Relationships Between Sandpipers and Horseshoe Crab in Delaware Bay: A Synthesis

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Abstract Recent and dramatic declines have been documented in several shorebird populations that stage in Delaware Bay during spring migration. As a result, considerable attention has been given to issues such as the reliance of sandpipers on Delaware Bay American horseshoe crab (*Limulus polyphemus*) eggs for refueling and how to best manage the horseshoe crab fishery to insure adequate resources for migratory shorebirds. In this chapter, we synthesize over 25 years of shorebird research and monitoring data in Delaware Bay to support the premise that horseshoe crab eggs are an essential element for migrating sandpipers during northbound passage through the bay. We then discuss long- and short-term trends in American horseshoe crab populations resulting from changes in demand and harvest regulations, and how this has affected shorebird population viability. Regulatory actions have led to recent increases in some demographic elements of the Delaware Bay crab population, but such changes have not yet translated into increased crab egg availability or population recovery indices in shorebirds. Because reduced availability of horseshoe crab eggs has severe consequences for migratory sandpipers at the individual and population levels, current conservation strategies that include harvest reductions on American horseshoe crabs in the Delaware Bay region must persist into the foreseeable future to insure the recovery of horseshoe crab populations and the long-term health of migratory sandpipers in Delaware Bay.

1 Introduction

Migrating animals have evolved complex and highly integrated behaviors and physiologies to overcome the considerable challenges they face during migration (Gauthreaux 1982; Berthold 1996; Dingle 1996). Birds are well known for the annual migrations, some of which are astounding marathons that carry

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individuals between the extreme ends of the earth (Baker 1978). Regardless of their journey's length or destination, individuals must stop along the migration route to rest and replenish energy stores (Moore et al. 1993).

The availability of suitable "stopover" habitats along the migration route that can provide the food resources necessary for birds to accumulate energy quickly and safely is essential to their ability to complete migration successfully (Moore et al. 1995). Destruction or degradation of a stopover habitat may compromise a bird's ability to reach its goal and for individuals migrating to the breeding grounds, this could affect nesting success and long-term population viability (Terborgh 1992; Skagen 2006). Rapid, human-induced alterations in global landscapes are having considerable consequences for migrating birds, especially those that travel long distances, because they likely encounter multiple perturbations en route to their destinations (Wilcove 2008).

Recent declines in American horseshoe crabs (*Limulus polyphemus*) have been acknowledged (Davis et al. 2006), resulting from dramatic increases in their harvest, especially in Delaware Bay. This has raised concern about the current status of horseshoe crabs, primarily because northward migrating sandpipers time their passage through Delaware Bay to coincide with major horseshoe crab spawning periods (Myers 1986). Upon arriving in the bay, sandpipers consume large quantities of crab eggs to replenish spent energy stores and prepare for their final flight to sub-Arctic- and Arctic-breeding grounds (Morrison 1984). Recent and alarming declines in some sandpiper populations that stage in the Delaware Bay during spring migration also have been documented (Morrison et al. 2001, 2006), suggesting an intrinsic and critical link between sandpiper population viability and horseshoe crab egg availability (Baker et al. 2004; Morrison et al. 2004; Niles et al. 2007).

Considerable contention has arisen regarding the extent of declines in horseshoe crab populations, the reliance of sandpipers on Delaware Bay horseshoe crab eggs, and how to best manage the horseshoe crab fishery to insure its long-term viability. In this chapter, we synthesize over 25 years of sandpiper research and monitoring data in Delaware Bay. We present results from these efforts in the context of migratory bird life history, ecology, behavior, and physiology to develop and support the premise that horseshoe crab eggs are an essential element for migrating sandpipers during passage through Delaware Bay. We then discuss recent declines in horseshoe crab egg availability in Delaware Bay and the negative consequences of these declines for migratory sandpipers at the individual and population levels.

2 Sandpiper Migration Systems

Sandpipers and their allies (Family Scolopacidae) are among the most migratory in the animal kingdom, often engaging in spectacular journeys between wintering grounds in the Southern Hemisphere and high latitude breeding areas in the Northern Hemisphere (Morrison 1984; Myers et al. 1987; Piersma and Baker 2000). Migration strategies of several species are typified by a series of non-stop, long-distance flights, each of which can be thousands of kilometers in length and take several days to complete (Morrison 1984; Wilson and Barter 1998; Battley et al. 2005; Piersma et al. 2005).

Interspersed between migration bouts are extended stopovers (Myers 1983; Cramp and Simmons 1983), which may constitute as much as 90% of the time individuals spend on the migration route (Hedenström and Alerstam 1997). During these intervening periods, individuals must accumulate energy stores, primarily as adipose tissue (Zwarts et al. 1990; Piersma and Jukema 1990; Gudmundsson et al. 1991; Hedenström and Alerstam 1998), to fuel subsequent legs of the migration, in many cases increasing their body mass 50–100% (Piersma and Jukema 1990; Piersma and Gill 1998; Battley et al. 2001; Baker et al. 2004). Rapid accumulation of energy stores is accomplished in several ways: eating more (i.e., hyperphagia), selecting diets with high lipid content, and increasing the assimilation efficiency of ingested food (Blem 1990; Stiles 1993; Bairlein and Gwinner 1994; Biebach 1996; Bairlein 1999). All of these mechanisms have been reported for migrating sandpipers (Zwarts 1990; Zwarts et al. 1990; Gudmundsson et al. 1991; Tsipoura and Burger 1999; Kvist and Lindström 2003; van Gils 2004; Battley et al. 2005).

Although adipose fat is the primary fuel for migratory flight (Ramenofsky 1990; Biebach 1996; McWilliams et al. 2004), long-distance migrants also deposit protein to build up flight muscle, heart and lung tissue that supports endurance flight (Piersma 1990; Piersma et al. 1999). Furthermore, many long-distance migrants are known to reduce the size of organs involved in metabolism (e.g., stomach, intestine, liver) just before initiating migration bouts (Jehl 1997; Piersma 1998; Piersma and Gill 1998; Biebach 1998; Piersma et al. 1999; Battley et al 2000). These must be rebuilt immediately upon arrival at a stopover or breeding site to accommodate the extensive feeding necessary to meet energy accumulation schedules (Piersma and Lindström 1997; Piersma et al. 1999).

Gudmundsson et al. (1991) suggest that Arctic-breeding sandpipers that complete migration in just a few long-distance flights punctuated by en route stopovers should adhere to a strategy that minimizes the time spent migrating (i.e., active flight and stopover periods). Timely arrival on the breeding grounds is paramount for Arctic-breeding sandpipers because of the short summer season typical of high latitudes (Drent et al. 2003). Optimal migration theory (Alerstam and Lindström 1990; Alerstam and Hedenström 1998) posits that "time-minimizing" species should select stopover sites that maximize energy intake and depart from sites when intake rates fall below what they will likely encounter at subsequent stopover locations. Frequently, time-minimizers will accumulate energy stores in excess of what is needed to reach the next stopover location (i.e., overloading) at high-quality stopover sites (i.e., those with high fuel deposition rates), allowing them to bypass low-quality sites (Gudmundsson et al. 1991; Lindström and Alerstam 1992). Overloading also may serve as insurance against sub-optimal fuel deposition conditions encountered en route. This excess accumulation can be especially important for sandpipers upon arrival on their Arctic-breeding grounds, when arthropod prey availability is low (Davidson and Evans 1989) and adverse weather conditions can cause high levels of mortality (Boyd 1992). Surplus energy stores are also used to reconstitute the metabolic and reproductive machinery reduced to facilitate migration (Farmer and Wiens 1999; Morrison and Hobson 2004; Morrison et al. 2005) and in some cases are mobilized for egg production in females (Morrison and Hobson 2004).

3 Delaware Bay: A Globally Important Sandpiper Stopover Site

The entirety of constraints faced by Arctic-breeding sandpipers during northward migrations and the intervening optimizing strategies shaping their behavior suggest that stopover site selection is a key component for successful breeding. Importantly, a disproportionately large number of sandpipers destined for Arctic-breeding grounds use a relatively small number of stopover sites (Myers 1983). These sites typically support hundreds of thousands to millions of individuals that represent hemispherically and globally significant portions of species populations (Myers et al. 1987). In North America, the most noteworthy are Gray’s Harbor and the Copper River Delta on the Pacific coast, Cheyenne Bottoms along the mid-continental flyway, and Delaware Bay on the mid-Atlantic coast (Senner and Howe 1984; Myers et al. 1987).

In the Western Atlantic, Delaware Bay is the last major stopover for several sandpiper species before flights to the breeding grounds (Myers et al. 1987), and alternative sites nearer the breeding grounds are unknown (Baker et al. 2004). Past estimates suggest that historically between 400,000 and 1,000,000 individuals passed through the bay annually during spring migration (Wander and Dunne 1981; Clark et al. 1993), although current estimates are lower (Clark personal communication). Significant proportions of the world’s Semipalmated Sandpipers (*Calidris pusilla*), Western Hemisphere’s Red Knots (*C. canutus rufa*), North America’s Ruddy Turnstones (*Arenaria interpres*), and the Atlantic coast’s Sanderlings (*C. alba*) pass through Delaware Bay during spring migration (Myers 1983; Morrison 1984).

Consequently, Delaware Bay has been designated as a hemispherically important site by the Western Hemisphere Shorebird Reserve Network, a “Wetland of International Importance” by the Ramsar Convention, and a globally significant Important Bird Area by BirdLife International. Three of the four primary species (i.e., Red Knot, Ruddy Turnstone, Sanderling) are listed as species of high conservation concern in the U.S. Shorebird Conservation Plan, while Semipalmated Sandpiper is listed as a moderate conservation concern species (Brown et al. 2001). Additionally, Red Knot is a candidate species for endangered species listing by the U.S. Fish and Wildlife Service.

4 The Importance of Horseshoe Crab Eggs to Migrating Sandpipers

Sandpipers arrive in Delaware Bay in late April through mid-May, many after completing non-stop transoceanic flights from northeastern South America (Morrison 1984), and depart from mid-May through the first week of June (Clark et al. 1993). Generally, they arrive in near-lean mass condition and deposit fuel stores over a 10–21 day stopover period (Atkinson et al. 2007; Mizrahi unpublished data).

The main attraction for sandpipers passing through Delaware Bay during spring migration appears to be the abundant and predictable eggs produced by the largest spawning population of American horseshoe crab (Shuster and Botton 1985; Myers 1986; Castro and Myers 1993; Tsipoura and Burger 1999; Gonzalez et al. 2001). Here we present several lines of ecological, physiological, and behavioral evidence that suggest an intrinsic link between migrant sandpipers and crab eggs.

4.1 Spatiotemporal Relationships

Perhaps the most obvious link is the uncanny arrival of sandpipers during the peak spawning period of horseshoe crabs (Shuster and Botton 1985; Myers 1986; Botton et al. 1988; Botton et al. 2003). Given appropriate water temperatures and tidal phase, Delaware Bay horseshoe crabs begin spawning on sandy beaches and creek mouths in late April through early May, just when the earliest arriving sandpipers are making landfall in Delaware Bay (Botton et al. 2003). As crab spawning activity increases through May, there is a coincidental increase in sandpiper numbers. In some years, spawning activity peaks as sandpipers are completing their stopover.

A second line of evidence is related to the spatial relationships between horseshoe crab eggs and sandpiper feeding areas. Egg availability within the Bay is not uniform in space or time, either within or among seasons (Botton et al. 1994; Smith et al. 2002a, 2002b), and this appears to have a direct affect on the distribution and abundance of sandpipers. Botton et al. (1994) reported that horseshoe crab eggs were the most abundant food item found on Delaware Bay beaches and that sandpiper numbers increased coincidently with increasing egg density. Sandpiper aggregations were most apparent at beach sites with distinct shoreline discontinuities (e.g., creek mouths, jetties) that tend to trap and concentrate free-floating eggs.

Karpanty et al. (2006) also found that the number of horseshoe crab eggs was the most important determinant of beach use by Red Knots. They found that the relative proportion of crab egg biomass (i.e., as a proportion of total prey biomass) was similar at sites used by Red Knots and randomly selected sites (i.e., 91 and 94%, respectively). However, overall egg biomass was more than three times greater at sites used by Red Knot compared with random sites. Red Knot habitat use appeared to shift from emergent marsh and peat-beaches to sandy beaches, especially around the high tide period. Greater numbers of loose eggs are available in beach swash zones during rising versus falling tides (Nordstrom et al. 2006) and birds appear to respond with greater foraging activity during this period (Burger et al. 1997).

4.2 Ecophysiological Relationships

Although a variety of prey may be available in Delaware Bay (e.g., bivalves, small crustaceans, polychaete worms, insect larvae), sandpipers exhibit a strong preference for horseshoe crab eggs (Myers 1986; Castro and Myers 1993). Free-ranging sandpipers depleted 80% of horseshoe crab eggs presented in feeding trials and, regardless of egg density, did not exhibit a give-up threshold (Gillings et al. 2007). In a diet selection study, Tsipoura and Burger (1999) found that horseshoe crab egg membranes constituted the majority of gut contents in all species they sampled. Additionally, depletion of undesiccated eggs in the wrack and swash zones is nearly complete during daily tidal fluctuations (Fraser personal communication).

These results are not surprising. When horseshoe crab eggs are present in surface sediments, search and ingestion time was near-instantaneous (Gillings et al. 2007). Their nutritional constituents are easy to digest and assimilation rates can be as high as 70% (Castro et al. 1989; USFWS 2003), resulting in the highest energy accumulation rates in Red Knots worldwide (Piersma et al. 2005) and among the highest recorded in vertebrates (i.e., 5–7 times greater than basal metabolic rate, Atkinson et al. 2007). Plasma triglyceride and phospholipid levels measured in Semipalmated Sandpipers during stopovers in Delaware Bay are greater than at any stopover along the Atlantic coast or on Caribbean wintering grounds prior to spring migration initiation (Lyons et al. 2008) and among the highest observed in migrating sandpipers (Mizrahi et al., in preparation). Circulating levels of these metabolites can be used to infer fattening rates (Jenni-Eiermann and Jenni 1994, 2003) as they are involved in lipogenesis and adipose tissue deposition (Ramenofsky 1990).

This is principally because horseshoe crab eggs are rich in lipids comprised of 16- (stearic acid) and 18-carbon (palmitic acid) fatty acids and an 18:1 unsaturated fatty acid (oleic acid) (Haramis unpublished data). Fatty acids are the primary energy substrates for long-distance migratory flight (Jenni and Jenni-Eiermann 1998; Jenni-Eiermann and Jenni 2003; McWilliams et al. 2004) for several reasons. Fatty acids are twice as energy dense, per unit dry matter, as carbohydrates and protein. Fatty acids also are relatively anhydrous, thus can be stored with a minimum of additional water and weight. Weight can be an important constraint for migrants (McWilliams et al. 2004).

Haramis (unpublished data) found that fatty acid composition of adipose tissue from heavy Red Knots collected in Delaware Bay in late May were closely matched in type and concentration with those contained in horseshoe crab eggs, suggesting direct deposition of crab egg constituents to fat depots (McWilliams et al. 2004; Pierce and McWilliams 2005). Red Knot adipose tissue also contained two "essential" fatty acids (i.e., not synthesized by the organism but obtained through food intake), eicosapentaenoic acid and docosahexaenoic acid, both of which are constituents found in horseshoe crab eggs.

Using stable isotope methods, Haramis et al. (2007) provide several lines of evidence that support the thesis of a strong dietary link between migrating sandpipers and horseshoe crab eggs. They found that as body mass in free-ranging Red Knots and Ruddy Turnstones staging in Delaware Bay increased, their plasma $\delta^{15}N$ values increased asymptotically. This same pattern was exhibited by Red Knots and Ruddy Turnstones fed ad libitum horseshoe crab eggs during 32-day pen trials. Mean $\delta^{15}N$ asymptotic values in both free-ranging and captive birds were not significantly different, and as mass increased in both groups, these values converged on the mean $\delta^{15}N$ value found in horseshoe crab eggs (see Figure 2, p. 370, Haramis et al. 2007). In contrast, mean $\delta^{15}N$ values of local blue mussels (*Mytilus edulis*) and coquina clams (*Donax variabilis*), known bivalve prey of migrating sandpipers, were well below values for horseshoe crab eggs and plasma levels in free-ranging and captive sandpipers. Finally, Haramis et al. (2007) found that test subjects in pen trial exhibited mass gain rates consistent with those found in free-ranging knots and turnstones. They posit that low $\delta^{13}C$ fractionation values observed during feeding trials suggest that dietary lipids are rapidly assimilated and likely converted to adipose tissue with little biochemical alteration (Jenni and Jenni-Eiermann 1998; Jenni-Eiermann et al. 2002; McWilliams et al. 2004).

These relationships were evident in a similar study conducted with Semipalmated Sandpipers (Mizrahi et al., in preparation). That is (1) plasma $\delta^{15}N$ increased asymptotically in free-ranging individuals and captive birds fed exclusively on horseshoe crab eggs, (2) plasma $\delta^{15}N$ asymptotic values of each group were not significantly different, and (3) both groups gained mass rapidly and at similar rates, converging on the $\delta^{15}N$ values of horseshoe crab eggs as mass increased.

4.3 Alternative Food Resources?

Many sandpiper species respond to diminishing availability of preferred prey by switching to alternative prey (Zwarts and Drent 1981; Beukema 1993). In these cases, however, physiological condition can be severely compromised in the absence of suitable alternative prey (Goss-Custard et al. 2003). Botton et al. (1994) found relatively few macro invertebrates (i.e., > 1 mm, mostly small oligochaetes, nematodes, and insect larvae) on the Delaware Bay beaches they sampled and densities rarely exceeded 200 m^{-2}. Tsipoura and Burger (1999) found that some sandpiper species consumed various worm and insect prey, however, nutritional analyses and comparisons of profitability for migrating sandpipers have yet to be fully investigated.

Bivalves are generally favored by Red Knots in other parts of the world (Piersma et al. 1993), and certain species, such as *Gemma gemma*, can occur in high densities in Delaware Bay (e.g., Botton 1984). However, this and several other bivalves (e.g., *Mercenaria* spp., *Anomia* spp.) are not typically consumed by shorebirds (Skagen and Oman 1996) either because they are too large or their shells are too hard (Botton 1984). The availability of suitable bivalve prey (e.g., small *Mytilus* spp., small *Mya* spp.) is temporally and spatially patchy in Delaware Bay and nearby coastal areas (Sitters et al. 2005; Haramis et al. 2007), and densities do not appear high enough to allow a large numbers of staging sandpipers to meet their fuel deposition needs (Escudero and Niles 2001; Haramis et al. 2007). Even if suitable bivalve fauna were available at high densities in Delaware Bay or coastal sites in close proximity, the ability of Red Knots to double their mass in 3 weeks, as they do eating horseshoe crabs eggs (Baker et al. 2004), is unlikely. Red Knots feeding on blue mussels and gastropods (*Littorina* spp.) during 3-week spring stopovers in Iceland had half the fuel deposition rates as Delaware Bay knots (Alerstam et al. 1992).

Bivalves and other hard-shelled prey are less profitable than horseshoe crab eggs to consume for a variety of reasons related mostly to their shells. Shells must be crushed in the gizzard and are bulky, resulting in digestive constraints to intake rates and low digestive efficiency compared to soft-bodied prey (van Gils et al. 2003, 2005). Thus, time-minimizing migrants should select prey that minimizes digestive constraints (e.g., horseshoe crab eggs; van Gils et al. 2005). Furthermore, the gizzard, along with other digestive organs, undergoes dramatic reductions in size prior to long-distance migration bouts (Piersma et al. 1999). A predominantly bivalve diet would require Delaware Bay Red Knots to fully restore gizzard function to facilitate the processing of shells, which may be too costly for individuals constrained by the need to reach the Arctic quickly (van Gils 2005). van Gils et al. (2006) documented a negative relationship between gizzard size and mortality rates in Red Knots (*C. canutus islandica*) feeding on cockles in the Dutch Wadden Sea, implying that individuals with small gizzards were less able to obtain the energy needed from their food. Finally, the high protein-to-calorie ratio of bivalves can reduce the potential for fattening (Bairlein 1998; McWilliams et al. 2004).

5 Recent Changes in Egg Availability

The quantity of horseshoe crab eggs available to sandpipers migrating through Delaware Bay has been reduced in recent decades, likely due to the increased harvest of adult horseshoe crabs. During the 1990s, demand for horseshoe crabs for use as bait increased to accommodate the American eel (*Anguilla rostrata*) and rapidly expanding whelk (family Melongenidae) pot fisheries (ASMFC 1998 and addenda [2004a; 2006]). The eel fishery targets female crabs, whereas the whelk fishery uses both male and female crabs (ASMFC 2004b). The maximum Delaware Bay area (DE, NJ, MD, PA, and VA) horseshoe crab harvest in modern record occurred in the mid-1990s and was estimated at just under 2 million crabs landed annually (ASMFC 2004b), although historical records indicate that larger harvests may have been carried out in the late 1800s (e.g., 4 million in 1880, Kreamer and Michels, 2009). The current Delaware Bay estimate of horseshoe crab abundance reported by the Horseshoe Crab Technical Committee is 13.3 million crabs (ASMFC 2006).

Trawl surveys, landing reports, and egg density surveys indicate that horseshoe crab populations in Delaware Bay may have been affected by the rapid changes in harvesting activity that took place between 1990 and 2000 (Botton et al. 1994; USFWS 2003; Davis et al. 2006; Niles et al. 2007). For instance, surplus production models of fishery-dependent and -independent survey data from several different sources indicate that the relative biomass (B/B_{MSY}) of horseshoe crabs in the bay steadily declined from the mid-1990s to 2003 at an annual rate of approximately 7% (Davis et al. 2006). The models were recently updated and unpublished results indicate that biomass has been increasing since 2003 and may be approaching levels similar to the mid-1990s (D. Smith, personal communication). However, such trend analyses are tenuous at best, as the majority of abundance estimates derived from long-term sources are highly variable and occasionally conflict, (Davis et al. 2006; Smith et al. 2006) and statistically robust surveys that focus exclusively on horseshoe crabs have only recently been implemented. Furthermore, there is some concern about the use of the surplus production modeling technique to determine these trends because of assumptions inherent in the models (Brust et al. 2006). Current data from the most robust crab surveys (e.g., Delaware Bay spawning survey, Michels et al. 2008; offshore benthic trawl survey, Hata 2008; baywide tagging study, D. Smith, personal communication) do, however, indicate that male and juvenile crabs have been increasing at an appreciable rate in recent years. Although these same surveys suggest that female crab numbers have stabilized, return to former population levels is not yet apparent.

Other indices of horseshoe crab abundance (e.g., egg density, landings) also support the hypothesis that crab populations have been affected by changes in harvesting over the last two decades. For instance, horseshoe crab egg densities on New Jersey's Delaware Bay beaches fell from average counts of 40,000 eggs m^{-2} in the early 1990s (Niles et al. 2007) to approximately between 3,000 and 4,000 eggs m^{-2} in 2005–2007 (Kalasz et al. 2008), and data from 2007 reflect the lowest egg densities recorded in New Jersey in 8 years (Kalasz et al. 2008). Although average egg densities bay-wide and on Delaware beaches appear to be stable or increasing over the last 3 years, estimates have been driven primarily by increases in Mispillion Harbor, where the highest egg densities in the bay are recorded (Kalasz et al. 2008). Caution should be exercised when comparing egg densities between New Jersey and Delaware due to methodological differences in egg sampling employed in the two states (Kalasz et al. 2008). It is also difficult to assess temporal trends in egg densities due to the extreme variability in estimates among years, both for individual beaches and for the bay as a whole (Smith et al. 2002a, b, Pooler et al. 2003, Kalasz et al. 2008). The New Jersey Division of Fish and Wildlife (DFW) and Delaware DFW initiated a study in 2008 that aims to determine the comparability of egg density data across the two states (Kalasz et al. 2008), and should lead to clearer understanding of general trends in the bay.

Landing surveys indicate that the mean number of crabs per catch and mean catch per unit effort have also declined since the 1990s (USFWS 2003). However, these harvest indices have in part been driven by regulatory actions (see below) and have stabilized at low levels in recent years. Unfortunately, few data are available to assess the status of the Delaware Bay horseshoe crab population prior to 1990.

The density of spawning horseshoe crab females is also known to increase the process of bioturbation, through which buried eggs are released to the beach surface through intraspecific interference by competing females (Jackson et al. 2002; Smith 2007). Smith (2007) used a spatially explicit model to predict the percentage of horseshoe crab nests disturbed as a function of adult densities. The model predicted that the percentage of nests disturbed would increase linearly up to twice the 2004 spawning crab densities and asymptote at approximately 70% of nests. According to the model, the proportion of nests disturbed during peak spawning (i.e., second spring tide) in 2004 was approximately 45%, and at one-third this spawning level would be approximately 20%. It was also assessed that a minimum of roughly 5–9% of these disturbed eggs would be exhumed to the surface (i.e., 0–5 cm) through various processes (Smith 2007) and thus be available for consumption by most shorebirds. It is currently unclear what threshold densities of nest densities and nest disturbance levels are necessary to support target shorebird populations. However, it is known that this redistribution of eggs is crucial for sandpipers, as they are highly dependent upon eggs available near or at the surface (Tsipoura and Burger 1999). Furthermore, bioturbation by horseshoe crabs may also have indirect effects that can affect shorebirds. Through feeding and substrate agitation, crabs can disturb the benthic community, oxygenate substrates, and resuspend previously unavailable nutrients (Odell et al. 2005). Loss of these secondary processes could affect the availability of alternative resources for migrating sandpipers.

Concerns about the accelerated harvest and potential overexploitation of horseshoe crabs in Delaware Bay, chiefly due to their possible effects on migrating sandpipers, led to several regulatory actions at the regional and state levels to protect stock levels. The Atlantic States Marine Fisheries Commission (ASMFC) adopted a Fishery Management Plan for horseshoe crab in 1998 (ASMFC 1998), followed by addenda that established quota systems in 2000, 2001, 2004, and 2006. Legislative restrictions led to a 76% coast-wide reduction in bait landings between 1998 and 2005 (ASMFC 2006), and some surveys indicated that there was a 63% drop in landings in New Jersey and Delaware between 2003 and 2004 alone (Smith et al. 2009). In 2006, the state of New Jersey enacted a two-year moratorium on harvesting horseshoe crabs. Recently, the state passed legislation to further restrict the harvest, landing or possession of horseshoe crabs until the *rufa* Red Knot population reaches target recovery goals.

To date, changes in harvest regulations imposed since 1998 do not appear to have translated into increased bay-wide egg densities (Niles et al. 2007; Kalasz et al. 2008), although recent data from Delaware beaches are encouraging and suggest some site-specific increases. It is less clear how regulatory actions have affected the adult horseshoe crab population. Statistically robust surveys that focus exclusively on horseshoe crabs have only recently been initiated, including a 30-ft offshore trawl survey that started in 2001 (Hata and Berkson 2003). According to spawning surveys, which were redesigned in 1999 to provide better data for long-term trend analysis (Smith and Michels 2006), horseshoe crab activity on New Jersey and Delaware beaches has stabilized since 1999 (Smith et al. 2002b). However, most other available population estimates based on longer-term data sets show a continuous decline between 1995 and at least 2003 (Davis et al. 2006). Overall, 2003 biomass estimates from several sources suggested that levels remain less than 56% of those recorded in 1995 (Davis et al. 2006). This lack of population response may indicate a lag effect due to horseshoe crab age-to-recruitment, which is approximately 9–11 years (Shuster and Sekiguchi 2003).

6 Consequences for Sandpipers

6.1 Physiological Condition

The reduction in Delaware Bay horseshoe crab biomass has raised concern over future egg availability for migrating sandpipers as well as crab stock availability. Using a surplus modeling approach, Davis et al. (2006) predicted that under 2003 harvest levels (1356 tons), population recovery to B_{MSY} (spawning biomass that would produce maximum sustainable yield) would take at least 4 years, and four of seven models examined predicted that recovery would not reach B_{MSY} within 15 years. For sandpipers, such reductions in horseshoe crab biomass could negatively affect the quantity and availability of eggs needed for refueling.

Based on the equations of Kersten and Piersma (1987), and taking into account daily energy expenditure (Castro and Myers 1988) and modified assimilation rates based on Castro et al. (1989), the Delaware Bay Shorebird Technical Committee (USFWS 2003) estimated that a minimum of approximately 300 metric tons of eggs would be necessary to sustain current populations of six species of migratory sandpipers using the bay during spring migration (Ruddy Turnstone, Red Knot, Sanderling, Semipalmated Sandpiper, Dunlin [*C. alpina*], Short-billed Dowitcher [*Limnodromus griseus*]). Using this estimate, they calculated that 30,000–70,000 eggs m^{-2} would be needed to sustain all sandpipers passing through the bay (using an estimate of 423,000 individuals of the six primary species using the bay). This is likely a conservative estimate of densities needed to accommodate migratory sandpipers, as it does not take into account all species using the egg resource (e.g., Least Sandpiper, *C. minutilla*; gulls, family Laridae) and uses a low-end estimate of total sandpipers using the bay (i.e., estimates range from 400,000 to 1,000,000 individuals; Myers et al. 1987; Clark et al. 1993). The egg estimate also does not take into account the effects of intra- and interspecific interference competition on intake rates and resource accessibility (Stillman et al. 2002), or potential age differences in foraging efficiency (Caldow et al. 1999), which would likely be strongest when competitor densities are high and prey scarce (Caldow et al. 1999; Triplet et al. 1999). In Delaware Bay, competition between gulls and sandpipers for foraging space has been demonstrated in areas where horseshoe crab eggs accumulate (Burger et al. 2007). Finally, the estimate does not explicitly take into account the effects of horseshoe crab density on the vertical distribution, and thus availability of crab eggs, to sandpipers.

According to functional response models, Red Knot peck success is twice as high for surface eggs than for buried eggs, so that probing for buried eggs is not profitable unless they are present in extremely high densities (Gillings et al. 2007). Stillman et al. (2003) demonstrated that the number of eggs within the top 5 cm of sediment consumed per second ranged from near zero at densities of 300 eggs m^{-2} to two eggs per second at 25,000 eggs m^{-2}. Similar models predict that surface eggs can sustain current Red Knot populations at densities of 360 m^{-2}, as compared to 19,000 m^{-2} densities of buried eggs (Gillings et al. 2007). Haramis et al. (2007) further concluded that it would take an estimated 16 billion buried crab eggs to provide adequate resources for 40,000 Red Knots alone refueling in Delaware Bay. None of the 16 beaches surveyed in New Jersey and Delaware in 1999 during peak shorebird migration stopovers (23–24 May) contained densities of buried eggs in 0–5 cm cores above 30,000 eggs m^{-2} (i.e., densities deemed necessary to support all sandpipers using the bay), whereas 11 of them contained that density in deeper cores (0–20 cm, Pooler et al. 2003; USFWS 2003). According to recent comparable egg surveys conducted during May 21–28, only 4 of 11 beaches surveyed in Delaware and 1 of 12 beaches in New Jersey averaged this threshold egg density in the 0–5 cm stratum between 2005 and 2007 (Kalasz et al. 2008). In fact, only one new New Jersey beach surveyed in 2005–2007 ever exceeded densities of 30,000 eggs m^{-2} during the entire shorebird migratory period (i.e., May 1–June 6) in any year (Kalasz et al. 2008). While 64% of the Delaware beaches surveyed had egg densities above the threshold at least once during the migratory period, this usually occurred during the final week of the stopover period, when many individuals had already departed for the breeding grounds (NJDEP unpublished data).

Documented changes in sandpiper foraging ecology within Delaware Bay (Baker et al. 2004; Atkinson et al. 2007) and widespread declines in sandpipers along the Atlantic flyway (Morrison et al. 2006; Bart et al. 2007) indicate that current resource levels in the bay may be below the threshold needed to sustain populations that depend on Delaware Bay as a critical migratory stopover site. According to empirical models that account for body mass and morphometry (Kvist et al. 2001), Red Knots passing through Delaware Bay must reach target weights between 180 and 220 g to reach breeding grounds with sufficient energy stores (Piersma [2000] Energetics of body mass changes in red knots staging in Delaware Bay in May 1998. Unpublished report, Nether Inst Sea Res, Trexel, The Netherlands; Baker et al. 2004; Morrison et al. 2005). Red Knots must reach this target before a certain "departure" date that will allow them to complete their flight to the breeding sites at the appropriate time, as evidenced by mass gain rates that are two to three times higher toward the end of their migration stopover period than at the beginning (Atkinson et al. 2007). This pattern is especially pronounced in birds that arrive later in the season and in those at lower weights (Atkinson et al. 2007). However, the proportion of Red Knots reaching the target departure mass decreased significantly between 1997 and 2003 (Robinson et al. 2003; Baker et al. 2004; Niles et al. 2007). In 2003 and 2005, birds also did not increase mass gain rates toward the end of the stopover period, indicating that they were unable to attain rates of ingestion or assimilation to reach target weights within the limited departure window (Atkinson et al. 2007). This was likely a result of the lower egg densities available to sandpipers in recent years (Botton et al. 1994; Niles et al. 2007).

Similar patterns in weight gain have been observed in other sandpiper species using Delaware Bay during spring migration. For example, the proportion of Ruddy Turnstones captured in Delaware Bay that were at threshold departure mass (150 g) declined significantly between 1997 and 2002, although daily rates of mass gain during this period only declined slightly (Niles et al. 2001; USFWS 2003). Analysis of individually marked turnstones captured between 1997 and 2000 similarly revealed significant differences in mass gain among years, although there was no consistent negative trend in gain rates (Robinson et al. 2003). Mizrahi (1999) observed that based on energetic consumption models (Castro and Myers 1988) some Semipalmated Sandpipers captured in Delaware Bay from 1996 to 1998 likely did not have sufficient fat reserves to make it to their breeding grounds in Canada and that many of those that did reach the breeding grounds would have done so with few remaining energy stores. More recent data (2000–2007) show that Semipalmated Sandpipers captured in the bay were of significantly lower mass and demonstrated lower mass gain rates than were observed in the mid-1990s (Mizrahi, unpublished data). Based on these data, Semipalmated Sandpipers appear to be departing Delaware Bay at lower weights than in previous years (Mizrahi, unpublished data).

6.2 Population Responses

The changes in fattening rates observed in Delaware Bay during spring migration appear coincidental with population changes in several species of North American sandpipers (Morrison et al. 2001, 2006; Bart et al. 2007). For instance, the *rufa* subspecies of Red Knot, one of the smallest sub-specific populations of Red Knot known worldwide (Piersma and Davidson 1992), has declined from an estimation of 170,000 individuals in the late 1980s to approximately 20,000 currently (Gonzalez et al. 2001; Morrison et al. 2004). This is noteworthy because most *rufa* Red Knots stage in Delaware Bay during spring migration and evidence suggests that numbers in the bay are also declining precipitously. It was estimated that approximately 100,000 Red Knots passed through the bay annually during spring migration in the 1980s, with peak counts over 95,000 (Clark et al. 1993). In contrast, recent estimates are under 25,000 with peak counts under 15,000 (Niles et al. 2007, Morrison et al. 2007). Decreases in the *rufa* subspecies has also been especially pronounced in the Patagonia and Tierra del Fuego wintering areas (Morrison et al. 2004). A large proportion of Red Knots that migrate through Delaware Bay are known to winter in this region (Atkinson et al. 2007).

The Semipalmated Sandpiper population that breeds in eastern Canada and passes through Delaware Bay in spring (Morrison 1984) has decreased by approximately 43% since 1982 (Morrison et al. 2006), with significant changes in numbers observed along the Atlantic coast (Bart et al. 2007). A decline of 68% between 1982 and 2004 was estimated for the Bay of Fundy, through which approximately 75% of the global population passes during fall migration (Morrison et al. 2006). Declines have also been documented in eastern populations of several other sandpiper species that migrate through Delaware Bay in the spring and likely depend on horseshoe crab eggs, including Least Sandpiper (Morrison et al. 2006; Bart et al. 2007), Sanderling (Howe et al. 1989), Dunlin (Morrison et al. 2006), and Short-billed Dowitcher (Bart et al. 2007).

The dramatic declines in sandpiper numbers in recent years have caused alarm about the future sustainability of some populations. Some survival models indicate that the *rufa* subspecies of Red Knot that passes through Delaware Bay could be extinct by 2010 (Baker et al. 2004), based on the mean survival estimate from 1998 to 2001 (i.e., 53.9%). Annual survival rates from this period were highly variable (i.e., 45–63%, 95% CI), but were still well below those reported for *islandica* Red Knot, which ranged from 76% when the population was declining to 80% when the population was stable (Boyd and Piersma 2001). Modeling efforts by Hitchcock and Gratto-Trevor (1997) determined that among five sandpiper population parameters they considered (i.e., fecundity, adult mortality, juvenile survival, delayed recruitment, and immigration), adult mortality would have the strongest effect on population change. Adult sandpiper survival rates appear closely associated with body stores acquired during spring migration (Morrison et al. 2006). Baker et al.

(2004) reported that Red Knots departing Delaware Bay at low weights are less likely to be seen later in the flyway, implying lower survival. Data collected at Plymouth Beach, Massachusetts, during fall migration also indicated that fat levels in individual Semipalmated Sandpipers were positively associated with annual return rates (Pfister et al. 1998). Fecundity rates are also likely affected by the conditions encountered during stopover, as reproduction is predicted to decrease logarithmically as energy stores at departure decrease (Piersma and Baker 2000).

Although conditions at the breeding and wintering grounds also may impact sandpiper population health, several lines of evidence indicate that the loss of horseshoe crabs in Delaware Bay may be driving the negative trends observed in recent years for some species. Populations of some species that winter in Tierra del Fuego, but do not migrate through Delaware Bay (e.g., Hudsonian Godwit, *Limosa haemastica*), are stable or increasing (Morrison et al. 2004; Jehl 2007). Recent data also indicate that declines in the number of Semipalmated Sandpipers breeding in eastern Canada (e.g., Churchill, Manitoba) are attributable to mortality outside of the breeding season, as breeding success and habitat suitability have not appeared to change within the region (Jehl 2007). Several species that depend on Delaware Bay as their last stopover, but do not winter or breed in the same regions, are experiencing declines, such as Sanderling, Semipalmated Sandpiper, Least Sandpiper, Ruddy Turnstone, and Dunlin (Morrison et al. 2006, Jehl 2007). Some of the sharpest declines have been documented in species that rely heavily on surface horseshoe crab egg availability, such as Red Knot and Semipalmated Sandpiper, and which have also shown marked reductions in mass gain potential during stopover in Delaware Bay (Robinson et al. 2003; Baker et al. 2004; Niles et al. 2007; Mizrahi, unpublished data).

7 Conclusions

Several sandpiper species migrating in the Western Atlantic track the availability of horseshoe crab eggs in space and time during northbound passage to the breeding grounds. Historically, this meant that each spring hundreds of thousands of individuals converged on Delaware Bay, the epicenter of horseshoe crab spawning in North America, to exploit what was once a readily available and profitable food resource. Rapid energy accumulation, combined with efficient energy delivery that occurs during periods of intense exercise, such as long-distance flights, appear to underlie the strong relationship between migrating sandpipers and horseshoe crab eggs in Delaware Bay. That other prey items could provide the same synchrony in availability, economy of acquisition and processing, and nutritional effectiveness as horseshoe crab eggs seems unlikely.

The consequences of reduced crab egg availability are clear. Declines in weight gain potential of sandpipers staging in Delaware Bay can compromise their ability to complete migration successfully, survive harsh conditions they encounter frequently on the breeding grounds, or make the behavioral and physiological transitions necessary to initiate breeding. These outcomes, alone or in concert, can affect population viability adversely especially if diminished egg availability persists, as it has for nearly a decade. Dramatic population declines over the last decade in some species migrating through Delaware Bay are well documented and one, the Red Knot, is perilously close to extinction.

Although we provide clear evidence linking the viability of some sandpiper species with declines in Delaware Bay horseshoe crabs, acknowledging other threats that potentially contribute to declines in sandpiper populations is important. In some years, sandpipers arrive late to Delaware Bay or in poor physiological condition (USFWS 2003; Niles et al. 2007; Mizrahi, unpublished data), which could be related to conditions birds experience on their wintering grounds or at stopover locations in South America. Threats such as industrial development, oil exploration, and aquaculture, to name a few, could affect known sandpiper wintering and stopover areas (USFWS 2003). Although the core *rufa* Red Knot wintering areas along the Patagonia and Tierra del Fuego coastlines appear to be in good ecological condition and have not changed significantly in the last 15 years (USFWS 2003), much less is known about other wintering or stopover locations in South America. For example, in 2006 between 400 and 1,000 Red Knots died at a stopover site in Uruguay, apparently from harmful algal bloom contamination (Baker personal communication). Surveys conducted in the late 1980s along the northern coast of South America (Morrison and Ross 1989) have not been repeated, although this region supports nearly 85% of the world's Semipalmated Sandpipers and significant numbers of other sandpiper species (Morrison personal communication).

Human disturbance also can adversely affect sandpipers during the nonbreeding season (i.e., migration, wintering, Pfister et al. 1992; McGowan et al. 2002; Thomas et al. 2003). Observations during spring migration in Delaware Bay suggest that human disturbance can directly affect the use of certain beaches by sandpipers (USFWS 2003; Burger et al. 2007; Niles et al. 2007) and can exacerbate interspecific competition from gulls (Burger et al. 2007). However, actions to abate this problem (e.g., beach closures) have been implemented in Delaware Bay over the last few years (Niles et al. 2007).

We believe that although other perturbations may contribute to overall declines in Delaware Bay sandpipers, their affect is minor compared to the loss of a viable horseshoe crab population that consistently produces a superabundance of eggs. Since 1998, the ASMFC and state environmental protection agencies have taken measures to reduce the horseshoe crab harvest quota. Given that horseshoe crabs must be 9–11 years old before recruiting into the spawning population (Shuster and Sekiguchi 2003), these efforts must persist into the foreseeable future to insure the recovery of horseshoe crab populations and the long-term health of migratory sandpipers in Delaware Bay.

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