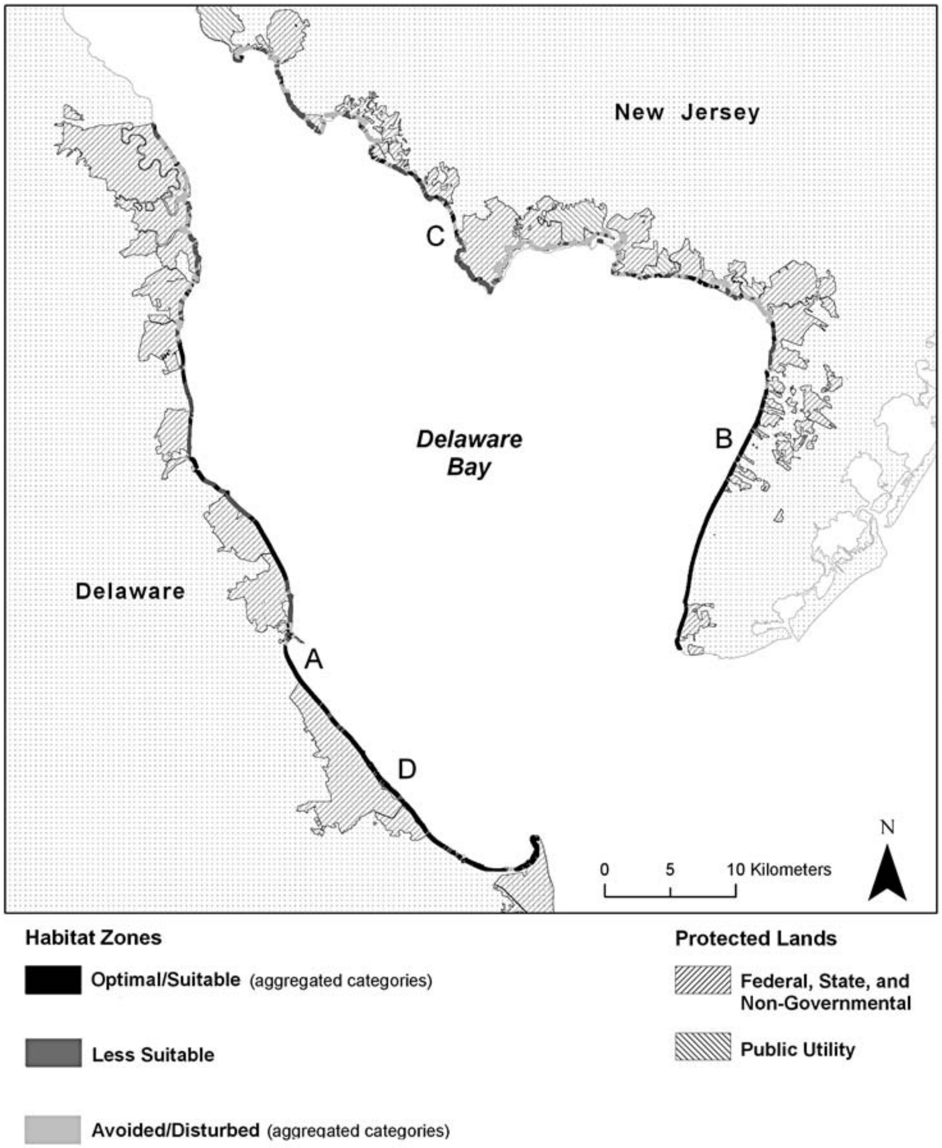

FIGURE 16. Map of horseshoe crab spawning habitat suitability with location of protected conservation lands. Several key locations have been annotated: (A) Slaughter Beach, (B) Cape May NWR, (C) Fortescue, and, (D) Broadkill Beach. Protected Lands GIS Data Sources: NJDEP, NJ Green Acres, TNC-NJ Chapter, DE Parks and Recreation.

A large portion of Delaware Bay shore has some form of conservation protection (Fig. 16). The New Jersey shore includes state-owned lands at Dennis Creek, Heislerville and Egg Island Wildlife Management Areas; USFWS-owned land (Cape May National Wildlife Refuge [NWR]); The Nature Conservancy (TNC) land; and the Public Service Electric and Gas Company land managed by TNC. The Delaware shore includes large areas in USFWS ownership at Bombay Hook and Prime Hook NWRs, state-owned land (Little Creek, Ted Harvey, and Milford Neck Wildlife Areas and Cape Henlopen State Park), and a significant amount of conservation land owned by TNC and Delaware Wildlands. However, in both states, large areas of shoreline are in private ownership and subject to habitat disturbance and loss. In New Jersey, while the intertidal beach is considered publicly owned, key beaches lie immediately adjacent to residential development including Villas, Reed's Beach, and Fortescue. In Delaware, private property ownership generally extends to mean low water. Similar to New Jersey, residential development in Delaware is adjacent to key beaches including Pickering, Kitts Hummock, Bowers, and Slaughter beaches. Port Mahon and Mispillion Inlet are different in that commercial use and bulkheading threaten critical Red Knot habitat. Regardless of residential proximity where the bayfront is accessible by car, human disturbance is a threat that can reduce the value of habitat for Red Knots.

Red Knot feeding ecology in Delaware Bay

The strong reliance of Red Knots on horseshoe crab eggs has been confirmed by stomach content analyses (Tsipoura and Burger 1999) and stable-isotope, diet-tracking studies, which show that horseshoe crab eggs are the main constituent of the Red Knots' diet during their stopover in Delaware Bay (Haramis et al. 2007). Other studies (Castro et al. 1989, Castro and Myers 1993) have estimated the daily requirement of shorebirds for horseshoe crab eggs based on the birds' energetic requirements. These show that Sanderlings would need 8,300 and Red Knots 30,000 eggs per day (Castro et al. 1989, Castro and Myers 1993, Hernández 2005). A more recent study using pen trials estimated that Red Knots need 13,000 eggs per day to maintain body weight and 24,000 eggs per day when fattening optimally (Haramis et al. 2007).

A key question, however, is not just how many eggs are required or consumed, but how important are horseshoe crab eggs to migratory fattening and to what extent alternative foods in the Delaware Bay environment are utilized. Haramis et al. (2007) conducted research in Delaware Bay from 2000–2004 that considered the trophic link between Red Knots and crab eggs using stable-isotope diet tracking and pen-feeding trials. He measured stable isotopes (SI, δ^{15}N signal) in the plasma of captive Red Knots that were fed exclusively on horseshoe crab eggs and compared these signals to free-ranging Red Knots. The close consistency in SI pattern of response and convergence of diet asymptotes between free-ranging and captive birds confirm the importance of crab eggs in the diet of Red Knots during stopover in Delaware Bay.

Throughout their worldwide range, Red Knots generally feed wholly or mainly on bivalves which are swallowed whole (Alerstam et al. 1992, Dekinga and Piersma 1993, Piersma et al. 1993, González et al. 1996). Therefore, the most likely alternative prey in the Delaware Bay system would be blue mussels, coquina clams, or ribbed mussels (*Modiolus demissus*). As filter feeders, bivalves are low in the food chain and have SI values that can be discriminated easily from crab eggs. This enabled Haramis et al. (2007) to show that while some Red Knots may consume bivalves, they do not form a significant part of the diet of most birds in Delaware Bay in spring. However, in most years a significant minority of birds (<30%) has been observed foraging on these alternative food resources. These tend to occur on the Atlantic coast of New Jersey and the majority of these birds are short-distance migrants (possibly *C. c. roselaari*) from wintering areas in the southeastern states of the U.S. (P. W. Atkinson et al., unpubl. data). It is hypothesized that these short-distance migrants are either able to arrive in Delaware Bay earlier than birds from South America and regrow their digestive apparatus to deal with the hard-shelled prey, or do not undergo the major physiological changes of gut size reduction that the long-distance migrants have to undertake to migrate in such long hops (P. W. Atkinson et al., unpubl. data). However, for long-distance migrants, particularly the birds from Tierra del Fuego, crab eggs are crucial to successful fattening and these birds are therefore likely to be more vulnerable to a decline in the availability of eggs than those that have not come so far.

Hernández (2005) analyzed prey-attack patterns (peck and probe rates), locomotion patterns (step rates), and the interactions between these patterns as a measure of foraging efficiency relative to egg density and patchiness. However, because he was not able to tell whether or not a peck or probe was successful, he could not determine the relationship between intake rate (eggs per second) and egg density, which is essential for measuring the critical egg densities that affect overall foraging success. Atkinson et al. (2003) describe the use of feeding pans containing known numbers of eggs, either on the surface or buried in the top 5 cm of sand, and placed these in foraging flocks of Red Knots in the field and recorded feeding rates and depletion. Knowing the relationship between egg density and egg-intake rate, and the daily egg requirements from the Haramis et al. (2007) study, it is possible to estimate the number of hours of feeding required for a given density of eggs.

From these experiments, Atkinson et al. (2003) determined that the number of eggs consumed per peck (i.e., success rate of pecks) increased asymptotically with egg density (Gillings et al. 2007). Whether present on the surface or buried in the sand, eggs consumed per second increase asymptotically with egg density (Fig. 17). Higher intake rates are achieved from pecking eggs off the sand surface and, even at very low surface egg densities, it is significantly more profitable to peck than probe (Fig. 18).

Daylight during staging is around 15 hr and crab eggs are laid near the high tide mark so birds theoretically could feed for most of daylight hours. Then, the required daily egg intake could be achieved by feeding on surface eggs at a density of only 360 eggs m^{-2}, or buried eggs at a density of 19,200 eggs m^{-2} (Table 7). However, the availability of eggs on the sand

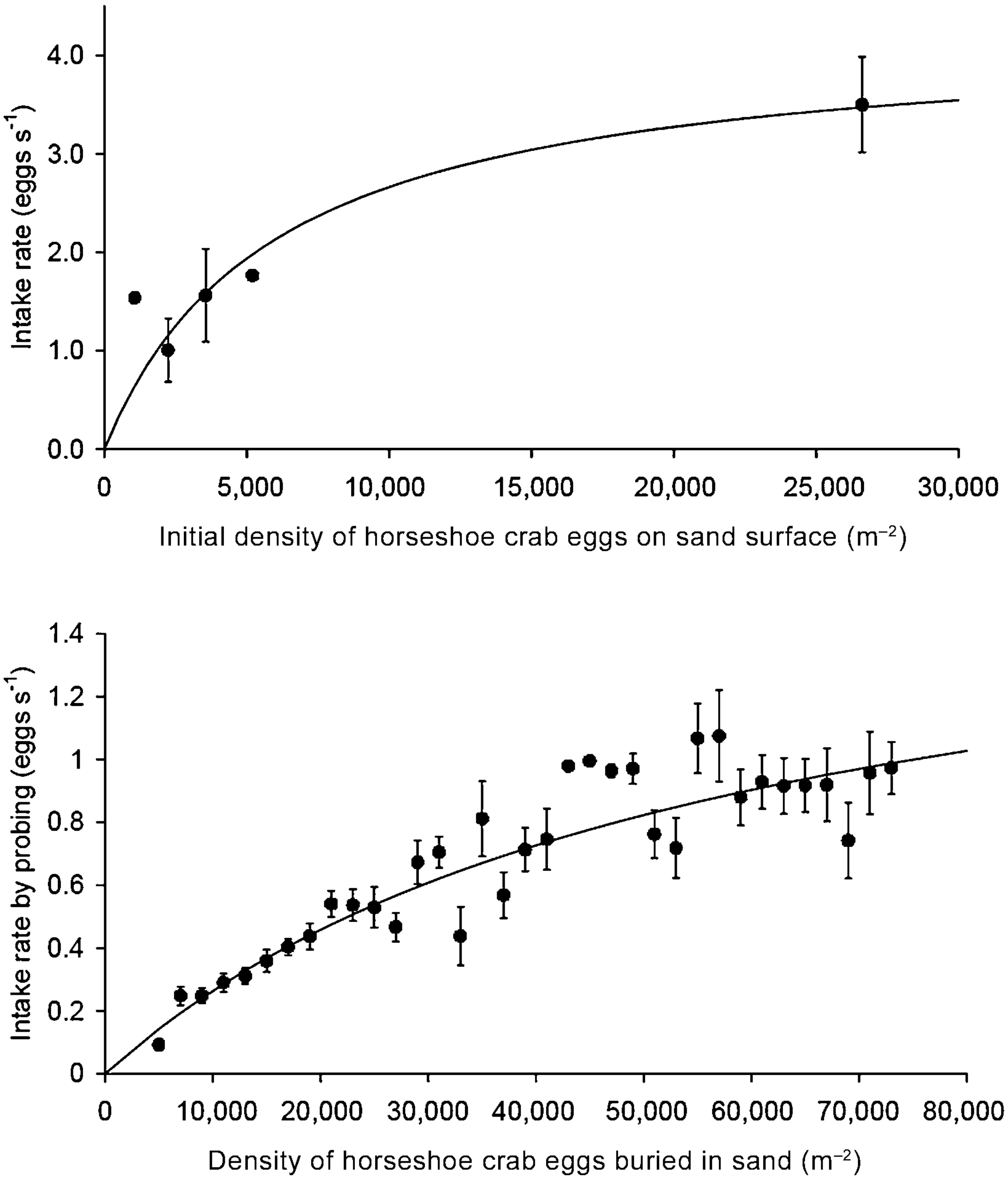

FIGURE 17. Functional responses relating the intake rate (eggs s^{-1}) achieved by Red Knots to the density of (upper) eggs present on sand surface and (lower) eggs buried and mixed in the top 5 cm of sand.

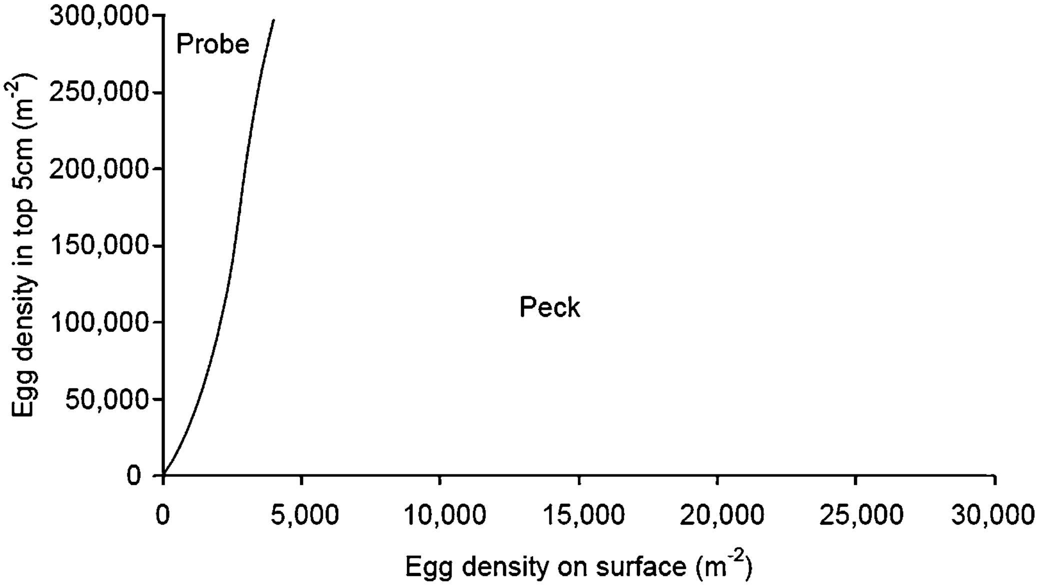

FIGURE 18. Density of eggs on the sand surface or buried and mixed in the sediment (down to 5 cm) will determine whether it is most profitable to peck or probe.

surface, and buried in the top 5 cm of sand are likely to vary through the tidal cycle with density of spawning crabs, wave action, and depletion by shorebirds and gulls. Furthermore, eggs remaining on the sand surface rapidly dry out (within an hour of deposition on hot windy days) and become hardened. During 10 yr of observations Red Knot have never been seen consuming these dessicated eggs and the Semipalmated Sandpiper (*Calidris pusilla*) is the only species having been seen consuming dessicated eggs and that only on one day (S. Gillings, pers. comm.; N. Clark, unpubl. data). These processes mean that optimal feeding is constrained to bouts of consumption of eggs freshly deposited on the sand surface by the falling tide and/or consumption of buried eggs where they are present at sufficiently high density.

Based on field studies in Delaware Bay between 2003 and 2004, Hernández (2005) predicted that a minimum density of at least 300,000 eggs m^{-2} was needed for Red Knots to completely maximize foraging efficiency on buried eggs. This fits well with predictions in Table 7. So far as we know, Red Knots do not feed on horseshoe crab eggs at night in Delaware Bay and cannot feed continuously

TABLE 7. THE AMOUNT OF TIME (HR) NEEDED TO ACHIEVE THE DAILY HORSESHOE CRAB EGG CONSUMPTION OF 24,000 FRESH EGGS (HARAMIS ET AL. 2007) IN RELATION TO EGG AVAILABILITY (EGGS M^{-2}) DEPENDENT ON WHETHER EGGS ARE: (A) FREELY AVAILABLE ON THE SAND SURFACE OR (B) BURIED WITHIN THE TOP 5 CM OF SAND.

(A) Surface egg density	Required feeding time	(B) Buried egg density	Required feeding time
360	15.0	19,200	15.0
500	11.3	50,000	8.1
1,000	6.7	100,000	6.0
2,000	4.3	200,000	4.9
3,000	3.6	300,000	4.5
4,000	3.2		
5,000	2.9		
10,000	2.5		
20,000	2.2		
30,000	2.2		

Notes: These calculations are based on intake rates from experimentally measured functional responses (Atkinson et al. 2003, Gillings et al. 2007). For reference, the density of eggs yielding a 15-hr foraging time (day length) is shown.

throughout the day as they need to spend time on other behaviors such as vigilance and preening. Moreover feeding areas are not available when the tide covers them, neither are surface eggs if they are subject to rapid desiccation at low tide on hot days. The foraging models also suggest that Red Knot foraging efficiency is adversely affected by decreased egg density and increased egg patchiness.

Studies by Haramis et al. (2007) and Hernández (2005) describe the importance of horseshoe crab eggs to Red Knots and the lack of alternative foods being used during stopover. Data from NJENSP indicate average egg densities in New Jersey in 2004 of around 3,200 eggs m^{-2} in the top 5 cm. If these were all on the surface they would theoretically be sufficient. However, in reality many of these will have been buried and those on the surface may have desiccated on hot days. Therefore, Red Knots may not be able to meet their energetic requirements during stopover due to insufficient numbers of eggs. In conclusion, low egg densities constitute a direct threat to migratory fattening in *C. c. rufa*. Moreover it has been demonstrated that low weight birds in Delaware Bay subsequently have a lower resighting rate in the flyway, implying lower adult survival (Baker et al. 2004).

Studies of Red Knots trapped twice during a single spring stopover show that the mean rate of mass gain of birds that arrive in mid May is around 4 g/d, but that late-arriving birds can achieve gains two–three times higher. This indicates that if there is sufficient food they have some flexibility and are able to make up for lost time (though it is likely that this comes at some physiological cost). This relationship broke down in 2003 and 2005 and late-arriving birds were apparently unable to achieve higher rates of mass gain because of inadequate food supplies (Atkinson et al. 2007).

In summary, feeding studies in Delaware Bay appear to go some way toward explaining why Tierra del Fuego wintering Red Knots have shown a sharp decline, but northern wintering populations have apparently been more stable. The southern birds are more reliant on horseshoe crab eggs, the availability of which has declined. Migration has become later in Patagonia and some evidence shows later arrival into Delaware Bay (Baker et al. 2004, Bala et al. 2005; K. Clark, unpubl. data). Late arrivals do not have the ability to recover lost time if egg numbers are not sufficient. In contrast, northern-wintering birds have shown no change in migration phenology and are less reliant on crab eggs. Therefore, if factors lead Red Knots to arrive late in Delaware Bay and/or in poor condition, it does not diminish the importance of the Delaware Bay food resource. If anything, it is increased because it is of critical importance in enabling the birds to recover quickly and reach the breeding grounds on time and in good reproductive condition.

Mapping horseshoe crab spawning habitat suitability

Lathrop and Allen (2005) used visual interpretation of high-spatial-resolution color-infrared digital orthophotography to provide the first comprehensive inventory and characterization of the Delaware Bay shoreline. Several categories of information were mapped that are relevant to the bayshore's value as horseshoe crab spawning habitat: (1) shoreline type and width, (2) presence of near-shore development, and (3) shoreline stabilization structures on both the fore-shore and back-beach. Sand beach dominates the foreshore of the Delaware side of the bay, while organic beach composed of either eroding peat banks or salt marsh dominates the New Jersey side (Table 8). Overall, about 54% of Delaware Bay's shoreline represents the horseshoe crab's preferred spawning habitat of sand beach (Fig. 16). These sand beaches are generally narrow in width, averaging only 10.9 m on the Delaware side and 5.9 m on the New Jersey side of the bay. Some of the widest beaches (some nearly 100 m in width) are found along the central and southern portions of Cape May in New Jersey and the central sections of the Delaware coast.

TABLE 8. CHARACTERIZATION AND LENGTHS OF THE DELAWARE BAY SHORELINE.

Shoreline type	Delaware Kilometers	Delaware (%)	New Jersey Kilometers	New Jersey (%)
Sand	67.50	(74.3%)	61.86	(41.7%)
Armor (fore-shore)	3.66	(4.0%)	8.35	(5.6%)
Organic	19.68	(21.7%)	78.10	(52.7%)
Total shoreline	90.84	(100%)	148.30	(100%)
Armor (back) [a]	2.67	(2.9%)	5.06	(3.4%)
Development	13.35	(14.7%)	5.72	(3.8%)

[a] Back-beach armor and developed area measurement are separate from the total shoreline measurement.

Beach stabilization structures (e.g., armoring practices such as bulkheading or riprap) account for 4.0% of the Delaware shoreline and 5.6% of the New Jersey side (Table 8). An additional 2.9% and 3.4% of the Delaware and New Jersey shorelines, respectively, also had some form of armoring in the back beach (Table 8), which may come into play as beaches erode and shorelines recede, exposing these structures in the future. About 8.0% of the Delaware Bayshore is subject to near-shore development. While some beaches in New Jersey and Delaware have had development removed (e.g., Thompson's Beach, New Jersey, and Big Stone Beach, Delaware), Lathrop and Allen's ground truthing surveys observed construction of new development and redevelopment on the Delaware side of the bay.

Using the mapped shoreline geographic information system (GIS) data, Lathrop and Allen (2005) classified the Delaware Bay shoreline into five categories of horseshoe crab spawning suitability based on criteria proposed by Botton et al. (1988). These were:

1. Optimal—undisturbed sand beach.
2. Suitable—sand beach with only small areas of peat and/or backed by development.
3. Less suitable habitat—exposed peat in the lower and middle intertidal zone and sand present in the upper intertidal.
4. Avoided habitat—exposed peat or active salt marsh fringing the shoreline, no sand present.
5. Disturbed—beach fill, riprap, or bulkheading.

Based on this more refined mapping assessment, about a quarter (23.9%) of Delaware Bay's shoreline was classified as optimal spawning habitat (34.5% of Delaware and 17.4% of New Jersey bayshore; Table 9). Only an additional 6.6% of shoreline came in the next, suitable, category (11.6% Delaware, 3.4% New Jersey). Most of the optimal and suitable spawning habitat is located in the lower parts the bay; the bay becomes more fragmented farther up (Fig. 19). Lathrop and Allen's map should be regarded as only a provisional assessment of spawning habitat suitability because it does not include site-specific consideration of beach morphology or wave energy characteristics that may also be important. Thus the map probably overestimates the amount of optimal habitat. For example, the lowest section of the Delaware shoreline (15 km south from Broadkill) and the southern third of the Cape May Peninsula (8.5 km) on the New Jersey side were mapped affording optimal or suitable habitat. However, Smith et al. (2002b) did not record high levels of horseshoe crab spawning on these beaches, presumably due to their greater exposure to the ocean leading to higher wave energies and less suitable beach morphology. It should be noted that in a few areas classified as disturbed, groins have resulted in low energy sandy beaches which are ideal for spawning horseshoe crabs. An example of this is Mispillion Harbor, which has the highest reported density of crab eggs in the whole of Delaware Bay.

Of the optimal spawning habitat, 39.5% has some form of conservation protection (i.e., federal, state, public utility, or non-governmental organization—41% Delaware, 37% New Jersey; Table 10). Therefore, while significant stretches of optimal habitat are protected, key sections have no formal protection (Fig. 16), though that does not necessarily mean that they are threatened. On the Delaware side, Slaughter Beach is one of the longest stretches of optimal habitat that is largely unprotected. Similarly several pockets of optimal or suitable habitat exist along the northern New Jersey bayshore (e.g., Fortescue and Gandy's Beaches) that are largely unprotected. Although a long section of optimal or suitable habitat would appear to be protected by the Prime Hook NWR (Fig. 16), this is only partially true because some stretches of the barrier beach are in private ownership and developed (e.g., Broadkill Beach) and only the back-bay marshes and adjacent uplands are in refuge protection.

TABLE 9. LENGTH OF SHORELINE IN DELAWARE AND NEW JERSEY ACCORDING TO SUITABILITY FOR HORSESHOE CRAB SPAWNING.

	Delaware		New Jersey	
Habitat suitability	Kilometers	(%)	Kilometers	(%)
Optimal	31.28	(34.5%)	25.69	(17.4%)
Suitable	10.56	(11.6%)	5.07	(3.4%)
Less suitable	28.98	(32.0%)	48.88	(33.1%)
Avoided	16.78	(18.5%)	58.84	(39.8%)
Disturbed	3.08	(3.4%)	8.31	(5.6%)
Total shoreline[a]	90.68		147.79	

[a] The five categories are adapted from Botton et al. (1988). Due to differences in GIS processing, the total shoreline lengths are slightly different compared with Table 8.

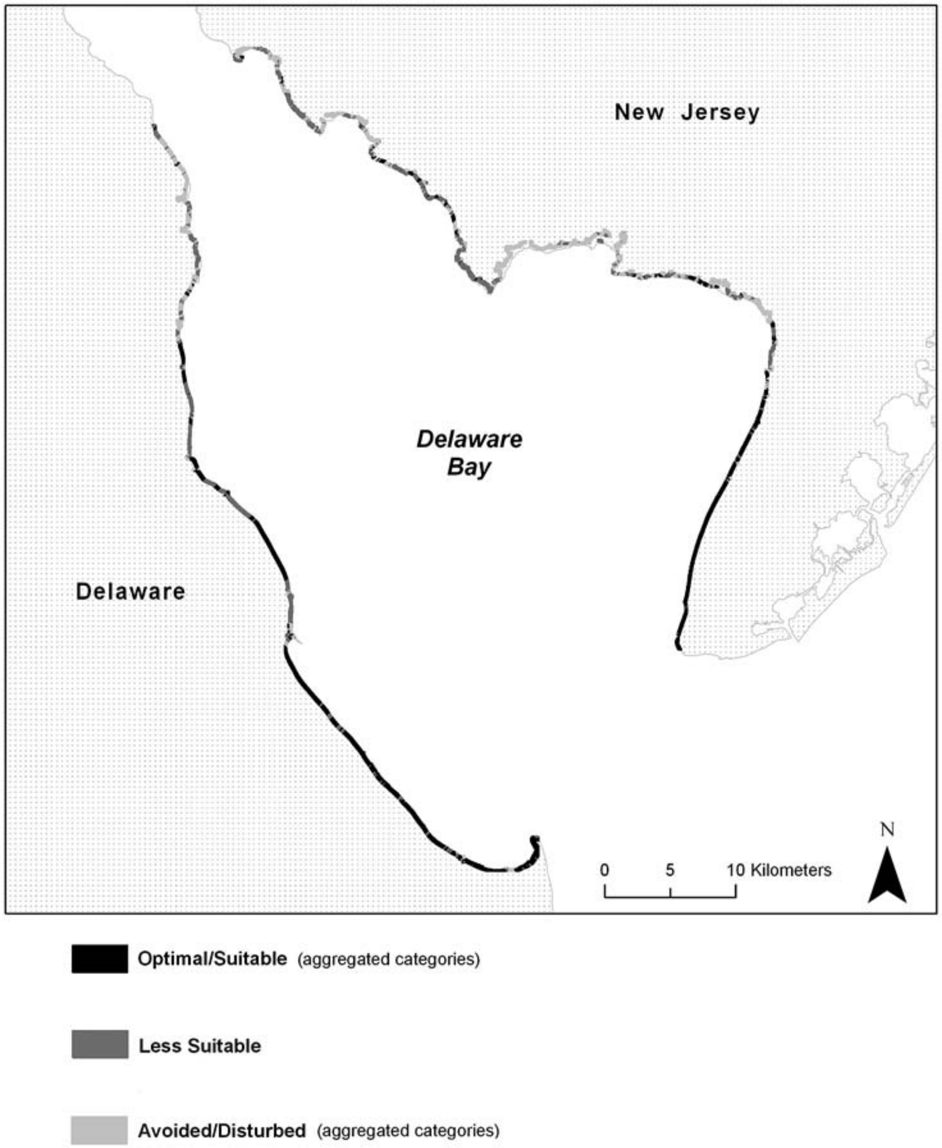

FIGURE 19. Map of horseshoe crab spawning habitat suitability on Delaware Bay based on beach sediment and development characteristics (Lathrop and Allen 2005). Note that this mapping does not include consideration of beach morphology or wave energy characteristics that may be also be important in determining the suitability of the beach as horseshoe crab spawning habitat or other human disturbance or habitat factors that might influence bird usage.

Mapping critical Red Knot habitat

During 1986–2005, weekly aerial shorebird surveys were carried out along the Delaware Bay shore over the 6-wk period of the spring stopover from the beginning of May to early June (Clark et al. 1993; K. Clark, unpubl. data). These data have been examined to determine which Delaware Bay beaches are most important for Red Knots. For the survey, the bayshore was divided into 81 segments of about 3 km each (48 in New Jersey and 33 in Delaware), which were geo-referenced to permit mapping. The survey data have been summarized for 5-yr periods. For each period, the aggregate number of Red Knots counted in each segment was

TABLE 10. LENGTH AND PERCENTAGE OF EACH SPAWNING HABITAT SUITABILITY CATEGORY IN CONSERVATION OWNERSHIP.

	In conservation ownership			
	Delaware		New Jersey	
Habitat suitability	Kilometers	(%)	Kilometers	(%)
Optimal	12.87	(41.1%)	9.62	(37.4%)
Suitable	0.74	(7.0%)	0.13	(2.6%)
Less suitable	18.57	(64.1%)	33.56	(68.6%)
Avoided	11.55	(68.8%)	48.87	(83.0%)
Disturbed	0.99	(32.1%)	0.53	(6.4%)

Notes: Conservation ownership may include federal, state, public utility, or non-governmental organization land that is primarily held for the conservation of wildlife or other natural resources. The percentages are based on the shoreline lengths shown in Table 8.

expressed as a percentage of the total aggregate number summed (across the whole study area for the entire 5-yr period). The survey data were analyzed as percentages to examine the spatial distribution of beach use on a relative, rather than absolute basis.

Comparison of the maps for the first and last 5-yr periods suggests that the spatial distribution of Red Knot use has changed (Fig. 20; K. Clark, unpubl. data). During 1986–1990, Red Knots were relatively evenly distributed along the New Jersey shore from Reeds Beach to Ben Davis Point. However, during 2001–2005, a greater concentration occurred from Norbury's Landing to Reed's Beach and from Egg Island Point to Gandy's Beach. During 1986–1990, the Red Knots were relatively evenly distributed along Delaware shore from Bowers Beach through Bombay Hook NWR with a major concentration in the Slaughter Beach-Mispillion Harbor area. During 2001–2005, however, a much greater concentration occurred around Slaughter Beach-Mispillion Harbor and around Bowers Beach. Mispillion Harbor consistently supports high concentrations of Red Knots, sometimes more than 20% of the entire bay population.

Other areas of the Bayshore were little used by Red Knots; for example, in New Jersey the Cape May Peninsula south of Norbury's Landing, and in Delaware the central and lowest sections (Big Stone Beach and Broadkill Beach to Cape Henlopen). These low Red Knot-use sections coincide with areas of low horseshoe crab spawning activity as recorded by Smith et al. (2002b). Lathrop and Allen (2005) classified other parts of the bayshore as less suitable and even as avoided as crab-spawning habitat in 2002, that were recorded as having medium-high Red Knot use in 1986–1990. In many cases, Red Knot use of these beaches had diminished by 2001–2005; for example the Bombay Hook NWR in Delaware and the Maurice River area in New Jersey (Fig. 20). Whether these changes are due to beach erosion and/or reduced numbers of horseshoe crabs or spawning activity is unknown.

In addition to the aerial surveys, ground surveys have been conducted by NJENSP to identify other high use areas for Red Knots during both spring and autumn stopover. In particular, large numbers of Red Knots have been recorded using the Hereford Inlet area on the Atlantic coast of Cape May and the adjacent marshes in spring. Fall ground surveys have also recorded significant numbers of Red Knots in the Hereford Inlet area. Stone Harbor Point and the nearby Nummy, Champagne, and Humphrey Islands include undeveloped sand beach, sandbar, mudflat, and salt-marsh habitats which afford critically important roosting areas, especially on spring high tides and at night. This area is also important for supplementary foraging by Red Knots in spring and as a main foraging area in autumn when surf clams and mussel spat are available.

In addition to the Delaware beaches identified from aerial surveys, International Shorebird Surveys (ISS) conducted in Delaware during the 1992–1997 spring migrations suggest that managed impoundments along Delaware Bay may also provide important habitat for Red Knots. Each year from 1993–1996, 1,200–5,300 Red Knots were recorded in an impoundment at the Ted Harvey Wildlife Area. Managed impoundments in Delaware may represent critical habitat for high-tide and nighttime roosts if conditions are suitable.

Maps showing the distribution of horseshoe crab spawning habitat and Red Knot use in Delaware Bay (Figs. 16, 19, and 20) identify the main areas that should be considered as critical habitat to support the Red Knot's spring stopover. Knot use is probably the better criterion because it not only reflects areas of high egg density but also the birds' other requirements, such as safety from predators and suitable and safe high water and nighttime roost sites. For example, coastal areas of Egg Island modeled as less suitable or avoided by spawning crabs, are

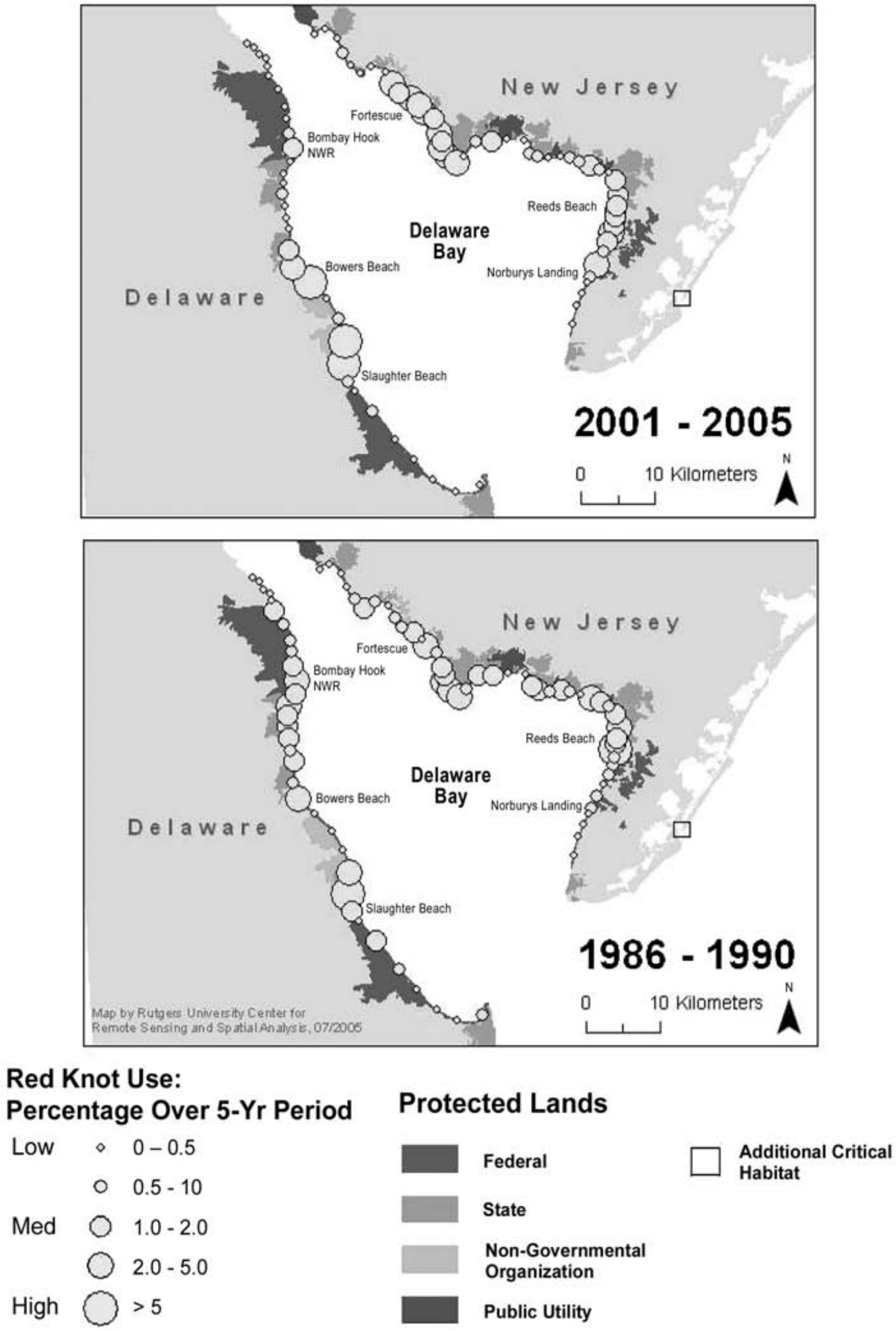

FIGURE 20. Map of percent Red Knot use for spring stop over between 1986–1990 and 2001–2005. Survey data summed across the 5-yr period and percent of total calculated for each beach segment (K. Clark, unpubl. data).

nevertheless valuable Red Knot habitat because they are used for roosting during day and night high tides. Their attraction is that they are protected by water channels from ground predators and are free from human disturbance.

On the basis of the most recent as well as the 1980s data, the Delaware Bay shore in New Jersey from Norbury's Landing to Dennis Creek should be considered critical Red Knot habitat. This portion of the Cape May Peninsula has been the focus of land conservation acquisition as part of the Cape May NWR. However, the significant gaps that still exist in the existing refuge boundaries (Fig. 16) should be a high priority for future acquisition or conservation management. Likewise, important stretches of shoreline in the Fortescue and Gandys Beach areas should be considered critical Red Knot habitat and prioritized for protection. The Hereford Inlet area, between Stone Harbor and Wildwood, and Stone Harbor Point should also be considered critical habitat due to its importance during both spring and fall migration.

The survey data suggest that some parts of the New Jersey shore between East Point and Moores Beach had higher relative use by Red Knots during 1986–1990 than more recently. This area has experienced considerable beach erosion and some stretches have a history of development and beach armoring. Therefore, it would seem possible that beach restoration might be feasible in this area (e.g., at Thompson's Beach). The most southerly portion of the Cape May Peninsula (south of Villas), while mapped as optimal/suitable horseshoe crab spawning habitat (and appearing as major gaps in conservation protection in Fig. 16), probably need not be considered as important Red Knot habitat due to its lower usage by spawning crabs and foraging Red Knots.

In Delaware, the shores in the vicinity of Bower's Beach and Slaughter Beach-Mispillion Harbor were recorded as critically important for Red Knots, but they are significantly lacking in protection due to private land ownership and density of residential development. These areas should be given priority for conservation acquisition or management in future. The area of Slaughter Beach-Mispillion Harbor should receive special consideration due to its outstanding concentrations of Red Knots (Fig. 20). The lowest section of the Delaware shore (south of Broadkill Beach), while mapped as optimal/suitable horseshoe crab spawning habitat (and appearing as major gaps in conservation protection, Fig. 16), probably should not be considered as critical Red Knot habitat due to its lower usage by spawning crabs and foraging shorebirds.

While it is the intertidal beaches that comprise the most important Red Knot habitat in Delaware Bay, Burger et al. (1997) have shown that migrant shorebirds, including Red Knots, move actively between the bay's habitats using them for foraging, resting, and other behaviors according to the state of the tide, date, and time of day. Though the beaches are of critical importance, during high tides (especially spring) the birds would be restricted to areas without sufficient food for profitable foraging and too close to vegetation and structures that could harbor predators. Therefore, Red Knots often go elsewhere, including nearby salt marshes, sand spits, and islands. On some occasions, Red Knots fly all the way across the Cape May Peninsula to use the extensive sandy beach, mud flats, and salt marshes in the vicinity of Stone Harbor for both foraging and roosting.

Evidence of decline in both the population of horseshoe crabs and the availability of their eggs for Red Knots

Currently, several surveys monitor the horseshoe crab population, the total density of eggs in the beaches, and the proportion of eggs in the upper 5 cm of sand that are potentially available to the shorebirds. Only two surveys, however, have been running long enough (and using consistent methods) to show how crab and egg numbers have changed over the period of increased horseshoe crab harvest which started in 1996. These are the DDFW trawl survey of crabs in Delaware Bay, which has focused on the in-bay population of crabs, and egg density surveys on the New Jersey bay shore since 1985. The egg density survey began in 1985–1986 by K. Williams, a contractor under NJDFW, and was continued by Rutgers University (M. L. Botton and R. E. Loveland) in 1990. Botton and Loveland analyzed the data collected by K. Williams in 1985–1986 in their subsequent study, using conversion factors derived from side-by-side sampling (M. L. Botton and R. E. Loveland, unpubl. data). The egg density survey has been carried out since 2000 by NJENSP. The Delaware Bay trawl survey shows a highly significant decline in the number of adult crabs in Delaware Bay (Fig. 21) and the New Jersey egg density survey shows a highly significant decline in the density of eggs in the upper 5 cm of sand in New Jersey (Fig. 22). In respect of both parameters, the main decline took place in the 1990s, before the Delaware Bay horseshoe crab spawning activity survey began in 1999 (Michels and Smith 2006) and before the horseshoe crab benthic trawl survey began in 2001 (Hata 2006). Both of these new and thorough

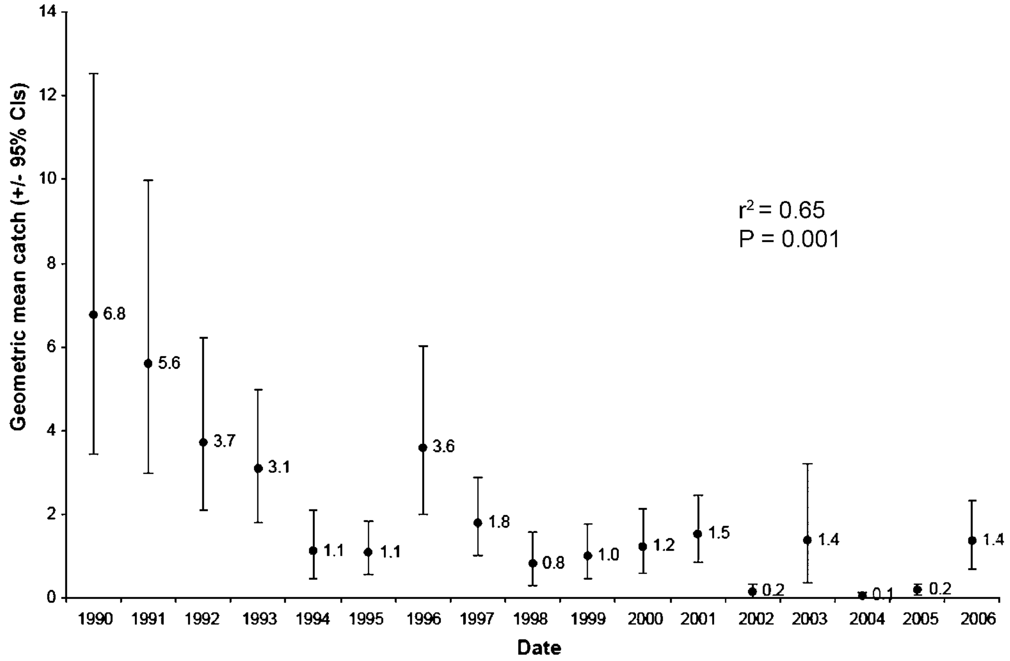

FIGURE 21. Number of horseshoe crabs in 30-foot trawls in Delaware Bay during May 1990–2006 (S. Michels, pers. comm.). The declining trend is highly significant ($r^2 = 0.65$, $P < 0.001$).

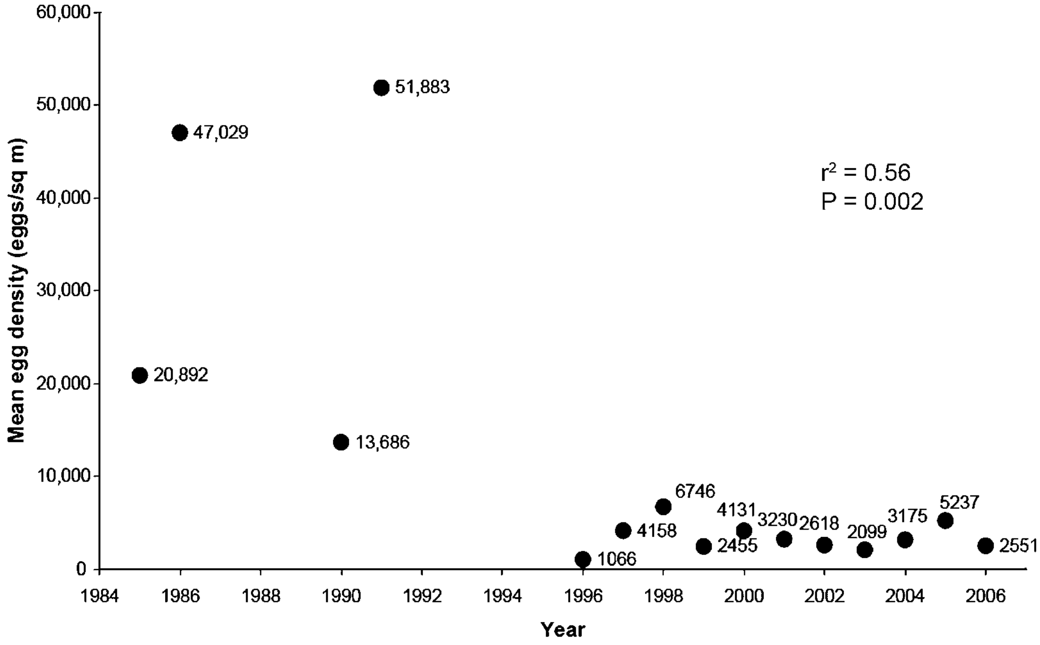

FIGURE 22. Density of horseshoe crabs eggs in the upper 5 cm of sand in the Delaware Bay beaches of New Jersey during late May 1985–2006. The declining trend is highly significant ($r^2 = 0.56$, $P = 0.002$). Source: 1985–1999 (M. L. Botton, pers. comm.; R. E. Loveland, pers. comm.); 2000–2006 (NJENSP, unpubl. data). Confidence intervals are not plotted because the raw data are not available for the earlier period and for the later period they are very small in relation to the scale. All data points relate to 2–6 sampling dates spread over May and early June and to core samples taken along transects between the high and low tide lines at 3-m intervals.

surveys indicated no major change in the size of the horseshoe crab population since they were instigated. The spawning activity survey shows that in 2003 and 2005 spawning was later than usual, probably on account of cold weather, and was much reduced in May. This led to a reduction in the availability of eggs during the peak Red Knot stopover and late-arriving birds in particular were unable to make the mass gains they needed (Atkinson et al. 2007). The confidence limits associated with the crab data preclude precise estimation of the scale of the decline, but it would seem to be of the order of 80% (based on geometric mean; Fig. 21). Similarly there is uncertainty about the scale of the decline in available eggs, but the data suggest somewhere in the range of 80–97% (Fig. 22).

Horseshoe crab spawning is greatly reduced by heavy on-shore wave action (M. L. Botton and R. E. Loveland, pers. comm.), and in some years long periods of winds from a particular direction lead to more crab spawning on one side of the bay than the other (the sheltered side, where the wind is offshore). For example, in 1997 persistent westerly winds led to far more spawning in Delaware than in New Jersey, but the reverse occurred in 2003 (L. J. Niles, unpubl. data). However, the fact that more Red Knots fed in New Jersey than Delaware every May from 2002–2005 (Fig. 23), including 2003 when winds were off-shore in New Jersey, indicates that on-shore winds alone are not responsible for the decreased densities of eggs on the New Jersey shore shown in Fig. 22.

Occasionally, (as on the Delaware shore in May 2003 [N. Clark, unpubl. data]) a storm will deposit large quantities of new sand on exposed beaches so that eggs already laid become buried so deeply that they are completely inaccessible to the shorebirds. Storms and wave action, as well as variation in the quality of different beaches as spawning habitat and depletion of eggs by foraging shorebirds and gulls mean that in any season considerable spatial and temporal variation occurs in the availability of eggs to Red Knots. The birds show a preference for foraging on beaches with high densities of available eggs; they also avoid concentrations of, and competition with, large numbers of gulls (Botton et al. 1994).

Studies of horseshoe crab spawning phenology show variation associated with seawater temperature; for example spawning was delayed by about 2 wk in 2003 when water temperatures averaged 2.8°C lower than the 1997–2002 mean (Weber 2003). This could have negative implications for the shorebird stopover if global warming results in a change in local seawater temperatures as a result of which the peak of spawning and the stopover do not coincide.

Egg-density sampling has not been carried out in Delaware for as long as in New Jersey and differences in methodology make comparison of trends between states virtually impossible. Therefore, no such comparisons are presented here. However, sampling in Delaware has demonstrated that one site, Mispillion Harbor, which is very well sheltered by long groins, is by far the most important horseshoe crab spawning location in the entire bay and often has eggs densities that are an order of magnitude greater than any other site sampled (Fig. 24).

The peak in the harvest of horseshoe crabs took place during 1996–1999 after which

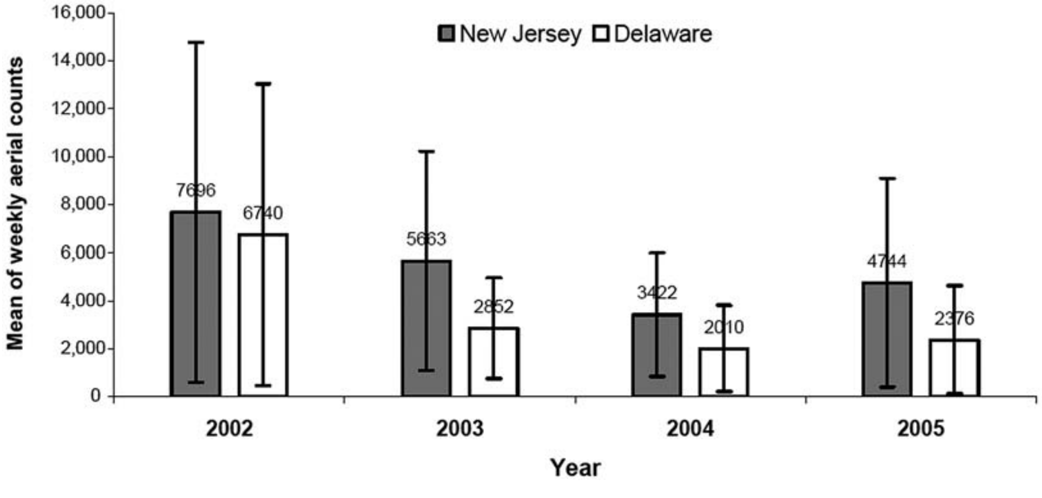

FIGURE 23. Mean of weekly aerial counts of Red Knots in New Jersey and Delaware in May 2002–2005.

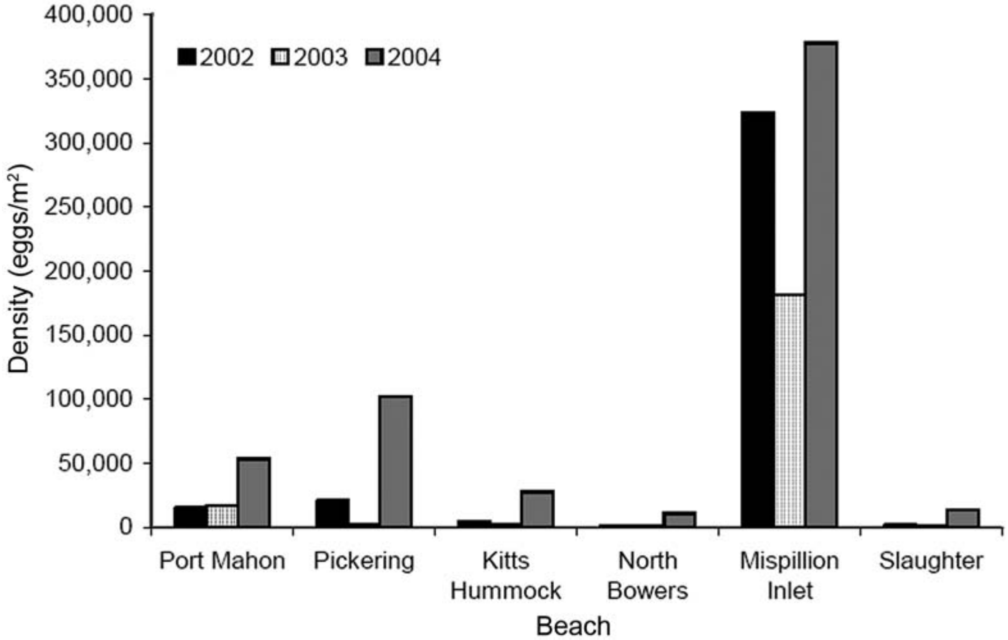

FIGURE 24. Mean densities of horseshoe crab eggs in the upper 5 cm of sand from beach transects sampled once in late May and once in early June at six sites on the Delaware shore of Delaware Bay during 2002–2004 ordered from north (Port Mahon) to south (Slaughter Beach) (Weber 2003, 2004). At each site on each sampling date, 20 core samples were taken along each of two transects covering 83% of the distance between the nocturnal high tide line and the tidal flat. Only the means for both transects are given by Weber so confidence intervals are not available.

harvest restrictions and management actions appear to have resulted in a more or less stable crab population, albeit at a relatively low level (Figs. 13, 21; Morrison et al. 2004). Crabs do not breed until 9–11 yr of age (Shuster et al. 2003), and thus measures already taken or even a complete cessation of all further harvest, may not be reflected by an increase in the breeding population of horseshoe crabs for several years.

MIGRATION AND STOPOVER HABITAT—SOUTHEASTERN UNITED STATES

In the southeastern U.S., Red Knots forage along sandy beaches during spring and fall migration from Maryland through Florida, and in Texas. During migration, Red Knots also use the tidal mudflats in Assateague Island National Seashore in Maryland and along the barrier islands in North Carolina (S. Cameron, pers. comm.; G. Therres, pers. comm.). In addition to the sandy beaches, Red Knots forage along peat banks for mussel spat in Virginia (S. Rice, pers. comm.; B. Truitt, pers. comm.; B. Watts, pers. comm.), and along small pockets of peat banks where the beach is eroding in Georgia (B. Winn, pers. comm.). Red Knots in Florida also utilize salt marshes, brackish lagoons, and tidal mudflats, in addition to mangroves in southern Florida (N. Douglass, pers. comm.; P. Leary, pers. comm.; Sprandel et al. 1997). In Texas, migratory Red Knots concentrate at the Bolivar Flats in Galveston County with smaller numbers on the outer beaches utilizing the tidal mudflats and salt marshes (W. Burkett, pers. comm.; B. Ortego, pers. comm.).

In Virginia, an invertebrate study was conducted in May 2000 (Truitt and Brown 2000). Nineteen days were spent in the field on Metompkin (12 d in peat bank habitat), Parramore (6 d in sandy beach habitat), and Fisherman Islands (1 d in sandy beach habitat); 105 core samples were collected for invertebrate analysis and counts were made of migratory Red Knots. The peat banks of Metompkin Island had both the highest density and diversity of invertebrate species (Table 11). The blue mussel was by far the most abundant invertebrate with densities ranging from 33,000 m^{-2} to 181,000 m^{-2}. Observations confirmed that the Red Knots were feeding on these mussels which covered the peat banks in dense mats. Other species noted in the core samples included six polychaetes, five amphipods, and

TABLE 11. TOTAL NUMBERS OF ALL BENTHIC INVERTEBRATES COLLECTED DURING TRANSECT SAMPLING ON METOMPKIN (MET), PARRAMORE (PARR), AND FISHERMAN ISLANDS (FISH), VIRGINIA, IN MAY 2000 (TRUITT ET AL. 2001).

Transect	Substrate	N core samples	Density/m^2	Dominant. species	Total N species
MET1	Peat	1,162	181,019	*Mytilus edulis*	12
MET2	Peat	213	33,115	*Mytilus edulis*	7
MET3	Peat	577	89,896	*Mytilus edulis*	10
PARR1	Sand	60	9,285	*Melitidae sp.*	5
PARR2	Sand	34	5,318	*Melitidae sp.*	5
FISH1	Sand	16	2,523	*Parahaustorius*	9
FISH2	Sand	5	861	*Parahaustorius*	5

one isopod. Of the three islands, Parramore had the least diversity, but the second highest density of invertebrates (Table 12). The Melitidae amphipods were by far the most abundant invertebrate species which suggests that they were the Red Knots' main prey. However, observations could not confirm this because the birds held their heads underwater in the wash of the waves while probing.

Fisherman Island had the second highest diversity of invertebrates and the lowest density. The amphipod *Parahaustorius longimerus* was the most abundant, along with three other amphipods, two polychaetes, and two bivalves. Ash-free dry weights were also the lowest among the three islands.

Metompkin Island offered the most food resources for Red Knots in terms of ash-free dry mass, while there was less at Parramore and least at Fisherman. This helps to explain the large numbers of Red Knots observed at Metompkin during past aerial surveys. Without information on stopover times, it is impossible to estimate what proportion of the flyway Red Knot population is supported by this island on migration, but it could be substantial. On 23 May 2005, a dusk count of the Hereford Inlet roost showed 20,000 Red Knots were in Delaware Bay. In the middle of the same day, an aerial count showed 9,150 on the coastal islands of Virginia (B. Watts, pers.comm.).

On Metompkin, the Red Knots roosted over high water on the beach adjacent to the peat banks. As soon as the banks became exposed, feeding activity began and continued for several hours. By half tide or just after, a marked decrease occurred in feeding and most birds were observed preening, loafing, or sleeping. Usually, just before low water, many birds would fly off to the north at a time when the most peat and blue mussels were exposed. This suggests that feeding on blue mussels the birds are able to satisfy their food requirements remarkably quickly.

It is significant to note that none of the core samples from the three islands contained the coquina clam., a common summer resident on many of the Virginia barrier islands. It is believed that in spring 2000, the Red Knot migration probably preceded this bivalve's seasonal migration from just offshore into the intertidal zone of the island beaches.

MIGRATION AND STOPOVER HABITAT—PANAMA

The upper Panama Bay is a critical staging area for shorebirds during the spring. Red Knots forage along the intertidal mudflats that extend several kilometers at low tide. They may also forage within mangroves and sandy beaches near Chitré (Buehler 2002).

MIGRATION AND STOPOVER HABITAT—MARANHÃO, BRAZIL

Maranhão is a migration stopover point during spring and fall for Red Knots. The Red Knots forage on the sandy beaches and mudflats of Campechá Island in the Lençóis Bay and Coroa dos Ovos and Ingleses islands in the Turiaçú Bay. Knots also use extensive mangroves that permeate the interior through the São Marcos Bay and the lower courses of several rivers. Among the important plant species are the red mangrove (*Rizophora mangle*), black mangrove (*Avicenia germinan*), and white mangrove (*Laguncularia racemosa*). The high primary productivity is important to migratory birds (I. Serrano, unpubl. data).

MIGRATION AND STOPOVER HABITAT—LAGOA DO PEIXE, BRAZIL

Lagoa do Peixe National Park is one of the largest stopover grounds for North American migratory waterbirds in the South American continent. The lagoon connects to the sea during winter through wind action, rain, and accumulated water volume in the lagoon, and these processes are supplemented by pumping in summer. This maintains a constant influx of salt water which sustains a rich fauna of

TABLE 12. NUMBERS OF EACH INVERTEBRATE SPECIES COUNTED DURING TRANSECT SAMPLING ON METOMPKIN, PARRAMORE, AND FISHERMAN ISLANDS, VIRGINIA IN MAY 2000 (TRUITT ET AL. 2001).

Species	Number of individuals 1 m from surf	Number of individuals 2 m from surf	Number of individuals 3 m from surf
Metompkin Island			
Bivalves			
Mytilus edulis	16,047	3,224	7,410
Cyrtopleura costata	82	89	264
Polychaete worms			
Nereis succinea	43	85	191
Mediomastus ambiseta	26	0	3
Loimia medusa	0	1	1
Chaetopteros fragment	0	0	1
Heteromastus filiformis	0	5	1
Capitellidae sp.			
Amphipods			
Jassa falcata	20	7	28
Caprela penantis	1	0	0
Eunice norvegica	1	0	0
Gammarus mucronatus	1	0	0
Erichthonius brasiliensis	13	0	0
Isopods			
Cirolana sp.	21	2	10
Miscellaneous			
Fish larvae	1	0	0
Mollusk siphon	1	0	0
Gastropod sp.	1	0	0
Nemertean spp.	3	0	4
Parramore Island			
Bivalves			
Cyrtopleura costata	57	27	
Polychaete worms			
Scolepsis squamata	32	21	
Amphipods			
Melitidae sp.	656	433	
Parahaustorius longimerus	7	1	
Crustaceans			
Emerita talpoida	2	4	
Fisherman Island			
Bivalves			
Cyrtopleura costata	6	12	
Ensis directus	8	0	
Polychaete worms			
Scolepsis squamata	1	2	
Lumbrinereis sp.	1	0	
Amphipods			
Parahaustorius longimerus	222	63	
Trichophoxus epistomus	1	5	
Haustorid sp.	1	0	
Monoculoides edwarsi	1	0	
Miscellaneous			
Nemertean spp	10		

invertebrates all year round. During both northward migration in March-April and southward migration in September-October, Red Knots use the lagoon and the ocean beach for foraging. However, peak numbers have declined from around 10,000 in the mid-1990s to <1,000 in 2003. In the lagoon, the Red Knots' principal prey is the mud snail (*Littoridina australis*; I. Serrano, unpubl. data).

MIGRATION AND STOPOVER HABITAT—PAMPAS REGION, ARGENTINA

In this region available shorebird habitat is found along >1,200 km of shoreline from Buenos Aires, in the mouth of Río de la Plata estuary, to Punta Alta near Bahía Blanca. Bahía de Samborombón and Bahía Blanca estuary contain extensive marshes and mudflats. Tide amplitude is low (2 m on average) and huge intertidal mudflats are present. South of Bahía de Samborombón (Punta Rasa), sandy beaches occur and Laguna Mar Chiquita contains a shallow permanent brackish lagoon connected to the sea.

The highest numbers of Red Knots have been seen during spring migration on ocean sandy beaches backed by dunes southward from Punta Rasa where the area has been heavily modified by urbanization to create appropriate conditions for tourism in summer (Ieno et al. 2004). Feeding studies showed that Red Knot's primary prey is the mud snail (Ieno et al. 2004).

MIGRATION AND STOPOVER HABITAT—PATAGONIAN SHORELINE, ARGENTINA

The Patagonian shoreline consists of the Buenos Aires Province coastline south of Bahía Blanca and includes Río Negro, Chubut, Santa Cruz, and Tierra del Fuego provinces. Critical feeding areas for Red Knots are associated with extensive sandy beaches and mudflats where the primary prey is clams (*Darina solenoides*; Escudero et al. 2003, Albrieu et al. 2004; M. A. Hernández et al., unpubl. data; P. M. González et al., unpubl. data), but also includes polychaetes (e.g., *Travisia olens*; M. A. Hernández et al., unpubl. data) and small crustacea (P. M. González, et al., unpubl. data). Other critical feeding habitats for Red Knots are the restingas, broad, wave-cut rocky platforms extending to the lower intertidal zone, where knots usually feed on blue mussels or another small mussel *Brachidontes rodriguezi* (González et al. 1996, Escudero et al. 2003).

The entire Argentinian coast from Bahía Blanca to the Beagle Channel (Tierra del Fuego) contains sandy beaches and sandflats, mudflats, and restingas which are often covered with a rich invertebrate fauna (Canevari et al. 1998). Gulfs and embayments are important coastal features, and the Patagonian (Tehuelche) gravels form beaches along the shoreline and occur in many places such as the area surrounding Península Valdés and the southern part of the Golfo San Jorge. Restingas are found in many areas below cliff beaches near San Antonio Oeste.

During high tide, foraging areas are usually covered by water and Red Knots roost along the upper shore of beaches, sandbars and shellbars, marshes, and other expansive coastal areas above high-tide line.

MIGRATION AND STOPOVER HABITAT—URUGUAY

The coastline of Uruguay was searched as part of the South American Atlas project in the mid-1980s; no Red Knots were found there (Morrison and Ross 1989). Recent enquiries indicate that Red Knots are recorded in Uruguay very infrequently and in only low numbers (P. M. González, unpubl. data).

WINTER HABITAT—UNITED STATES

As explained in the taxonomy section of this document, the subspecific status of the Red Knots that winter on the western and northeastern coasts of Florida and on the coast of Georgia, South Carolina, and Texas is uncertain. Therefore, on the basis that this population might be *C. c. rufa*, we present the following description of the habitats it occupies.

From South Carolina through Florida, Red Knots winter along sandy beaches. They may also utilize peat banks in Georgia and salt marshes, brackish lagoons, tidal mudflats, and mangroves in Florida. In Texas, wintering Red Knots occur along sandy beaches on Mustang Island and other outer beaches and tidal mudflats and salt marshes on Bolivar Flats.

WINTER HABITAT—CHILE

Bahía Lomas is the main wintering area of *C. c. rufa* in South America (Morrison and Ross 1989, Morrison et al. 2004). It is located near the east entrance of the Straits of Magellan on the northern coast of the main island of Tierra del Fuego (52°28′08″ S; 69°22′54″ W; Fig. 25) and is mainly dominated by intertidal mudflats which tend to be smooth and sandy towards the edges and highly channelled toward the middle. The flats extend for about 50 km and on spring tides the intertidal distance reaches 7 km in places. The substrate of the bay comprises a large area of mud slopes with channels that diminish towards low water.

Since 2003, an ecological study has been conducted on the tidal flats of Bahía Lomas. The main objective has been to determine the composition, distribution, and abundance of the benthic community with special reference its trophic relationship with the Red Knot wintering population. The results indicate that the flats are dominated by three invertebrates: the clam *Darina solenoides*, an amphipod, and a polychaete (Table 13; Espoz et al. 2008). Although each has its own characteristic distribution with respect to tide level, they all tend to increase in abundance towards low water. Of the three species, *Darina solenoides* is the most abundant (Fig. 26) and stable isotope analysis shows that wintering Red Knots are mainly assimilating carbon and nitrogen present in that species (Fig. 27). Therefore *Darina* would appear to be the Red Knots' main

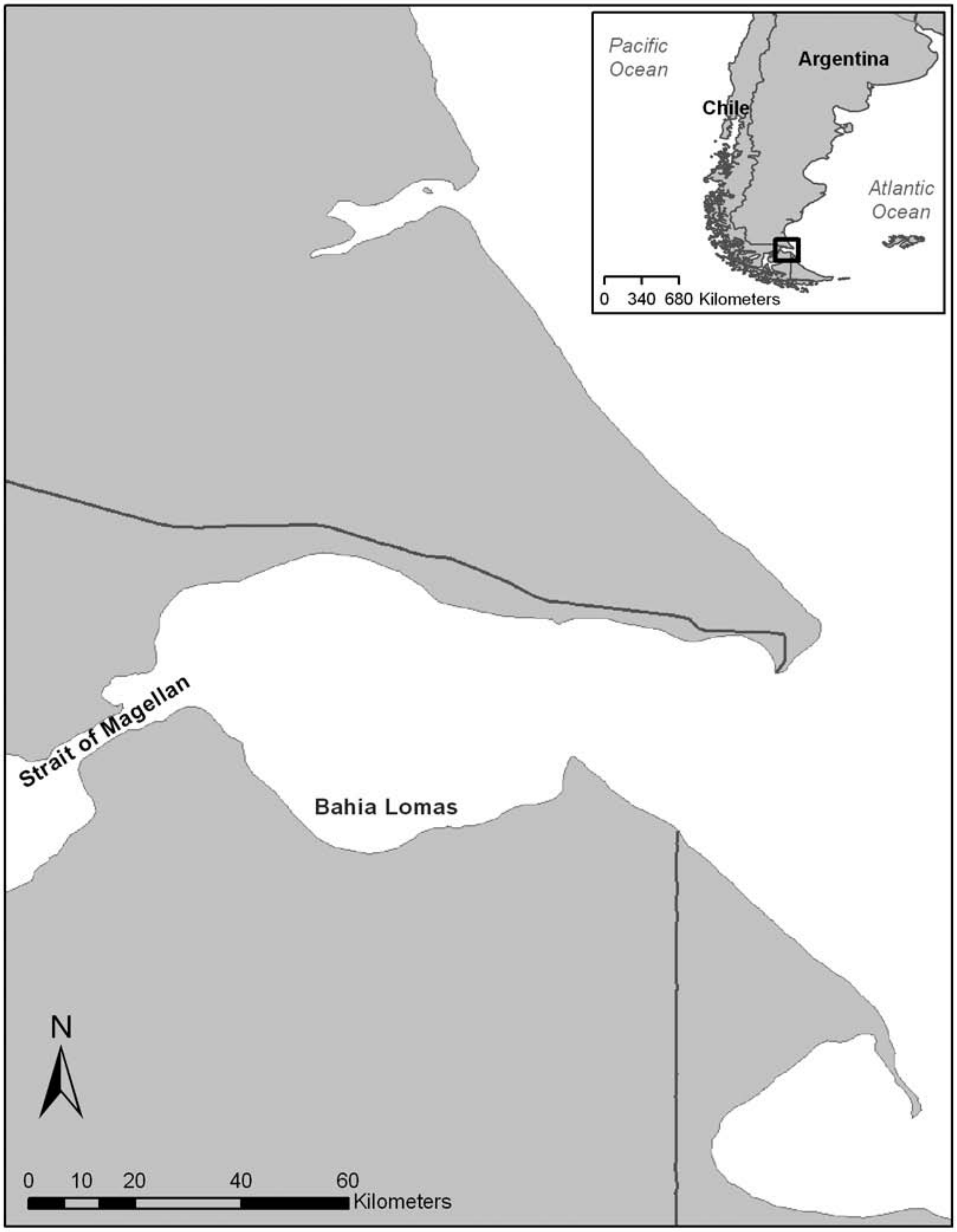

FIGURE 25. Location of Bahía Lomas in Tierra del Fuego, Chile.

TABLE 13. INVERTEBRATES RECORDED IN TRANSECT SAMPLING AT BAHÍA LOMAS, CHILE, AND THE RELATIVE ABUNDANCE OF EACH.

	N	%
Mollusca, Bivalvia		
Darina solenoides	1,815	51.3
Bivalvia (unidentified species)	3	0.1
Mollusca, Gastropoda		
Gastropoda (unidentified species 1)	4	0.1
Gastropoda (unidentified species 2)	3	0.1
Polychaeta		
Paraonidae		
Paraonidae (unidentified species)	875	24.8
Phyllocidae		
Eteone sp.	331	9.4
Nephtyidae		
Aglaophamus sp.	13	0.4
Opheliidae		
Travisia sp.	13	0.4
Euzonus sp.	29	0.8
Spionidae		
Scolelepis sp.	23	0.7
Scolecolepides sp.	165	4.7
Glyceridae		
Glycera sp.	1	0.03
Polychaeta (unidentified species)	11	0.3
Crustacea		
Isopoda 1	13	0.4
Amphipoda (unidentified species 1)	178	5.0
Amphipoda (unidentified species 2)	1	0.03
Others		
Insecta	3	0.1
Insect larvae	20	0.6
Nematoda	20	0.6
Nemertea	11	0.3
Unidentified	3	0.1

prey at Bahía Lomas, just as might be expected in view of the prey taken by Red Knots worldwide (Piersma 1994).

WINTER HABITAT—ARGENTINA

Wintering Red Knots in Argentina are now largely confined to Bahía San Sebastián and Río Grande in the Province of Tierra del Fuego. Knots feed mainly within the mudflats of Bahía San Sebastián and along sandy beaches, mudflats, and restingas in Río Grande (P. M. González, unpubl. data).

WINTER HABITAT—BRAZIL

The main wintering area of Red Knots in Brazil is on the coast of the state of Maranhão where they forage along sandy beaches, tidal mudflats, and mangroves (I. Serrano, unpubl. data).

WINTER HABITAT—PANAMA

A small number of Red Knots winter in the Upper Panama Bay where they utilize the soft, silty mud in the tidal mudflats near Panama City (Buehler 2002).

POPULATION SIZE AND TRENDS

In breeding habitats, Red Knots are thinly distributed across a huge area of the Arctic, where we have no comprehensive understanding

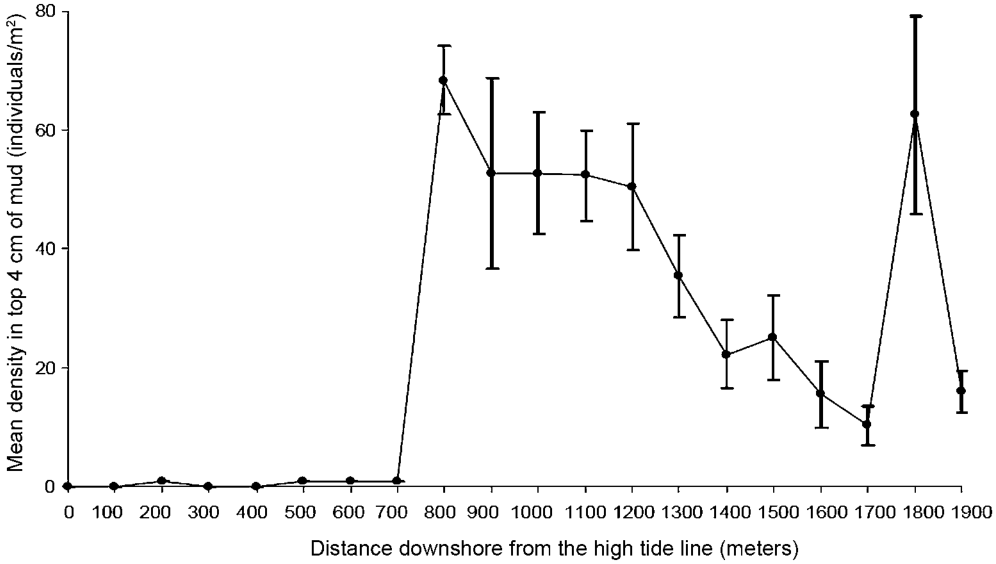

FIGURE 26. The intertidal distribution pattern of *Darina solenoides* at Bahía Lomas, Chile (Espoz et al. 2008).