Effects of Horseshoe Crab Harvest in Delaware Bay on Red Knots: Are Harvest Restrictions Working?

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*Each May, red knots (*Calidris canutus rufa*) congregate in Delaware Bay during their northward migration to feed on horseshoe crab eggs (*Limulus polyphemus*) and refuel for breeding in the Arctic. During the 1990s, the Delaware Bay harvest of horseshoe crabs for bait increased 10-fold, leading to a more than 90% decline in the availability of their eggs for knots. The proportion of knots achieving weights of more than 180 grams by 26–28 May, their main departure period, dropped from 0.6–0.8 to 0.14–0.4 over 1997–2007. During the same period, the red knot population stopping in Delaware Bay declined by more than 75%, in part because the annual survival rate of adult knots wintering in Tierra del Fuego declined. Despite restrictions, the 2007 horseshoe crab harvest was still greater than the 1990 harvest, and no recovery of knots was detectable. We propose an adaptive management strategy with recovery goals and annual monitoring that, if adopted, will both allow red knot and horseshoe crab populations to recover and permit a sustainable harvest of horseshoe crabs.*

Keywords: red knot, Calidris canutus rufa*, Delaware Bay, horseshoe crab,* Limulus polyphemus

New World red knots (*Calidris canutus rufa*) migrate annually from Arctic breeding grounds to the southern tip of South America and back, covering more than 30,000 kilometers (km). Each May, red knots and other shorebirds stop at Delaware Bay on the US eastern coast (figure 1), where they feed on eggs of spawning horseshoe crabs (*Limulus polyphemus*). For red knots, it is the final stop before a single direct flight to Arctic breeding grounds (Morrison and Harrington 1992, Harrington 2001), where, on arrival in early June, weather is uncertain and feeding conditions are poor. Therefore, body reserves gained on Delaware Bay are crucial for both the flight to the Arctic and survival and successful breeding (Baker et al. 2004, Morrison and Hobson 2004, Morrison et al. 2005, 2007).

In the 1980s, Delaware Bay was recognized as a critical migratory stopover for six shorebird species—red knot, ruddy turnstone (*Arenaria interpres*), sanderling (*Calidris alba*), semipalmated sandpiper (*Calidris pusilla*), dunlin (*Calidris alpina*), and short-billed dowitcher (*Limnodromus griseus*)—with peak counts of more than 400,000 individuals; estimates are that more than 1 million shorebirds used the bay in spring (Myers et al. 1987, Clark et al. 1993). Delaware Bay, the first stopover ranked of "hemispheric importance" in the Western Hemisphere Shorebird Reserve Network (Myers et al. 1987), by 1990 had gained repute as one of the world's most spectacular shorebird stopovers, comparable with the Copper River Delta in Alaska, the Wadden Sea in Europe, and the Yellow Sea in Asia. Delaware Bay had also spawned an ecotourism industry with an estimated worth of $34 million (Eubanks et al. 2000).

Horseshoe crabs, especially egg-laden females, had been harvested historically as bait for minnow and eel, but their abundance and ease of collection when spawning made them a prime target as bait for an emerging conch fishery in the early 1990s. In the five years between 1992 and 1997, the reported harvest of crabs grew 20-fold from about 100,000 to more than 2 million (figure 2), at an estimated value of $11 million to $17 million (Manion et al. 2000). Because no states had mandatory reporting, the true increase is uncertain, but the number of hand-collecting permits for Delaware grew from 10 in 1991 to 132 in 1997, indicating a large increase (Whitmore and Greco 2005). The growth in harvest led to a

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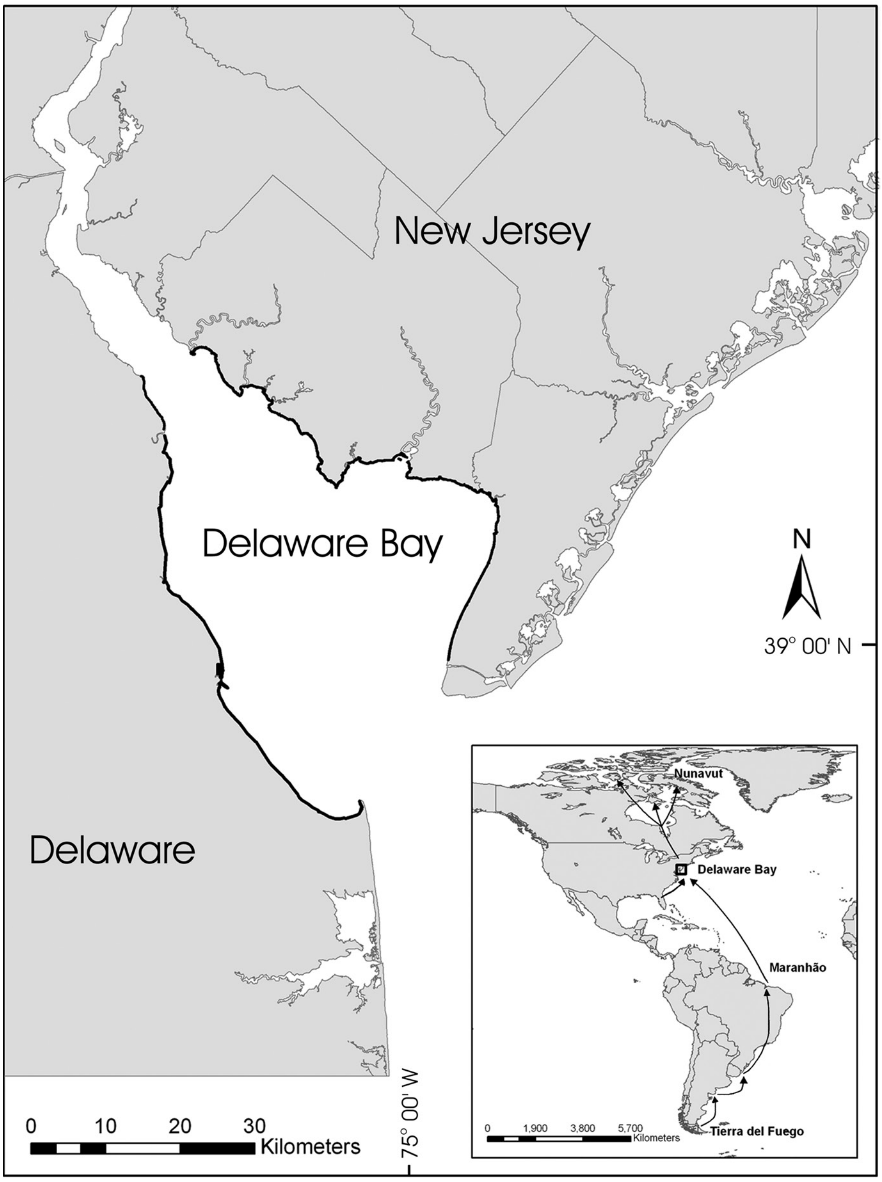

Figure 1. Delaware Bay and the main parts of the shore used by red knots (dark lines) during their spring migration. The inset portrays the entire migration route from Tierra del Fuego in Chile and Argentina to the Arctic.

dramatic decrease in spawning crabs and thus in the availability of crab eggs for shorebirds (Michels 2000), and shorebird numbers on Delaware Bay were soon falling fast; peak counts of knots in 2003–2007 averaged 66% less than counts for 1998–2002 (figure 3, box 1).

By 1997, the Atlantic States Marine Fisheries Commission (ASMFC) began to implement restrictions, and some states (New Jersey, Maryland, and Delaware) had already begun to implement restrictions (ASMFC 1998, 2006a). The notable exception is South Carolina, which in 1991 limited the use of horseshoe crabs for biomedical purposes only, and required crabs to be returned to the water after bleeding (10% to 15% of crabs do not survive the bleeding process; ASMFC 1998). Early restrictions, such as stopping the harvest during the shorebird stopover, were aimed at reducing the disturbance to feeding birds, but they did little to reduce the harvest. By 2004, the ASMFC and states had restricted annual harvests of Delaware Bay horseshoe crabs to about 600,000, from a high of more than 2 million. Although the 2004 harvest was only a quarter of the 1998 peak, it was still well above harvests thought to have occurred before the sharp increase in the early 1990s (figure 2). In 2006, concern that harvest restrictions were not founded in good science led to a review by the ASMFC stock assessment committee, which concluded that the harvest still exceeded production (ASMFC 2006b). Since May 2008 there has been a moratorium on the harvest of female horseshoe crabs in Delaware, and a moratorium on the harvest of all horseshoe crabs in New Jersey.

Abundant horseshoe crab eggs are a particularly valuable food resource for time-stressed, long-distant migrants, including red knot, ruddy turnstone, and sanderling (Tsipoura and Burger 1999), as they are easily digested and metabolized into fat and protein (Castro and Myers 1993, Haramis et al. 2007). The digestive organs of knots arriving after a direct flight from South America are reduced in size (Piersma and Gill 1998) and are initially inadequate to support feeding on knots' usual prey—hard-shelled bivalves (e.g., *Mytilus edulis*; Niles et al. 2008). An abundant supply of soft, easily digested, energy-rich horseshoe crab eggs allows birds to feed at high rates when they arrive, rebuild their organs and muscles, and achieve mass gains among the highest ever recorded in knots (Atkinson et al. 2007, Haramis et al. 2007). Consequently, the stopover duration of Delaware Bay knots is much shorter (10 to 14 days) than comparable stopovers in other parts of the world (21 to 28 days) (Piersma et al. 2005). However, a major disadvantage of this reliance on horseshoe crab eggs is that no similar, easily digested alternative food is available in the bay if the egg supply is reduced. Although some knots (particularly the Florida wintering population [Niles et al. 2006]) appear to have a different strategy and do take bivalves on the Atlantic coast of New Jersey, for the majority, switching to alternative prey does not seem to be an option. Knots migrating long distances from Tierra del Fuego would have to arrive earlier and stay longer in Delaware Bay to refuel adequately and depart on time, as there is only a short time window for successful breeding in the Arctic.

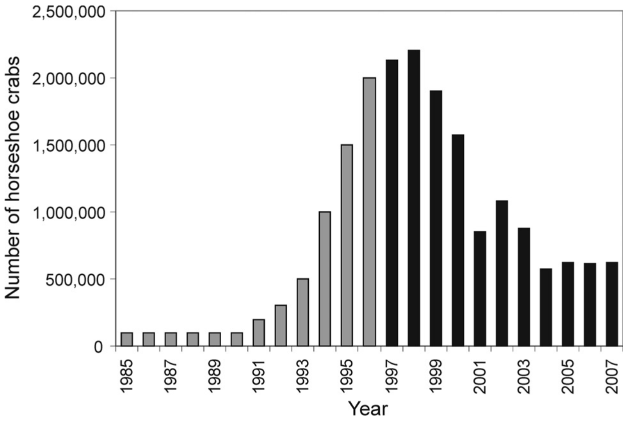

Figure 2. Harvest of horseshoe crabs reported by mid-Atlantic states. Gray bars represent the estimated harvest, according to interviews with state marine fish biologists from Delaware and New Jersey (reliable harvest reports are not available for years prior to 1997). Black bars represent the sum of the harvest reported to the Atlantic States Marine Fisheries Commission by New Jersey, Delaware, Maryland, Virginia, and New York.

Box 1. "Green Eggs and Sand": A Resource for Teachers.

The conflict between fishermen using horseshoe crabs as bait and conservationists demanding a healthy shorebird stopover mirrors other conflicts around the United States over multiple uses of resources: the spotted owl and forest products industry, wolves and sport hunters in Alaska, and Pacific salmon and water resources in the Pacific Northwest. A teachers' curriculum program called "Green Eggs and Sand" takes advantage of the controversy on the Delaware Bay to provide teachers with a window into the complexities of resource conflicts and the methods used to resolve them. Working with biologists, the program creators designed a curriculum guide to help middle-school and high-school teachers learn of the complex life history of each animal and their interrelationships. Then they focus on how fishery management decisions are made, the resource-use conflict, and the difficulties of resolution. They conclude with a discussion of similarly contentious issues throughout the country. For more on this program, contact Cindy Etgen at *www.dnr.state.md.us/education/are/ges.html.*

Horseshoe crabs lay eggs 15 to 20 centimeters (cm) below the beach surface (Botton et al. 1994), a depth that is inaccessible to shorebirds. Eggs become available to shorebirds in two ways. If the density of spawning horseshoe crabs is high, individual females unearth existing egg masses when laying their own eggs, bringing eggs to the surface, where they are available to shorebirds. Eggs are also brought to the surface by wave action, which loosens sand and eggs (Botton et al. 1994, Smith 2007). Without a large population of horseshoe crabs, most eggs remain buried and unavailable to shorebirds. Eggs brought to the surface are lost to horseshoe crab recruitment even if they are not eaten by shorebirds because they quickly desiccate and die. As early as 1997, concern over the increased horseshoe crab harvest and its effect on the Delaware Bay stopover prompted intensive shorebird studies; researchers used cannon-net capture to monitor mass gain and individually marked birds to estimate annual survival. Such studies have focused particularly on red knots, ruddy turnstones, and sanderlings; however, it is the red knot that has been the cause for most concern. Red knots that stop over in Delaware Bay belong to separate populations that breed in the central Canadian Arctic and winter in Tierra del Fuego, northern Brazil, and Florida. Tierra del Fuego knots belong to the *rufa* subspecies, one of six red knot subspecies that together have a circumpolar Arctic breeding distribution. The taxonomy of the other two populations is currently under investigation, but they are also believed to be *rufa.* The knots that use Delaware Bay and the populations in all three wintering areas have suffered a major collapse (Morrison et al. 2004, Niles et al. 2008).

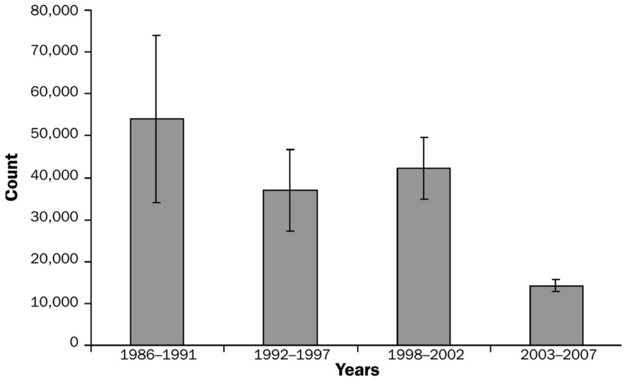

Figure 3. Mean peak counts of red knots observed on aerial surveys of Delaware Bay 1986–2007 in five- to six-year periods (bars are ±95% confidence intervals).

Rufa is listed as endangered under the Bonn Convention and is proposed for endangered status in Brazil (Niles et al. 2008). In April 2007, the US Fish and Wildlife Service determined that *rufa* warranted "threatened" listing under the Endangered Species Act (50 C.F.R. 17), but chose not to list it because of insufficient staff and fiscal resources, as well as the lower priority of *rufa* relative to other candidate species. In April 2007, the Committee on the Status of Endangered Wildlife in Canada classified the southern wintering population of *rufa* as endangered and the north Brazil (Maranhão) and Florida populations as threatened (COSEWIC 2007).

In this article we review more than a decade of studies of red knots, horseshoe crabs, and horseshoe crab eggs in Delaware Bay. We ask whether, after nine years of reduced horseshoe crab harvest, conditions for knots in Delaware Bay have improved. We suggest a recovery paradigm—a series of assumptions about how the recovery of horseshoe crabs and knots can be accomplished—and propose recovery parameters that should be monitored to ensure that recovery proceeds as anticipated. Finally, we describe current monitoring programs, particularly of shorebirds in Delaware

Bay, and show that with minor modification, they can provide information needed to monitor the recovery process. We believe the horseshoe crab–red knot conservation issue provides an excellent opportunity to employ an adaptive management approach (Williams et al. 2001) and stress those principles throughout. We also believe that new initiatives are needed to ensure the sustainability of the horseshoe crab harvest.

Horseshoe crabs: Trends in population size and the density of their eggs

Several surveys during the past 20 years (ASMFC 2004) of adult horseshoe crabs in Delaware Bay have led to various analyses, but all show similar results (ASMFC 2005, 2006a, Botton et al. 2003, Carmichael et al. 2003, Hata and Berkson 2003, 2004, Swan 2005, Smith and Michels 2006, Smith et al. 2006, Smith 2007, Sweka et al. 2007). To illustrate the population trend, we use standardized data collected since 1990 by Delaware Division of Fish and Wildlife. A 30-foot trawl net was towed for 20 minutes (covering about 2 km), once per month from March to December, on each of nine transects across the Delaware side of the bay. As the location of tows has varied, we treated the annual totals as independent estimates obtained using stratified random sampling. This survey was criticized in an ASMFC peer review in 1998 (ASMFC 1998) because, as a finfish survey, it was not designed specifically for horseshoe crabs. However, it is the only reliable long-term survey of horseshoe crab numbers in Delaware Bay. The peer review also suggested a new offshore trawl survey, which began in 2000; we report on that survey in this article.

The Delaware 30-foot trawl surveys showed a decline of 88% ($r^2 = 0.76$, $p < 0.001$) in the mean number of crabs caught per transect during the period 1990–2005 (figure 4). In 2006 and 2007, the catch increased to a level similar to that of the late 1990s, but those figures are still much lower than the levels of the early 1990s. It takes 10 years for horseshoe crabs to become sexually mature (Schuster and Sekiguchi 2003), so the declines shown by the trawl surveys may well be the result of growing harvests in the early and mid-1990s, with the increase in 2006 and 2007 a consequence of harvest restrictions that began in 1998. Therefore, a recovery of adult horseshoe crabs may be under way.

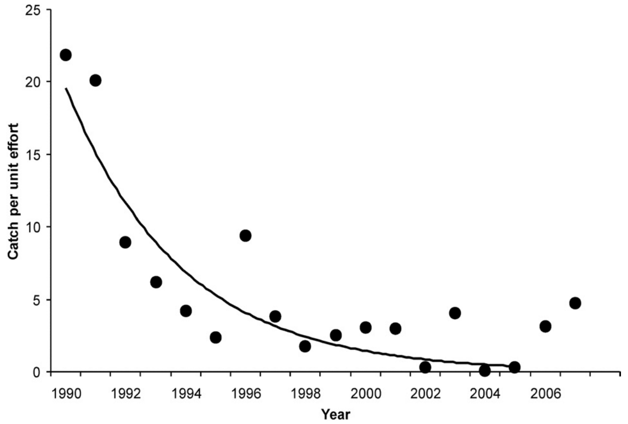

Figure 4. Number of adult horseshoe crabs caught on standardized surveys in Delaware Bay conducted by the Delaware Division of Fish and Wildlife. An exponential curve is fitted to the years 1990–2005.

Two other surveys can be used to assess whether an increase in horseshoe crab numbers started in 2006. Hata (2008) reported results from trawl surveys conducted since 2002 in the ocean off Delaware Bay; these surveys measured primiparous (prebreeding adult) and multiparous (breeding adult) horseshoe crabs. The mean catch was 35.0 in 2005, 65.1 in 2006, and 77.0 in 2007, indicating an approximate twofold increase from 2005 to 2006–2007. Counts of spawning crabs have been made since 1999 on Delaware Bay beaches (Michels et al. 2008). Between 2005 and 2007, the mean number of males per square meter (m^2) increased from 3.23 (standard error [SE] 0.29) in 2005 to 3.99 (SE 0.33) in 2006 to 4.22 (SE 0.38) in 2007, but the mean number of females per m^2 showed little change: 0.82 (SE 0.07) to 0.99 (0.07) to 0.89 (0.07), respectively. In summary, recovery may be starting, but considering the long period of sexual maturation, results from more years of surveying are needed to measure the strength and persistence of this trend.

Surveys suggest a decrease in egg numbers similar in magnitude to the approximately 90% decline in adult horseshoe crabs shown by the Delaware 30-foot trawl survey. In 1991 and 1992 in Delaware Bay, Botton and colleagues (1994) estimated the density of eggs in the upper 5 cm of sediments (available to shorebirds) of six beaches selected to cover a range of conditions (e.g., habitat composition, disturbance). Average densities per m^2 ranged from 3125 to 721,354 (mean 226,562). An annual egg-density monitoring program that began in 1996 used varying survey methods in its first four years. Since 2000, samples have been taken on six beaches at 3-meter (m) intervals between the high- and low-tide lines (the areas in which knots forage) between two and six times during May and June. We estimate the trend in egg density by assuming that in 1990 and 1991, it equaled the mean of the values reported by Botton and colleagues (1994)—226,562—and that it then dropped to the level reported in 1996 (figure 5). Results since 1996 have shown no significant trend (slope = –0.00005, $p > 0.5$). The mean density during this period was 3406, a decline of about 98% from the estimated density in the early 1990s. This estimate of the scale of decline should be viewed with caution because of the small sample size and substantial variation in density in the early years, but it is clear that egg density has declined very substantially (> 90%) as the numbers of crabs have declined. In view of the evidence that spawning female horseshoe crabs have not increased in number, it is not surprising that as of 2007, there has been no sign of an increase in egg density. However, if horseshoe crab populations are recovering, as suggested by trawl surveys, egg densities should begin to improve within the next few years.

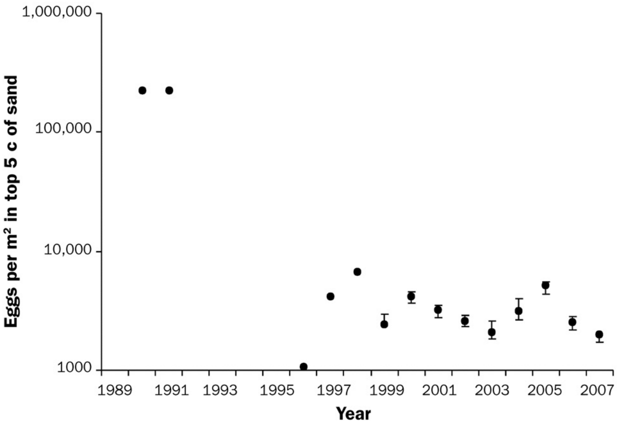

Figure 5. Estimated density of horseshoe crab eggs (eggs per square meter in the top 5 centimeters of sand) on Delaware Bay beaches. Data for 1990–1991 are from Botton and colleagues (1994). The y-axis is log scale, and the bars are ±1 standard error. Data on variation are not available for 1990–1991 or 1996–1999, so error bars cannot be shown.

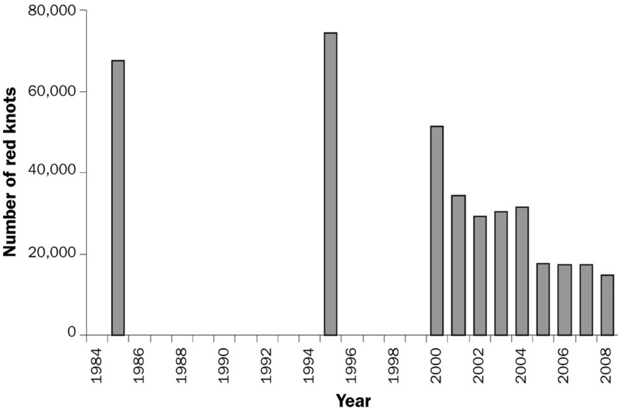

Figure 6. Number of red knots counted during surveys of their wintering grounds in southern South America, 1985 and 2000–2008, and estimated using capture-recapture methods in 1995 (González et al. 2004).

Red knots: Trends in population size

The best information about trends in the number of *rufa* knots is from surveys on wintering grounds. Historically, most *rufa* wintered in southern South America from Tierra del Fuego north to Río Colorado in Patagonia (Morrison and Ross 1989, Morrison et al. 2004, Baker et al. 2005a). Estimates of wintering numbers there were made in 1985 using aerial surveys (Morrison and Ross 1989), in 1995 using capture-recapture methods (González et al. 2004), and annually since 2000 using aerial surveys (Niles et al. 2008). Because aerial surveys are treated as complete counts, statistical analysis is not necessary, but estimation errors may occur if flocks are missed or their numbers over- or underestimated. Consistency of method and timing keeps such errors to a minimum.

The population size was about the same in 1985 and 2000, but it dropped rapidly thereafter (figure 6). Numbers in 1985 and 2008 were 67,546 and 14,800, respectively, indicating a decline of 78%. Baker and colleagues (2004) concluded that the Tierra del Fuego population fell by almost 50% between 2000 and 2002 because adult survival declined from an average of 85% for 1994–1995 through 1997–1998 to 56% for 1998–1999 through 2000–2001, and recruitment into the second-year cohort declined by 47%. After briefly stabilizing at 25,000 to 30,000 birds between 2002 and 2004, the population again plunged to between 17,000 and 18,000 in 2005–2007 and then to 14,800 in 2008 (COSEWIC 2007, Niles et al. 2008).

Smaller numbers of knots winter in northern Brazil at Maranhão and in the southeastern United States, mainly Florida. Surveys of Maranhão revealed 8324 birds in 1985 (Morrison and Ross 1989), 7575 in 2005 (Baker et al. 2005b), and about 3000 in 2006 (Niles et al. 2008).

Knots wintering in the southeastern United States, particularly on the Florida gulf coast, have not been surveyed systematically. Niles and colleagues (2008) suggested that the historic population might have been 7500 to 10,000 birds, but emphasized uncertainty about the true number. In Florida, the highest counts during winter were 5000 in 1978, 6500 in 1979, between 4000 and 5000 in 2004, and 2142 in 2006 (Niles et al. 2006). In 2006, 4569 knots were counted in a sample winter survey of southeastern United States (Niles et al. 2006). The number of knots seen in Georgia in winter has varied from hundreds to nearly 5000, but there are insufficient data for trend estimation. Even smaller numbers are reported during winter from South Carolina and farther north and from Texas.

Since 1986, four to six weekly aerial surveys of shorebirds have been conducted in Delaware Bay during northward migration in May and early June. The survey covers most bay beaches used by knots, but not the Atlantic Coast at New Jersey, where small numbers can be found foraging; therefore, it does not record total numbers but provides an index of stopover population size. Peak aerial counts (figure 3) show a sharp decline from 1998–2002 to 2003–2007, and the 2007 peak (12,375) was the lowest ever recorded.

Red knots: Trends in weight gain

Since 1997, red knots have been captured, banded, and weighed, and sometimes recaptured in the same year during spring migration in Delaware Bay. The main spring stopover period lasts from the beginning of May until the first week of June, though small numbers of birds may arrive earlier or stay later. Peak numbers usually occur during 14–28 May, after which time the majority of red knots have departed Delaware Bay for the Arctic. We have insufficient data to show how knot weights have varied in the earliest part of the stopover, before 14 May. During 14–20 May, when the majority of birds arrive, their weights have shown considerable year-to-year variation (probably a reflection of differences in arrival dates and arrival weights), but there has been no significant long-term trend (figure 7a). However, during 21–27 May, and 28 May to 3 June, when most birds depart, weights have shown a quadratic relationship with year, declining strongly in the early years, and then flattening out (figure 7a, 7b). Similarly, the proportion of knots weighing 180 grams (g) by 26–28 May, the main departure period, dropped significantly from between 0.6 and 0.8 g in 1997–1998 to between 0.14 and 0.4 g in 2006–2007 (figure 8). The decline in weight late in the stopover period could result from a trend for birds to arrive later or from slower weight gain because of reduced food supplies. Although some birds arrive late every year, there is no evidence (e.g., from aerial counts) of a systematic trend toward later arrival. Analysis of within-year recaptures of knots in Delaware Bay (1998–2005) by Atkinson and colleagues (2007) showed that early arrivals increase mass at approximately 4 g per day, but arrivals later in May can achieve mass gains two to three times higher, thereby making up for lost time. However, this relationship broke down in 2003 and 2005 when birds arriving later in May failed to make high rates of mass gain because of inadequate food supplies. This study indicates that birds arriving later in the stopover period require a superabundant supply of horseshoe crab eggs because they have less time than earlier arrivals to gain sufficient weight to fly to Arctic breeding grounds, survive adverse weather or low food resources, and breed successfully. Knots at a low weight in Delaware Bay, controlling for date, have significantly lower survival than heavier birds (Baker et al. 2004). Therefore, it is likely that the main reason for the decline of the red knot population is reduced availability of horseshoe crab eggs, their primary food resource on Delaware Bay.

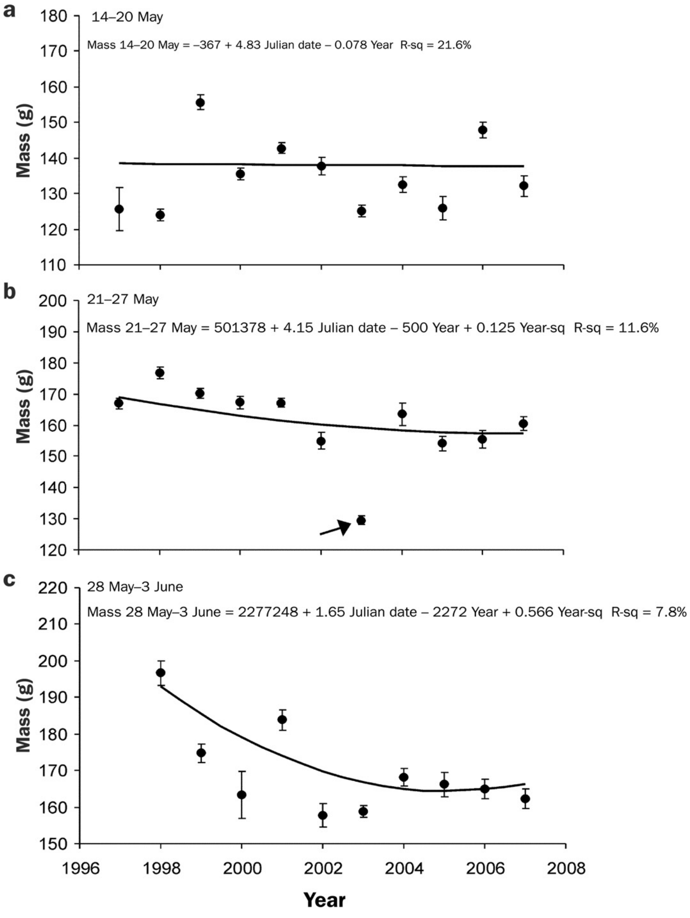

Figure 7. Mass (in grams) of red knots in Delaware Bay during three weeks of their spring stopover: (a) 14–20 May, (b) 21–27 May, and (c) 28 May–3 June, plotted against year. Trend lines are those predicted by the equations using the dataset means for the Julian date. All predictors in each equation are significant at $p \leq 0.001$ *except for year in the equation for 14–20 May, which is nonsignificant (*$p = 0.53$*). The equation for 21–27 May does not include the data for 2003 (marked by the arrow), which was an atypical year when large numbers of red knots arrived late, leading to very low weights in the latter part of the normal stopover period. Bars are ±95% confidence intervals.*

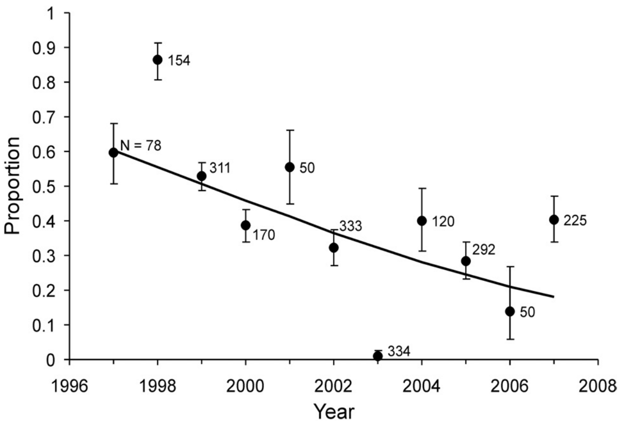

Figure 8. Proportions of red knots with 95% confidence intervals in the more than 180 gram (g) body-mass category in Delaware Bay near the departure time each year (26–28 May) over 1997–2007. Numbers are total birds sampled. The trend was fitted using binary logistic regression of body mass greater than 180 g (1 = yes, 0 = no) on year (continuous independent variable), with sigma-restricted parameterization where the year coefficient = –0.194, standard error = 0.015, and $p < 0.001$.

Botton and colleagues (2003) reviewed the synchrony of horseshoe crab breeding and the timing of shorebird migration. They pointed out that variations in the peak period of horseshoe crab spawning, caused by yearly variations in water temperature, can further contribute to inadequate mass gains in shorebirds if peak spawning occurs before birds arrive or after they depart. They also noted that peak spawning periods have narrowed as the horseshoe crab population has decreased.

Trends in other shorebird species

Several other shorebird species forage on horseshoe crab eggs in Delaware Bay during spring migration. Between 1998 and 2007, all of these species showed declines; those for ruddy turnstone were large and highly significant (table 1). Excluding red knot, shorebirds overall declined by an average of 50% during the period 1998–2007. For several species, the declines were large in absolute terms (table 1). The peak count of shorebird species other than red knot declined by a combined total of more than 14,000 birds per year; ruddy turnstones alone declined by 8145 per year.

Table 1. Trends in the number of shorebirds recorded from aerial surveys of Delaware Bay beaches, 1998–2007.

	Species					
Variable	**Ruddy turnstone**	**Semipalmated sandpiper**	**Sanderling**	**Short-billed dowitcher**	**Dunlin**	**All**
Slope	–8145	–3017	–1039	–849	–1057	–14,106
P value	0.001	0.545	0.102	0.097	0.424	0.071
Decline	77%	28%	48%	64%	29%	50%

Worldwide, similar declines in Arctic-breeding shorebirds have been reported in flyways where food resources have been depleted or habitat lost at the last major stopover before the flight to the Arctic. Among the causes of food depletion is mechanical shellfish harvesting in the Wadden Sea of northwestern Europe (Piersma 2007), and intertidal habitat has been lost to reclamation around the shores of the Yellow Sea in East Asia (Barter 2002, Moores 2006).

Summary

In the past eight years, horseshoe crabs and their eggs in Delaware Bay have declined to the extent that critical food resources for migrant red knots and other shorebirds are not sufficient to provide the nutrition needed to enable birds to continue migration and reach the Arctic in good enough condition to survive and breed successfully (table 2; Baker et al. 2004, Niles et al. 2008). Since 2000, despite a reduced horseshoe crab harvest, neither the horseshoe crab population nor egg densities have rebounded (adult horseshoe crab numbers, however, may be starting to rise). Horseshoe crabs take 10 years to reach sexual maturity, so recovery rates are likely to be slow. Not surprisingly, knot populations may still be declining. If listing the red knot is to be avoided, and its recovery is desired, we suggest that harvests be reduced further until horseshoe crab numbers, horseshoe crab egg densities, and red knot numbers recover to 1990 levels.

Table 2. Summary of changes in horseshoe crab and red knot populations, 1980–2007.

Decade	Major changes
1980–1989	Horseshoe crab harvest probably at low to moderate levels; high horseshoe crab and red knot populations.
1990–1999	High horseshoe crab harvest; horseshoe crab populations and horseshoe crab eggs decline by at least 80%; red knots and red knot weights begin to decline by the late 1990s.
2000–2007	Horseshoe crab harvest is reduced by the ASMFC through four addendums to the original management plan. Despite reductions and additional cuts made by New Jersey and Delaware, including a moratorium on harvest in New Jersey, the total harvest remained higher than estimated in the 1980s; horseshoe crab population stable at a low level; red knot population size and departure weights decline sharply; *rufa* red knots are recognized as threatened under the Bonn Convention and in Brazil, Canada, and the United States.

Bringing the bay back: A recovery strategy for horseshoe crabs and red knots

The evidence outlined above leads to a strong inference about the primary reason *rufa* knots have declined: greater harvest of crabs led to a sharp reduction in horseshoe crab eggs available to shorebirds. The decline in egg densities coincided with a decline in departure weights of knots, and resulted in lower annual survival of adults and reduced recruitment of juveniles. Reduced overwinter survival or mortality during migration could potentially be secondary factors exacerbating the decline of knots. Annual survival has not yet been partitioned into these seasonal components, but rare mortalities, such as the loss of 312 adults (and possibly 1000 more) migrating through Uruguay in April 2007 (Niles et al. 2008), have been recorded. Nevertheless, major population declines have occurred after the birds departed Delaware Bay (Baker et al. 2004), and only following years when feeding conditions in the bay were poor. Thus there can be no doubt that the Delaware Bay food supply has played a critical role in *rufa*'s decline.

The following paradigm provides a rationale for *rufa* recovery. To restore the population, adult survival and recruitment of juvenile birds need to improve. To achieve this goal, the number of birds reaching threshold departure weights of 180 g in Delaware Bay needs to increase; this requires greater egg densities during the migration stopover period. Therefore, horseshoe crab populations need to grow, which requires low harvests until they rebound to former levels. The recovery plan could be set out (figure 9) in terms of a target for the *rufa* population (goal); targets for adult survival; juvenile recruitment and proportion of knots reaching adequate departure weight in Delaware Bay (objectives); and targets for egg densities, horseshoe crab populations, and number of horseshoe crabs harvested (strategies). We now suggest quantitative criteria and standards (targets) for the goals, objectives, and strategies. All are intended to achieve our recovery vision of "healthy, economically important horseshoe crab and red knot populations" (figure 9). Formulation of the recovery plan is an ideal opportunity to apply the principles of adaptive management (Williams et al. 2001), the iterative decisionmaking process that reduces uncertainty of management decisions by informing future actions through system monitoring. Adaptive management, or adaptive resource management (ARM), can be characterized as "learning by doing," and has been used throughout the field of resource management, most recently and successfully in the management of waterfowl (Nichols et al. 2007). In 2007, ASMFC authorized both their horseshoe crab and shorebird technical groups to initiate an ARM project on horseshoe crabs and shorebirds. Here we propose specific actions and identify their expected consequences to help inform the ARM process.

Vision: Healthy, economically important, horseshoe crab and red knot populations

Stage	Description	Criterion	Standard (target)
Goal	*Rufa* red knot populations	Number of birds in winter	80,000 birds
	↑		
Objectives	Survivor rate	Annual adult survival rate	80%
	↑		
	Adult weight	Body weight upon departure from Delaware Bay	180 grams (60% of birds)
	↑		
Strategies	Horseshoe crab eggs	Density (top 5 centimeters)	50,000 per square meter (50% of suitable habitat)
	↑		
	Horseshoe crab adults	Number per trawl in Delaware Bay	15 (or equivalent from other surveys)
	↑		
	Horseshoe crab harvest	Harvest within 80 kilometers of Delaware Bay	To be determined by industry

Figure 9. Vision, goal, objectives, and strategies for recovering horseshoe crabs and rufa *red knots. The arrows represent the progression of recovery and numeric targets that characterize it: for example, increased horseshoe crabs and egg densities (strategies) lead to increases in red knot departure weight and survival (objectives), leading to recovery of the red knot population (goal).*

As these actions are taken, monitoring will reveal whether anticipated effects occur and will provide evidence to revise the recovery model as needed.

Recovery goals. The goal is a "restored" *rufa* population. Niles and colleagues (2008) proposed that rebuilding the *rufa* population to the 1980 level, estimated at 100,000 to 150,000 birds by Morrison and Harrington (1992), was a reasonable conservation goal. It is usual to establish recovery targets (conditions that would warrant delisting) that are smaller than the former or ideal population level, especially when the size of the historical population is uncertain. If we take the lower bound of the 100,000-to-150,000 range as a conservative estimate of the historical population, a recovery target of 80,000 seems reasonable. More specifically, we suggest two conditions for considering that *rufa* knots are recovered: (1) the population is consistently above 80,000, and (2) threats to the population have been rigorously assessed and no factors are known that would be likely to cause a reduction to below 80,000.

Recovery objectives. Objectives include increasing adult survival and Delaware Bay departure weights. As noted above, Baker and colleagues (2004) showed that annual survival rates of adult *rufa* were about 85% in the late 1990s, which is very similar to the 85.8% reported by Boyd and Piersma (2001) for *islandica* knots (which breed in northeastern Canada and winter in Europe) during 1985–1995 when their population was stable. To be conservative, we suggest an initial target for adult survival of 80%.

Baker and colleagues (2004) showed that annual survival was related to Delaware Bay departure weight, and departure condition was also shown to be significantly linked to survival in *islandica* knots departing from their final spring stopover area in Iceland (Morrison et al. 2007). Survival appeared to become asymptotic at a departure weight of about 180 g, which has been cited as a "healthy" departure weight (e.g., Niles et al. 2008). Since 1997–1998, the proportion of birds weighing at least 180 g at the end of the stopover has decreased from between 0.6 and 0.8 g to between 0.14 and 0.4 g (figure 8). We therefore propose that the weight target be at least 180 g for 60% of the birds when they leave Delaware Bay for their Arctic breeding grounds.

Recovery strategies. Strategies include increasing the density of horseshoe crabs and their eggs and maintaining a reduced horseshoe crab harvest. Defining egg density targets requires specification of an area and a minimum egg density within the area. Niles and colleagues (2008) identified bay beaches that historically provided "optimal" and "suitable" feeding conditions for knots, categories that apply to about half the bay beaches. We suggest using these areas in defining the target for horseshoe crab eggs. Work by Botton and colleagues (1994) suggests that egg densities in good habitats, before crabs declined in the 1990s, sometimes (in two of seven beaches studied) exceeded 200,000 eggs per m^2 in the top 5 cm of sand. This density, however, may have been more than sufficient for knots and other species that feed on the eggs. For example, Botton and colleagues (1994) estimated that the entire shorebird population might be sustained on a density of 44,000 eggs per m^2 in the top 5 cm of sand. We therefore propose that 50,000 eggs per m^2 in the top 5 cm is a reasonable initial target. Achieving this goal on all beaches is probably not realistic, however, because suitability for spawning has been determined only remotely (Niles et al. 2008). Achieving the target density on 50% of the beaches in each state seems reasonable as an initial goal until the relationships between horseshoe crab egg densities, beach conditions, and depletion of eggs by shorebirds are better understood. Our targets may have to be adjusted in the light of future studies, including those evaluating the impact of gulls, which also consume numerous eggs (Burger et al. 2004).

The number of horseshoe crabs needed to produce the target egg density is also difficult to estimate. The best approach is probably to express the target in terms of the catch on standardized surveys. Although the Delaware 30-foot trawl was designed for finfish, it is the only survey of horseshoe crabs that was made before the decline of the horseshoe crab population, and thus it is the most informative benchmark. We suggest that a sustained mean catch of 15 to 20 horseshoe crabs per tow is a reasonable target because it is similar to numbers obtained in 1990 and 1991 (figure 4). However, the number of horseshoe crabs and the estimated harvest that can be sustained are now the focus of a new effort by the ASMFC; the US Fish and Wildlife Service; and the states of New Jersey, Delaware, Maryland, and Virginia. This joint effort, being carried out by shorebird and horseshoe crab biologists, will use all available information to create a new quantitative model whose chief aim is to estimate harvests that allow sufficient eggs for migratory shorebirds. This joint committee will be responsible, then, for estimating suitable horseshoe crab densities and harvests. However, it may well take several years before the model is accepted within the regulatory framework of the ASMFC and its recommendations implemented.

The recovery of the Delaware Bay shorebird stopover, and particularly the red knot population, depends on the recovery of the horseshoe crab population. Therefore, a conservative strategy—a small harvest or no harvest—would be a wise approach until it is clear that horseshoe crab populations are recovering and likely to reach the target.

Secondary recovery parameters. Although our recovery paradigm may appear reasonable, there is no guarantee that it covers all actions needed to restore horseshoe crab and red knot populations. For example, problems for knots might occur on their breeding or wintering grounds or elsewhere on their migration route, or Delaware Bay may become unsuitable for some other reason. So in addition to the primary recovery parameters identified above, certain secondary recovery parameters need to be monitored. The following are three parameters that seem particularly important:

1. The proportion of the red knot population that uses Delaware Bay. A minority of knots has always stopped over in spring at other sites on the eastern coast of the United States, but recent information suggests that more red knots may be bypassing Delaware Bay than did in the past. This could reflect improved conditions at other sites as well as poorer conditions in the bay. Nevertheless, the proportion of the population that visits the bay is a key parameter for assessing its recovery.

2. Productivity. Annual production of juvenile knots might possibly be measured in late summer at a series of sites used during southward migration. A productivity index might be defined by using either the young-to-adult ratio or the number of young passing through each location. This approach is fraught with problems, however, as adults and juveniles generally migrate at different times and may winter in different areas. A better method might be to monitor the ratio between adults and second-year birds that winter together.

3. Recruitment into the breeding population. Another means of measuring recruitment is to monitor the birds migrating north for the first time through Delaware Bay. This would assess the number of new adults by comparing estimates of the size and survival of the previous year's adult population with the total number stopping over in Delaware Bay in the current year.

Monitoring recovery

Here we briefly describe ways to monitor primary and secondary recovery parameters. Detailed methods, such as sample size and power estimates, will be reported elsewhere. Our goal here is to show that a rigorous program, at a reasonable cost, is feasible. We hope this will encourage the many groups working on knots and crabs to coordinate their efforts to achieve these accuracy targets and monitor progress.

Monitoring *rufa* population size. Monitoring *rufa* population size is best done by counting birds on their wintering grounds. Aerial surveys already cover Tierra del Fuego, the most important area. The only sources of error are missing locations with birds, conducting surveys before all birds have arrived or after some have left, or counting errors. Careful evaluation of these factors is needed, but at present it appears that accurate counts can be made in Tierra del Fuego. Aerial surveys are required every year to monitor ongoing status and to determine when population changes occur, making it possible to discern which factors are driving population change and whether conservation measures are effective.

Much better information is needed from Brazil and the southeastern United States. Given the relative ease with which *rufa* could be counted in Florida and Georgia (compared with other wintering areas), and their status as a threatened species, obtaining accurate counts from these areas should be given particularly high priority.

Monitoring *rufa* survival rates. A major research and monitoring program focused on migrant shorebirds has been under way in Delaware Bay for many years. Since 1997, about 700 knots have been captured annually, along with similar numbers of ruddy turnstones and sanderlings. Each year, several thousand resightings are recorded of each species, making this program one of the most intensive for any migratory wildlife species.

Annual adult survival rates may be estimated from between-year recaptures and resightings of marked birds. Not all *rufa* knots pass through Delaware Bay, and at least a few visit the bay in some years but not in others. Therefore, survival rates for the *rufa* population as a whole can be estimated reliably only if they are based on data from throughout the flyway. Additionally, it is also important to monitor the annual survival of each wintering population separately because each faces differing conditions.

Monitoring *rufa* weights. This study has demonstrated the value of determining the status and condition of individual birds by monitoring their weights. It also affords one means of assessing the general state of environmental conditions in

Delaware Bay. Therefore, it is important to continue monitoring the weights of red knots, as well as those of ruddy turnstones and sanderlings, every three or four days from 14 May to 3 June, as done in the past.

Delaware Bay departure weights can be estimated using capture and within-year recapture data (Atkinson et al. 2007). The model can be refined through time (on the assumption that each version provides essentially unbiased estimates). Within each year, capture and resighting data can be used to estimate arrival and departure times for samples of birds. These data can be used along with weight at capture and the model to estimate the departure weight for each bird. This analysis would permit estimation of the proportion of birds weighing more than 180 g when they leave the bay. To corroborate this estimate and to provide backup in case within-year recaptures are insufficient for estimation, the proportion of birds weighing more than 180 g during 26–28 May should be monitored routinely (see figure 8), though this may not reflect the success of the stopover if migration phenology changes for some reason—for example, because of the effects of global warming.

Monitoring horseshoe crab parameters. Studies cited above measure horseshoe crab abundance, egg densities, and harvest rates (Botton et al. 1994, Smith 2007, Hata 2008, Michels et al. 2008). Egg densities in surface sediments are ephemeral. Even without wind-induced waves, eggs in the top 5 cm of sediment are readily entrained by small waves as they wash across a beach; then, as the tide recedes, eggs may be left exposed on low-tide flats or in the high-tide wrack line. Exposed eggs quickly desiccate. Thus, samples of surface-sediment eggs from beaches are very variable across time and space, so accurate estimation requires frequent sampling—possibly more frequent than currently practiced—and perhaps a model-based estimation approach. The best sampling plan and sample size needed for that plan therefore warrant more attention.

Monitoring secondary recovery parameters. Given estimates of *rufa* population size from the winter surveys, the proportion of the birds using Delaware Bay can be estimated as follows: The survey period (L days) must be long enough so that all birds visiting the bay are present sometime during the period (though some may arrive before or leave later). We assume that the aerial surveys are a systematic sample from this period and yield an unbiased estimate of the number of birds present at the time of the flight. Under these assumptions, it may be shown that $L\bar{x}/\bar{t}$ is an essentially unbiased estimate of the number of knots visiting the bay, where $\bar{x}$ is the mean number of knots recorded per survey and $\bar{t}$ is the average number of days that knots are in the study area during the survey period, estimated from resighting surveys.

Monitoring productivity by reference to the number or proportion of juveniles during southward migration is very difficult because, mainly, they migrate separately. Moreover, that method does not allow us to estimate the productivity of each of the wintering populations (which may have distinct breeding distributions). Juveniles and adults of the Tierra del Fuego population winter in different places, and this may also apply to the wintering populations of Florida and Maranhão. Thus, the only practical means of measuring productivity in each population is by reference to the ratio between adult and second-year birds that winter together.

Recruitment can be measured by partitioning change in population size into recruitment and adult survival rates. Let Y_i be population size in year *i.* We may express change in population size between two years as

$$\frac{Y_{i+1}}{Y_i} = \frac{Y_iS_i + A_{i+1}}{Y_i} = S_i + R_i \qquad (1)$$

where S_i is the proportion of the Y_i birds that survive until the next May, A_{i+1} is the number of birds first appearing in Delaware Bay (i.e., "additions") in year $i + 1$, and R_i is recruitment in year *i.* S_i may be estimated from between-year captures and resightings. R_i may be estimated as

$$r_i = \left(\hat{Y}_{i+1}/\hat{Y}\right)_i - s_i$$

where s_i is the estimator of S_i. The estimates of productivity can also be used to improve the estimate of recruitment.

Estimating these parameters for a dispersed, long-distance migrant is daunting, and there are few other widespread, threatened species for which such data are available. But as shown above, programs have been running for several years that, with minor changes, will enable us to estimate all of the parameters. The results will provide a nearly unprecedented opportunity to monitor the vital statistics of *rufa* and horseshoe crabs and to determine progress in relation to recovery goals. It is critical that these programs be continued, refined, and placed on a sound institutional basis.

Concluding remarks

Our analysis shows that the best chance for halting and reversing the decline of the red knot would be through restoration of horseshoe crabs and their eggs to levels prevailing in the early 1990s. As numerous ASMFC reports have demonstrated, the horseshoe crab harvests of the 1990s were not sustainable, nor were the lower harvests of later periods, because the population continued to decline. By restoring the horseshoe crab population to a level that produces egg densities similar to those of the early 1990s, Delaware Bay could once again provide critical food resources to knots and other migrant shorebirds, as well as a sustainable harvest of crabs.

The horseshoe crab–red knot issue highlights the disparity that exists between our ability to monitor, manage, and conserve terrestrial and marine animals. For red knots, we know almost exactly the size of their population and can monitor annual survival to an accuracy of just a few percentage points. In contrast, there is great uncertainty about the size of the horseshoe crab population, the numbers that can be harvested without adverse impact, and the number of horseshoe crabs necessary to support migratory shorebird populations. According to the latest (2003) estimate, the Delaware Bay horseshoe crab population numbers 20 million; however, this estimate is based on only 48 recaptures out of 17,543 marked individuals, so the 90% confidence intervals are large (13 million to 28 million) (Smith et al. 2006). Moreover, the debate about the size of the harvest that should be permitted has been bedeviled by a lack of understanding of what the population can stand. Conservationists have argued for a complete cessation of harvest as the most responsible risk-averse approach; regulatory authorities have acted to reduce the harvest but without any real understanding of what it should be. On the basis of data up to 2005, the Horseshoe Crab Stock Assessment Subcommittee of the ASMFC concluded that "the current harvest appears to be in excess of the maximum sustainable yield" (ASMFC 2006b).

Worldwide, and particularly in America, fisheries have exploited the resources of the seas with inadequate regard for sustainability; for example, the Pew Oceans Commission (2003) noted that "almost a third of US fish populations that had been studied were already overfished or being fished at unsustainable rates," concluding that "we catch too many fish, and far too quickly, for nature to replace." For horseshoe crabs and the red knots that depend on them to thrive again, we need a better understanding of how to conserve and manage the resources of the oceans.

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