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A Review of the Biology and Management of Horseshoe Crabs, with Emphasis on Florida Populations

Susan D. Gerhart



Florida Fish and Wildlife
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Cover Photograph

Mass spawning of horseshoe crabs in Safety Harbor, Florida.
Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute

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A Review of the Biology and Management of Horseshoe Crabs, with Emphasis on Florida Populations

Executive Summary

The horseshoe crab, *Limulus polyphemus*, lives in waters along the Atlantic and Gulf of Mexico coasts of the United States. They are related to spiders and scorpions, and their ancestors date back 500 million years. Although all horseshoe crabs in the United States belong to the same species, genetics studies have shown that they form discrete populations; horseshoe crabs on the Atlantic coast are genetically different from those on the gulf coast.

Horseshoe crabs bury their eggs in nests dug into the beach; when larvae hatch, they live in the sand for a while before emerging to live in the water column. Within days, the larvae settle to the bottom and metamorphose into juveniles. As they grow, the juveniles move farther offshore. Horseshoe crabs reach sexual maturity after 9–11 years and then live about 10 more years after that.

In some areas, horseshoe crabs spawn only during high tides around the full and new moons. In other areas, spawning is not synchronized with the lunar or tidal cycles. The timing of spawning most likely depends on the morphology of the beach and the range of the tides. Eggs are fertilized outside the female's body, either by a male that is attached to the back of her carapace, or by other males (satellite males) that surround the attached pair.

Some aspects of horseshoe crab biology are well studied. The blood contains a substance called Limulus Amebocyte Lysate (LAL), which clots in the presence of bacterial toxins and functions as part of the crab's immune system. The two compound eyes are made up of multiple components that form separate images; eight other eyes only detect changes in light levels. Adult horseshoe crabs feed mainly on clams and worms. Adults have few predators, but shorebirds and fish feed on their eggs. Many organisms attach to the carapace of the horseshoe crab; most are harmless, but some are parasitic.

Horseshoe crabs are harvested by three fisheries. The bait fishery uses horseshoe crabs to catch eel and conch, principally in the mid-Atlantic states. In Florida, only a small number of eel fishermen are licensed to harvest horseshoe crabs for bait. The marine-life fishery collects horseshoe crabs live for resale as aquarium and research specimens. This is the main horseshoe

crab fishery in Florida; more than 22,000 horseshoe crabs were harvested in 2005. Harvesters for the biomedical fishery collect horseshoe crabs temporarily to remove blood and then release the animals. LAL is extracted and used to test for bacterial contamination in drugs and medical devices. Florida does not have a biomedical fishery at this time.

Horseshoe crab stock assessments are limited in their ability to estimate sizes of horseshoe crab populations because some basic aspects of their biology (e.g., reproductive output, size at maturity, stage-specific mortality) are not known or have been studied only in small areas of their range. In Delaware Bay, where horseshoe crabs are most abundant and most studied, estimates of population sizes and dynamics have been attempted. In Florida, most research has been on reproductive behavior, but other important data is missing. The Fish and Wildlife Research Institute is currently conducting studies on beach nesting sites, reproductive timing, spawning behavior, and population genetic structure.

The horseshoe crab bait fishery in the United States is managed through the Atlantic States Marine Fishery Commission Fishery Management Plan. This plan sets quotas for the number of horseshoe crabs that can be harvested in each Atlantic-coast state and requires certain monitoring and research projects. The State of Florida has established bag limits and licensing procedures for the horseshoe crab fishery in Florida.

Currently, license holders with marine-life endorsements may take up to 100 horseshoe crabs per day. An increase in this number would have both biological and management impacts. Because marine-life harvesters are concentrated in South Florida and capture mostly juveniles, such an increase could threaten the ability of that population to replenish itself. The Atlantic States Marine Fisheries Commission Horseshoe Crab Management Board has recently made note of the high number of horseshoe crabs harvested in Florida that are not counted under the management plan quota. Should they decide to include the marine-life fishery in the management plan, restrictions on harvest would likely result in a reduction in allowable landings.

A Review of the Biology and Management of Horseshoe Crabs, with Emphasis on Florida Populations

Introduction

The North American horseshoe crab, *Limulus polyphemus*, is not a true crab (Subphylum Crustacea) but is a member of the Subphylum Chelicerata. This subphylum includes spiders and scorpions and is named for the chelicerae, a set of appendages found near the mouth. *Limulus* and three other species of horseshoe crabs belong to the Class Merostomata (*meros* = thighs, *stoma* = mouth; the mouth is located between the legs). The other three species live in waters off Japan and southeastern Asia. The Japanese species is called the helmet crab, *kabutogani* (*kabuto* = helmet, *gani* = crab; Y. Kiryu, personal communications), a name also used in the past in the United States. Other names include the horsefoot crab and the king crab.

Horseshoe crabs range from Maine through Florida on the Atlantic coast; in the Gulf of Mexico, horseshoe crabs live principally along the Florida and Yucatán coasts. Horseshoe crabs are scarce in the rest of the gulf, possibly because tidal frequency and amplitude are insufficient or the temperature and moisture content on the beaches are not appropriate for nesting (Shuster, 1979). Shuster determined that horseshoe crabs are a temperate species based on differences in body sizes in different areas. The largest horseshoe crabs are found along the mid-Atlantic bight, and size decreases to the north and south; the smallest horseshoe crabs are found along Florida beaches. The highest abundance of spawning horseshoe crabs is on beaches along the mid-Atlantic coast, from New York to Virginia (Botton and Ropes, 1987).

The horseshoe crab is often called “a living fossil” because the morphology of the extant species remains quite similar to species found in the fossil record. The earliest recognizable ancestor of the horseshoe crab, *Aglaspida*, lived during the Cambrian period around 500 million years ago, along with trilobites and giant water scorpions. During the Jurassic period, about 150 million years ago, *Mesolimulus* displayed morphology nearly identical to *Limulus* (Novitsky, 1984). Thus, horseshoe crab morphology has remained relatively unchanged since the age of the dinosaurs.

Horseshoe crabs are harvested in many areas of their range as bait for the eel (*Anguilla rostrata*) and conch (*Busycon* spp.) fisheries. In certain areas, har-

vesters in the biomedical fishery collect horseshoe crabs to obtain their blood, which is used in the pharmaceutical industry. In Florida, some horseshoe crabs are fished for eel bait, but they are fished principally by the marine-life industry, which collects the animals live for resale as aquarium, research, or educational specimens. The regulations for the horseshoe crab fisheries are developed by each state in compliance with the Atlantic States Marine Fisheries Commission (ASMFC) Horseshoe Crab Management Plan. The Florida Fish and Wildlife Conservation Commission (FWC) Division of Marine Fisheries Management (DMFM) develops recommendations for regulation of all marine fisheries in Florida. At the FWC Fish and Wildlife Research Institute (FWRI), the Crustacean Fisheries group studies marine arthropods, including horseshoe crabs. At the request of DMFM, this report was written to provide information on the biology, stock status, and management of horseshoe crabs and the implications relevant to the request for an increased bag limit by harvesters in the marine-life industry.

The Biology of Horseshoe Crabs

Since Thomas Hariot first described the horseshoe crab in 1588, it has become one of the most studied invertebrates in the world. The majority of studies have been conducted in the Delaware Bay region, where horseshoe crabs are most abundant. In Florida, researchers have studied horseshoe crabs in the Panhandle (see Rudloe references), near Cedar Key (see Brockmann references), and in the Indian River Lagoon (see Ehlinger references). The following is a brief summary of the general biology of this animal, with emphasis on known differences between Florida horseshoe crabs and those found in other parts of the United States.

Basic Biology

ANATOMY

The body of the horseshoe crab has been described as “tank-like” or “helmet-shaped.” It consists of two main parts: the cephalothorax and the abdomen (Figure 1). The cephalothorax is actually the head and thorax

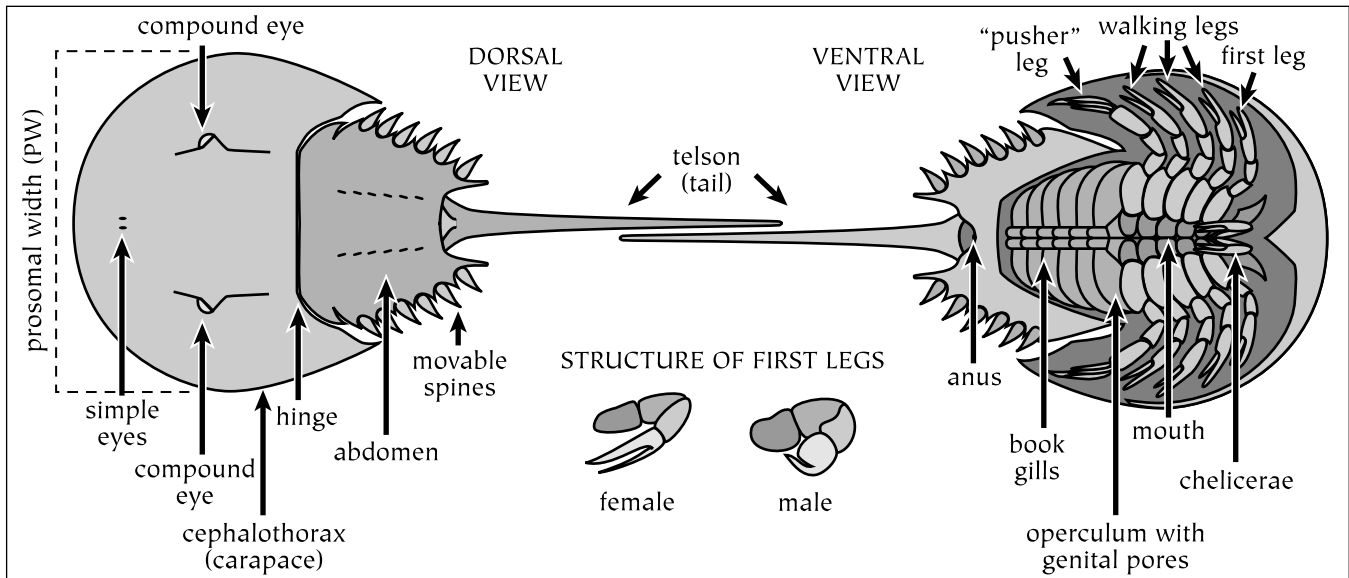


Figure 1 The external anatomy of a horseshoe crab.

fused together and is also called the prosoma. The most prominent features of the cephalothorax are the two compound eyes, located near the front, and the numerous legs underneath. The abdomen, also called the opisthosoma, attaches to the cephalothorax by a hinge joint that allows flexion. The book gills, which are used for oxygen exchange, dominate the underside of the abdomen. A hard shell, called the carapace, covers each part of the horseshoe crab. The carapace is an exoskeleton made of chitin, a polysaccharide, and provides an attachment point for muscles.

The color of the carapace can range from light gray or tan to almost black. In Florida, horseshoe crab carapaces are lighter in color than in more northern areas, most likely because the substrate on which they live is lighter and the water is less turbid (Shuster, 1979). The carapace of older animals may be covered with fouling organisms and injuries, such as cracks and punctures incurred during mating.

The appendages on the cephalothorax occur in pairs, and some are specialized for specific uses (Figure 1). The first pair of appendages on the cephalothorax is the chelicerae, which have small claws at the end that help manipulate food into the mouth. Next are five pairs of walking legs. The first four pairs also have small claws; in mature males, the first pair of claws are enlarged and modified for grasping the female carapace during mating. The last pair of walking legs, the pusher legs, do not have claws; instead they have four leaf-like processes that are used for pushing and for stirring up sediments when the horseshoe crab burrows or lays eggs. The base of each walking leg has a structure called a gnathobase that consists of a flat, spiny surface that is used for grinding food. A very small pair

of appendages called chilaria help manipulate food to the mouth.

The abdomen bears six pairs of book gills. The first pair is fused and creates the operculum, which protects the next five pairs. On the underside of the operculum are the genital pores, the exit points for eggs and sperm. Each gill has many folds, which increase the surface area for gas exchange. When the gills move, the folds flutter like the pages of a book, thus the name. The gills also serve as paddles when the crab is swimming. The final appendage is the telson, the spike-like tail. The telson attaches to the abdomen by a ball joint, which allows a wide range of motion. The horseshoe crab uses the telson to help right itself when it is overturned but does not use it as a weapon.

One can distinguish adult male and female horseshoe crabs in several ways. In general, the male carapace is more convex, its edges are more flared, and it is much smaller than the female. The first pair of legs in adult males have claws called claspers that are modified for reproduction. These claspers are larger than the other claws and resemble boxing gloves (Figure 1). Females and juveniles have the same size and shape of claws on all the walking legs. The genital pores also differ between sexes. In males they are located at the peaks of hard, conical projections; in females they are softer and appear as elliptical slits.

LIFE CYCLE

Horseshoe crabs begin life as embryos in unshelled, greenish eggs (Figure 2). Eggs are laid in nests on the beach at a mean depth of about 15 cm beneath the surface of the sand (Rudloe, 1979). Each clutch, or group of eggs, contains between 2,000 and 30,000 eggs (Cohen

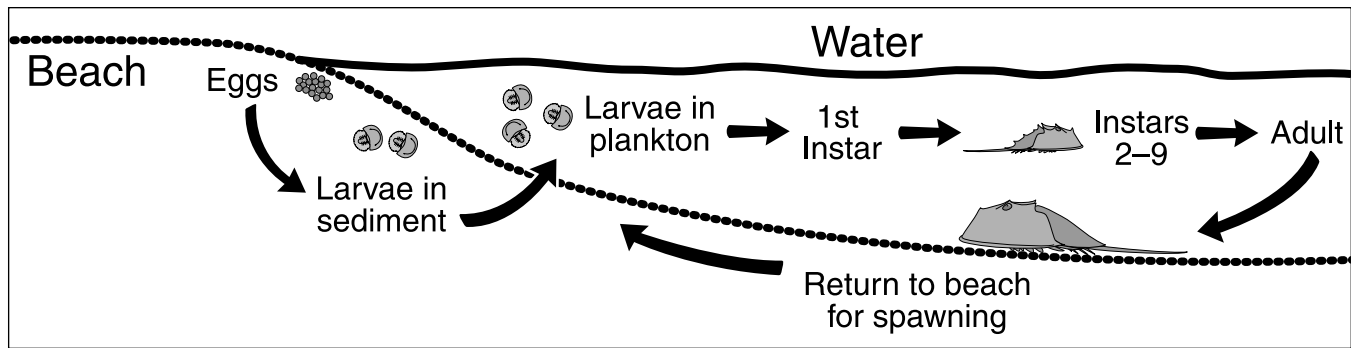


Figure 2 The life cycle of a horseshoe crab.

and Brockmann, 1983). After fertilization, each egg consists of a central yolk, an embryo, and a thick outer membrane. The embryo goes through 21 stages of development over two to four weeks (Shuster and Sekiguchi, 2003). Conditions associated with high water levels, such as hydration and agitation, trigger hatching (Ehlinger and Tankersley, 2003). Eggs on some beaches along the Florida west coast hatch en masse, although this has not been seen on beaches along Delaware Bay (Shuster and Sekiguchi, 2003). An estimated 0.06% of eggs survive to hatching (Carmichael *et al.*, 2003).

Horseshoe crabs in the next life stage are called trilobite larvae because they resemble the ancient trilobites. The larvae are swimmers that eventually molt to the more recognizable crawling form. After hatching, larvae remain buried in the sediment in the general area of the nest. They swim in the water that is trapped between sand particles, moving to the surface at high tide and back down again at low tide. With each upward movement, some larvae are exposed and either washed away by waves or eaten by birds (Rudloe, 1979). Larvae emerge from the sand at high water, either during the high tide associated with the full or new moon or during a storm event with strong onshore winds (Rudloe, 1979; Botton and Loveland, 2003). Some larvae in northern areas overwinter in the sand for up to eight months, emerging in early spring before the arrival of bird predators (Botton *et al.*, 1992). In the Indian River Lagoon (IRL), larvae are found in the plankton (floating in the water column) during April through August. These larvae show no periodicity of emergence from the beach because tides in the IRL are virtually nonexistent; instead, they emerge from the sand into the water approximately eight weeks after adults spawn (Ehlinger *et al.*, 2003). After they emerge into the open water, larvae stay close to the shore and are probably not distributed over long distances (Botton and Loveland, 2003). The larvae remain in the plankton for six to eight days before settling on the bottom and molting to the first juvenile stage (Rudloe, 1981; Shus-

ter, 1982). During their transition from the plankton to the benthos (bottom community), only about 2.5% of larvae survive (Botton *et al.*, 2003b).

The first instar, or post-larval stage, averages approximately 5 mm prosomal width (PW; Rudloe, 1981) and looks similar to the adult but has longer spines and a shorter telson (Shuster, 1982). Juveniles live on the tidal flats; in contrast to larvae and adults, juveniles are most active in the two hours before the daytime low tide and stay buried in the sediment at other times. They also bury in winter when temperatures drop below freezing (Rudloe, 1981). By the end of the first year, most juveniles have reached instar 7 and measure about 40 mm PW. Only 33 out of every one million larvae that emerge from the beach survive to this stage. Juveniles stay in the intertidal region until they reach 90 mm PW, moving farther offshore as they grow (Rudloe, 1981). The sex ratio at this stage is approximately 1:1 (Carmichael *et al.*, 2003). Large subadult (not yet sexually mature) horseshoe crabs have been dredged from waters as deep as 246 m (Shuster, 1982).

Subadults mature on the continental shelf off the northern Atlantic coast at 132–168 mm PW. Maturity takes 9–11 years and 17–18 instars (Shuster and Sekiguchi, 2003; Carmichael *et al.*, 2003). The size and time to maturity vary, depending on location; in Florida, horseshoe crabs mature at a smaller size than northern crabs and may mature in less time as well. Females are larger than males because of either greater growth with each molt or more molts before maturity (Shuster and Sekiguchi, 2003). Large size in females may be an advantage because females must tow males during the spawning season and a large body can contain more eggs (Botton and Loveland, 1992). The largest female and male horseshoe crabs captured were 340 mm and 232 mm PW, respectively (Shuster, 1979). Adult sex ratios on spawning beaches and in trawls always show more males than females. Although these ratios may be the result of male-biased sampling techniques, Carmichael *et al.* (2003) found sex ratios of 2.3:1 (male:female) when diving over adult habitat.

Males are more abundant, perhaps because females molt more frequently, and mortality increases during molting. The age and size at maturity of female horseshoe crabs are difficult to estimate; males develop claspers at maturity, but females lack any outward signs. The only way to determine maturity in females is to look for mature eggs in the reproductive system by either cutting a section of the carapace or palpating the eggs from the gonopore.

By using indirect aging methods, researchers have estimated that horseshoe crabs live up to 20 years. Botton and Ropes (1988) aged horseshoe crabs based on the age of slipper shells (*Crepidula* spp.) attached to the carapace. The oldest slipper shells attached to a horseshoe crab carapace were eight years old; assuming that the horseshoe crab last molted at maturity (9–11 years of age), it would be 17–19 years old. Other researchers tagged horseshoe crabs and added the time of recapture to the age of maturity, obtaining similar ages (Ropes, 1961; Swann, 2005). Researchers using each of these methods assumed that horseshoe crabs did not molt after reaching sexual maturity; however, some evidence indicates that molting may occur in adults. Usually, adults are separated into broad age categories based on amount of wear, color, and degree of fouling of the carapace (Haefner *et al.*, 2002).

REPRODUCTION

Reproduction in horseshoe crabs has been studied extensively. The seasonal timing of reproductive activity varies from region to region. In Delaware Bay and on Cape Cod, horseshoe crabs appear on beaches to spawn (release sperm and eggs) from mid-May to mid-June (Cavanaugh, 1975; Shuster, 1982; Barlow *et al.*, 1986; James-Pirri *et al.*, 2005), although older individuals begin spawning earlier and end later than younger ones (Smith *et al.*, 2005). In Florida, spawning occurs year-round, peaking in March through May (Rudloe, 1980; Ehlinger *et al.*, 2003; H. J. Brockmann, personal communication; personal observations).

Many horseshoe crabs spawn on the full and new moons (spring tides). This pattern is not absolute and is not valid in all areas where horseshoe crabs spawn. In Delaware Bay and areas of Maine, horseshoe crab spawning coincides with the full and new moons at the beginning of the season but not at the end of the season (Smith *et al.*, 2002b; Shaller *et al.*, 2005). On Cape Cod, spawning in some areas occurs every day during the breeding season, regardless of the lunar cycle (Cavanaugh, 1975; Leschen *et al.*, 2006) but in other areas is associated with the new and full moons (James-Pirri *et al.*, 2005). In Florida, the timing of spawning varies within the state. On Mashas Sands and surrounding areas of the Panhandle, horseshoe crabs

come to the beaches only during spring tides, never during neap tides (Rudloe, 1980). However, in St. Joseph Bay only 50 miles away, horseshoe crab spawning is not synchronized with the lunar cycle (Rudloe, 1985). Around Cedar Key, more horseshoe crabs spawn during the full moon than the new moon, but they also spawn throughout the lunar cycle (Cohen and Brockmann, 1983; Brockmann, 2005). Finally, in the IRL horseshoe crabs show no lunar spawning pattern (Ehlinger *et al.*, 2003).

In addition to variation in their seasonal patterns of spawning, horseshoe crabs also show a great amount of variation in their daily patterns. Horseshoe crabs preferentially lay eggs during periods of high water, which may be caused by high tides or wind. On Cape Cod, horseshoe crab spawning peaks about one hour after high tide, and more animals are on the beach during the higher of the two daily tides (Barlow *et al.*, 1986; Widener and Barlow, 1999). In Delaware Bay, spawning is affected more by wave height than by tide height—when waves are too high, horseshoe crabs do not come to the beach (Smith *et al.*, 2002b; Pooler, 2005). In the Mashas Sands area of Florida, spawning activity occurs within two hours of the high tide, but in summer it occurs only during the nighttime high tide (Rudloe, 1980). In the Cedar Key area, more horseshoe crabs are on the beach during the higher of the two tides, whether during the day or the night; however, if the tide does not exceed one meter, almost no animals come ashore (Brockmann, 2005). In the IRL, spawning occurs throughout the tidal cycle (Ehlinger *et al.*, 2003). Horseshoe crabs may also be deterred from approaching the beach by adverse environmental factors, such as strong off-shore winds and cold temperatures (Brockmann, 2005; Ehlinger *et al.*, 2003).

Why are some populations in synchrony with the lunar and tidal cycles and others are not? Penn and Brockmann (1994) found that on Delaware Bay beaches, tidal amplitude and beach draining are greater than on beaches near Cedar Key. The aerobic sediments suitable for egg and larval development are therefore higher on the beach in Cedar Key. The water generally reaches this level of the beach only during the high spring tides, so horseshoe crabs in this part of Florida spawn mostly at these times. In Delaware Bay, the high tides may reach the aerobic part of the beach even during neap tides, so horseshoe crabs spawn throughout the lunar cycle. Similarly, in the IRL where tides are only approximately 5 cm, horseshoe crabs may spawn at any time because there is little difference between spring and neap tides or between high and low tides. Thus both beach morphology and tidal amplitude appear to influence spawning.

Horseshoe crabs are unusual among marine in-



Figure 3 A pair of horseshoe crabs in amplexus. The female is on the bottom.

vertebrates in that they leave the water to spawn. Beach nesting comes with obvious risks: animals are exposed to extreme temperatures, low moisture, and the risk of being stranded. In addition, they must synchronize with other individuals to assure reproduction. This decreases the number of opportunities they have to reproduce while increasing competition for mates and nesting space. These risks are offset by the benefits of good conditions for egg and larval development and protection of eggs from many marine predators (Botton and Loveland, 1989; Penn and Brockmann, 1994).

Female horseshoe crabs approach the beach from offshore while the males are swimming parallel to the beach. As a female crosses this “stag line,” a male will almost always attach to her carapace. In most cases, a male attaches to the first female he encounters, but both very small and very large males may wait for females closer to their size (Suggs *et al.*, 2002). The male uses his claspers to hold on to the trailing edge of the female’s cephalothorax, overlapping her abdomen, in a position known as amplexus (Figure 3). Over time, a female develops mating scars at the attachment and overlap points. Males find females visually, although they often attach to other objects of similar shape and size (Brockmann, 1990). After the male grabs the female, she tows him to shore, where she burrows near the water line. Males that don’t attach to a female (satellite males) often come ashore alone and gather around an attached pair. Females rarely approach the beach alone.

To make a nest, the female burrows into the sand, digging with her pusher legs to create a slurry of sand

and water (Shuster and Sekiguchi, 2003). She then extrudes her eggs and stirs them into this mix. At the same time, the male or males release their sperm to fertilize the eggs. After releasing a clutch, the female may move forward slightly and begin again. Each clutch takes an average of eight minutes to be extruded, and each female can lay up to 15 clutches during one beach visit (Brockmann, 1990). Neither completion time nor clutch size are correlated with female size (Brockmann *et al.*, 2000); however, larger females develop more eggs than do smaller females, so they probably produce more clutches or nest more often (Leshcen *et al.*, 2006). When nesting is complete, the attached pair return to the water together. Horseshoe crabs find their way back to the water principally by following the slope of the beach (Botton and Loveland, 1987). During the spawning season, they bury in the sediment near shore until the next nesting event (Brockmann, 2003a). In one study, 95% of tagged females spawned repeatedly, often on consecutive nights and near the same spot on the beach (Brousseau *et al.*, 2004). Satellite males return to the same beach more often during a spawning season than do females or attached males (Cohen and Brockman, 1983).

Many more males than females approach the beach during spawning season. On Cape Cod, the ratio of males to females can be as high as 10:1 (Cavanaugh, 1975) but is usually closer to 2.5:1 (James-Pirri *et al.*, 2005). In the Florida Panhandle, the sex ratio is usually around 3.5:1 (Rudloe, 1980). The presence of satellite males represents an alternative reproductive strategy



Figure 4 Mating pairs of horseshoe crabs with satellite males.

in this species (Figure 4). Near Cedar Key, approximately half of the mating pairs had at least one satellite male (Cohen and Brockmann, 1983). Amplexed and satellite males do not differ significantly in size (Cohen and Brockmann, 1983; Brockmann, 1990; Loveland and Botton, 1992), but the condition of the carapace (number of injuries, amount of fouling, damage to eyes, etc.) may determine if a male attaches to a female (Brockmann and Penn, 1992; Duffy *et al.*, 2006). Males in good condition attach to females more often than those in poor condition, either because they have a greater ability to find females or a greater ability to stay attached. In fact, males in good condition will stay offshore if they cannot attach to a female rather than become satellites. Males in poor condition will act as satellites, and those in intermediate condition will switch strategies as needed (Brockmann, 2002).

What are the advantages of having two reproductive strategies? Attached males are in the best position to fertilize the eggs but cannot eat or bury (Botton and Loveland, 1992). Satellite males are often in poor condition and seem unable to attach or stay attached to females. By releasing sperm near the female, each satellite male has the potential to fertilize some of her eggs (Brockmann *et al.*, 2000). The success of fertilization does not depend on male size, but satellite males are more likely to be attracted to larger females, possibly because the greater surface area around her nest increases the chance that their sperm will reach the eggs (Brockmann, 1996). The combination of these two reproductive strategies means that most males pass on

their genes to some extent, and nearly all eggs are fertilized (Loveland and Botton, 1992).

The reproductive organs of the horseshoe crab consist of tubular gonads coiled extensively throughout the cephalothorax. Gametes (eggs or sperm) can mature anywhere along the length of this tube and then pass through gonoducts in the abdomen to the gonopore (Makioka, 1988). Female horseshoe crabs are determinant spawners, meaning that all eggs they will lay during a spawning season develop at the same time and are stored until needed (Leschen *et al.*, 2006). Based on mean egg volume, the average female holds approximately 450 ml of eggs, enough for 22 clutches. At a rate of 5–7 clutches per tide, she could be empty in 3–4 tides (Shuster and Botton, 1985).

Horseshoe crabs have external fertilization, which means that the sperm fertilize the eggs outside of the female's body. Spawning behavior increases the chance of the gametes coming together. Eggs remain viable after release for up to 40 minutes at 28°C; sperm remain viable for up to two hours at the same temperature (Brockmann *et al.*, 2000). Horseshoe crabs are the only arthropods that have free-swimming sperm, and these sperm travel at least 20 cm to reach the eggs (Brockmann, 2003b). A male can increase the chance of his sperm fertilizing eggs by altering the flow of water around the nest or by being in the closest position to the female's gonopore. For this reason, the attached male has the greatest chance of fertilizing the eggs, although his success is reduced to 51% when one satellite male is present and to 23% when two or more

satellite males are present. On average, 74% of larvae that survive hatching are fathered by satellite males (Brockmann *et al.*, 2000).

OTHER ANATOMY AND PHYSIOLOGY

Because of its pharmaceutical use, the blood of horseshoe crabs has been studied by many researchers. Horseshoe crabs have an open circulatory system, which means the blood does not stay in blood vessels throughout its circuit but pools around the organs in sinuses before returning to the heart. The heart is elongated, extends about half the length of the body, crosses the joint between the cephalothorax and the abdomen, and lies just beneath the carapace. The blood leaves the heart via a large anterior artery and returns through eight ostia, or openings, along the side (Shuster and Anderson, 2003).

The blood of the horseshoe crab is more properly called hemolymph because it is a mixture of blood and lymph. Hemolymph makes up one-third of the body mass and contains two types of cells: the numerous amebocytes and the more scarce cyanocytes. Cyanocytes produce hemocyanin, the oxygen-carrying molecule found in horseshoe crabs, as well as in other arthropods and mollusks (Leibovitz and Lewbart, 2003). The hemocyanin floats freely in the hemolymph, and the copper in the molecule gives it a characteristic blue color. The amebocytes function in the immune response. When the animal is injured or when bacteria are present, the amebocytes become motile and develop an adhesive coating. This causes clotting of the blood and prevents excessive bleeding or transport of bacteria (Armstrong, 2003).

Vision is perhaps the most studied aspect of horseshoe crab physiology. Horseshoe crabs have two large compound eyes that are composed of individual units called ommatidia (Figure 5). Each ommatidium contains a lens and a cornea. Because the neural reaction to light is fairly simple to follow, horseshoe crab vision has been studied in depth. The compound eyes detect movement but do not form clear images. Barlow *et al.* (1982) showed that males use their vision to find mates based on shape, movement, and contrast with the sediment. Adult horseshoe crabs are active at night, and the sensitivity of the compound eyes increases one million times after sunset (Barlow and Powers, 2003). This response is hormonally controlled and involves changes to the ommatidia that decrease the resolution of the eyes but increase the field of view (Barlow *et al.*, 1980).

The compound eyes are not the only eyes on a horseshoe crab; in fact, they have a total of ten eyes. Near the front of the carapace are two median ocelli, which have lenses, form images, and are sensitive to ultraviolet light (Barlow and Powers, 2003). The other



Figure 5 The compound eye of a horseshoe crab.

eyes only detect light and do not form images. They include two rudimentary lateral eyes near the compound eyes, one endoparietal eye between the median ocelli, two ventral eyes on the underside near the mouth, and a set of receptors along the telson.

Other aspects of horseshoe crab anatomy and physiology are not as well studied as their blood and vision. The digestive system consists of a simple alimentary canal located below the heart, with the mouth in the middle of the cephalothorax between the legs. Food is manipulated toward the mouth by the chelicerae and other appendages and ground by the gnathobases of the legs. The esophagus runs through the center of a doughnut-shaped brain. A gizzard further grinds the food, and a digestive gland excretes enzymes to complete digestion. Salt and water excretion take place in coxal glands, which open at the base of the walking legs, and in the gills. In water above 23‰ salinity, horseshoe crabs maintain the same salinity inside their bodies as in the surrounding environment. In water below 23‰ salinity, horseshoe crabs osmoregulate by retaining ions (such as calcium) at the coxal glands or actively taking up ions at the gills, which allows them to maintain an internal salinity that is higher than the surrounding environment (Towle and Henry, 2003).

Finally, like all arthropods, horseshoe crabs must molt to grow. When an individual is ready to molt, a new, soft, and folded exoskeleton begins to form beneath the old one. The old carapace splits along the forward edge, allowing the animal to crawl out. The now-soft animal is highly permeable to water and swells up, increasing in size. Then the exoskeleton absorbs minerals from the seawater that harden the carapace. After the carapace hardens, the horseshoe crab loses the excess water, leaving it room to grow into its new carapace. The time between molts and the time for a molt to occur both increase as the horseshoe crab increases in size; large animals take up to 12 hours to molt (Shuster and Sekiguchi, 2003). For many years, horse-

shoe crabs were believed to have a terminal molt (no molting after maturity), because no one had ever seen a mature horseshoe crab molting. However, Carmichael *et al.* (2003) showed that the average final instar juvenile would need to grow 20%–92% with one molt to achieve the average size of adults, much higher than the expected maximum growth increment of around 20%. Other evidence for continued molting after maturity includes discoveries of adult-sized molts on beaches and molts with mating scars.

Ecology

HABITAT

Horseshoe crabs lay eggs on sandy, low-energy beaches. When females approach a beach to spawn, they can discriminate between beaches with different biochemical characteristics, probably via water-borne cues (Botton *et al.*, 1988). Some portion of the population spawns in marginal habitat, but in these areas, egg and larval mortalities are high (Smith *et al.*, 2005). Embryos and larvae can tolerate a broad range of temperatures and salinities, traits necessary for animals that live in the fluctuating environment of intertidal beach sediments. Embryos are less sensitive to high salinities than to high temperatures; they can develop to larvae in salinities of 10–70‰. The optimal temperature for embryonic development is 30°–33°C, but 35°C is lethal (Ehlinger and Tankersley, 2004). Although larvae survive across a wide range of environmental conditions, their development is slowed by high temperature, high salinity, or low salinity (Laughlin, 1983; Ehlinger and Tankersley, 2004). After larvae metamorphose to juveniles, they live on intertidal flats near their natal beach (Shuster, 1979). The smallest juveniles live at the lower limit of the intertidal zone; juveniles move farther offshore as they increase in size (Rudloe, 1981). In Delaware Bay, most juveniles move to deep water by September of the year they hatch (Burton *et al.*, 2005).

While on the beach, adult horseshoe crabs encounter many risks, principally exposure to high temperature and desiccation. Although adults have a lower tolerance to extreme salinities than larvae and juveniles do, they have a higher tolerance to high temperatures (Ehlinger and Tankersley, 2004). Annually, approximately 10% of horseshoe crabs that come to the beach to spawn die from desiccation while stranded. Horseshoe crabs can become stranded when they cannot find their way back to the water or when wave action or males jostling for position around a female cause them to overturn. An unattached male is especially vulnerable to being overturned without a female to stabilize him. Once overturned, a horseshoe crab may right itself with its telson, but a missing or injured telson decreases the chance that

a horseshoe crab will be able to turn over. Because the risk of overturning correlates to weather conditions, some animals reduce that risk by not spawning during the roughest weather (Botton and Loveland, 1989). Horseshoe crabs also appear to prefer spawning on narrow beaches, possibly because the risk of stranding is lower (Smith *et al.*, 2002a). Stranding occurs more often on flat beaches; Botton and Loveland (1987) found that both blinded and sighted horseshoe crabs could find their way to the water on sloped beaches, but both had difficulty on flat beaches. If stranded upright on the beach between high tides, horseshoe crabs can bury in the sediment to conserve energy and keep their gills moist. Older males strand significantly more often than younger males, either because they are more likely to be unattached or because they have more trouble righting themselves when overturned (Penn and Brockmann, 1995).

During the spawning season, between trips to the beach, adults remain 100–400 m offshore in 8–30 m of water (Rudloe, 1980; Barlow *et al.*, 1986). When they are not spawning, adult horseshoe crabs live on the continental shelf. About 20% bury in the sediment, and the rest crawl along the surface (Carmichael *et al.*, 2003). Trawls have captured adults in waters up to 290 m deep off North Carolina (Botton and Ropes, 1987) and up to 246 m deep off Delaware Bay (Shuster, 1982); no trawling for horseshoe crabs has been conducted off the coast of Florida. The greatest depth at which a horseshoe crab has been observed was at 1,097 m by a remotely operated camera approximately 200 miles east of Charleston, South Carolina (Botton and Ropes, 1987).

POPULATION STRUCTURE

Based on differences in carapace sizes between areas, Shuster (1979) suggested that horseshoe crabs form discrete populations. Genetic studies have supported this idea. In 1970, Selander *et al.* found high genetic variation both within and between populations. In particular, they found a difference in polymorphism (a measure of genetic variation) between Atlantic and Gulf of Mexico populations. Saunders *et al.* (1986) used more advanced techniques to find a major genetic break in the Atlantic populations somewhere between Brunswick, Georgia, and Cape Canaveral, Florida. This was not surprising because northeast Florida is a transitional area between warm temperate and subtropical zones, and many other species have genetic breaks there; however, they did not find genetic breaks in horseshoe crab populations in other transitional areas. Saunders *et al.* (1986) also found some evidence of genetic differences between horseshoe crabs on the Atlantic and gulf coasts of Florida. King *et al.* (2005) conducted the largest study so far of horseshoe crab

population genetics. They sampled throughout the species' U.S. range and defined four management units based on genetic discontinuities: Gulf of Maine, mid-Atlantic, Atlantic Florida, and Gulf of Mexico Florida. They found gene flow (integration of genes into a population) between neighboring populations of horseshoe crabs, which is most likely due to migration of male crabs, but more distant populations were isolated from one another. They also sampled horseshoe crabs from the Yucatán peninsula, Mexico, and found them to be very different genetically from the U.S. populations, perhaps different enough to be a separate species. King *et al.* sampled extensively along the Atlantic coast but at only three sites in Florida: the northern IRL, Cedar Key, and St. Joseph Bay. Researchers at FWRI are currently sampling other areas along the Florida peninsula to better understand where the break occurs between the Atlantic Florida and Gulf of Mexico Florida populations.

Gene flow may be limited on an even smaller scale. Pierce *et al.* (2000) found genetic evidence for restricted interaction between Delaware Bay and Chesapeake Bay horseshoe crabs. Tagging studies by Swan (2005) also showed that movements of horseshoe crabs are restricted between these two bays. James-Pirri *et al.* (2005) found similar results in a tagging study at several locations along Cape Cod. Burger *et al.* (2002) found the type and level of heavy-metal deposition in the carapace of horseshoe crabs to be very different even between geographically close populations. If horseshoe crabs moved between areas, their exposures to heavy metals should be similar. Similarly, stable isotope studies have shown that horseshoe crabs remain in specific areas for long periods of time (O'Connell *et al.*, 2003; Carmichael *et al.*, 2004).

COMMUNITY RELATIONSHIPS

Horseshoe crab larvae do not feed; they depend on left-over yolk to nourish them while their digestive systems complete development (Shuster and Sekiguchi, 2003; Botton *et al.*, 2003c). Juvenile diet changes with growth: instars 2–4 feed on organic matter in the sediments, instars 5–11 feed on mostly crustaceans and polychaetes, and instars higher than 11 feed on prey similar to those consumed by adults (Gaines *et al.*, 2002). Adult horseshoe crabs are generalists, feeding on almost any prey they can capture. Botton and Ropes (1989) identified 50 different groups of organisms from the stomach contents of adult horseshoe crabs, including mollusks, arthropods, polychaete worms, and vascular plants. Horseshoe crabs eat principally bivalves, which make up 93% of the weight of their diet and 94% of their calorie intake. Although vascular plant material and organic

matter are not efficiently assimilated by horseshoe crabs, they may be important in providing components to build chitin (Carmichael *et al.*, 2004). Horseshoe crabs find prey using chemoreceptors on their claws and on their gnathobases. They use their legs and gills to stir up sediment and water and then capture prey with their legs (Botton, 1984; Botton *et al.*, 2003c).

Horseshoe crabs have different predators at different stages of their life cycle. The most studied feeding relationship is that between horseshoe crabs and migrating shorebirds. This relationship was first recognized in the 1980s (Botton *et al.*, 2003a). Each year many shorebirds migrate from their wintering grounds to their breeding grounds, often over great distances. The Red Knot (*Calidris canutus rufa*), for example, travels from the southern tip of South America to the Canadian Arctic. These birds make their last stop each year in Delaware Bay before heading to their breeding grounds; this stop usually coincides with the spawning season of horseshoe crabs. They must eat a tremendous amount to store enough energy to fly to the Arctic and lay their eggs, and much of this energy comes from horseshoe crab eggs. Botton *et al.* (1994) estimated that the entire migrating shorebird population in Delaware Bay would require 44,000 eggs/m² to meet their energy needs. Although each horseshoe crab egg contains very few calories, the huge numbers of eggs on the beach during the spring spawning season may provide enough food for these birds to increase their body weight by 70%–80% (Tsipoura and Burger, 1999). Despite the high numbers of eggs consumed, shorebird predation has little impact on the horseshoe crab population. The eggs that are eaten have washed to the surface or have been excavated by later-spawning females. Exposure to heat and desiccation would prevent survival of these eggs anyway.

Not all shorebirds migrate to South America. Many birds winter in Florida instead, particularly on the west coast, and many birds that do migrate to South America stop in Florida on their return north. Sprandel *et al.* (1997) surveyed 60 sites in Florida and found that of the nine sites with the highest migrating shorebird abundances, six were in Tampa Bay, two were in Florida Bay, and one was in Apalachicola Bay. However, there were no reports of large numbers of shorebirds co-occurring with peak numbers of spawning horseshoe crabs at any of these sites (Wallace, 2000). Because populations of horseshoe crabs are relatively small in Florida, their eggs provide a less dependable food source than those in Delaware Bay do; therefore, the presence of horseshoe crab eggs in the diet of Florida shorebirds is probably opportunistic (N. Douglas, personal communication).

Other animals besides migrating shorebirds prey on horseshoe crab eggs. Resident birds, particularly gulls, also feed on eggs, often chasing away the smaller shorebirds. Many small fish, such as killifish, can reach the nests near the waterline (Cohen and Brockmann, 1983). In the areas where horseshoe crabs nest subtidally, eggs are eaten by larger fish, including striped bass, white perch, weakfish, kingfish, and flounder. Sometimes eels and catfish consume the eggs even as they are being laid. These same predators also feed on horseshoe crab larvae. As small juveniles, horseshoe crabs are preyed on by blue crabs, spider crabs, hermit crabs, and fiddler crabs (Botton *et al.*, 2003c).

Large subadult and adult horseshoe crabs have few predators. They are too large and their carapace is too hard for many animals to eat them. Loggerhead turtles feed on horseshoe crabs by turning them upside down and scooping out the carapace with their beak (Botton *et al.*, 2003c). Occasionally, sharks and alligators may feed on adult horseshoe crabs (Shuster, 1982; G. Ehlinger, personal communication). If overturned on the beach, horseshoe crabs may be attacked by Herring and Black-backed gulls, which feed on the exposed gills and legs. After death, flies and beetles lay their eggs in the carcass, and amphipods feed on the remains. Chitin-decomposing bacteria attack the carapace quickly, but decomposition is slow, taking four months to decrease the weight of the carapace by half (Botton and Loveland, 1989).

Horseshoe crabs have symbiotic relationships with other organisms. Many organisms, such as barnacles, bryozoans, mussels, and slipper shells, attach to the hard carapace (Leibovitz and Lewbart, 2003), although a protein secretion covering the carapace in healthy horseshoe crabs seems to prevent heavy fouling (Harrington, 2000). Other symbionts do not attach to the carapace. Juvenile pinfish and juvenile blue crabs will follow a horseshoe crab as it ploughs through the sediment. The digging action stirs the sediment, bringing organic particles into the water where the fish and crabs can eat them. These animals also temporarily use the horseshoe crab for shelter by hiding under the carapace when predators approach. In fact, a pinfish will defend its horseshoe crab "territory" against other pinfish (Rudloe, 1985).

Some symbionts harm the horseshoe crab. Ciliates (single-celled "protozoans"), turbellarid worms, and nematodes can become parasitic (Leibovitz and Lewbart, 2003). Some worms lay eggs on the book gills, creating atrophied areas that provide entry points for bacteria (Groff and Leibovitz, 1982). The most common infection is a green alga that grows into the carapace. The alga fuses the old carapace to the new

underlying carapace, preventing molting. It also breaks down the carapace, eventually damaging the eyes and ligaments; it finally invades the heart, causing death (Leibovitz and Lewbart, 2003).

Horseshoe crabs interact indirectly with other organisms by altering their habitat. Foraging horseshoe crabs burrow approximately one-third of their body height into the sediment, disrupting the entire bottom community (Rudloe, 1985). In some areas with pits dug by horseshoe crabs, both diversity and abundance of other benthic species decrease (Woodin, 1978); in other areas, burrowing horseshoe crabs resuspend organic matter from the sediments and increase the abundance of species in the surrounding water (Kreuter and Fegley, 1994). Increased organic matter in the sediment near horseshoe crab nesting areas may also increase the abundance of some other benthic species. In one study, sediment samples from areas without eggs contained 500 nematodes/10 cm³, but sediment samples from areas with eggs contained 5,000 nematodes/10 cm³. The nematodes do not actually penetrate the eggs but feed on the shells after the eggs hatch (Hummon *et al.*, 1976).

Horseshoe Crab Management

Fisheries

The fisheries for horseshoe crabs have changed over the years. Before anyone discovered a commercial use for horseshoe crabs, they were considered a nuisance species in the U.S., particularly to the shellfish fishery. Horseshoe crabs are responsible for most juvenile surf clam (*Spisula solidissima*) mortality (Botton and Haskin, 1984). Some municipalities even offered a bounty for each telson a person brought in to show that they had killed a horseshoe crab (Ruteki *et al.*, 2004). Horseshoe crabs in Asia were (and still are) occasionally eaten (Shuster *et al.*, 2003). Beginning in the mid-1800s, horseshoe crabs were ground up for fertilizer. This fishery was fairly large, with landings of a few million horseshoe crabs per year. Ground horseshoe crabs and eggs were also fed to poultry and hogs. The fertilizer business began to decline in the 1930s and ended completely in the 1970s (Shuster, 2003). Around this time, other uses were found for horseshoe crabs.

THE BAIT FISHERY

Two different fisheries use horseshoe crabs for bait: the eel fishery and the conch fishery. The eel fishery targets mature female horseshoe crabs because their eggs attract eels. Florida has a small eel fishery on the St. Johns River; for the 2005–2006 season, 8 harvesters

bought eel permits, which allow them to catch horseshoe crabs for bait (K. Bonvechio, personal communications). Because of bag limits in Florida, most eel fishers have turned to alternative baits; in Florida, only 75 horseshoe crabs were landed in 2004 for bait, and none were landed in 2005 (FWC, 2006c). The conch (*Busycon* spp.) fishery uses both male and female horseshoe crabs as bait. Horseshoe crabs are usually chopped in half or into quarters and placed in bait bags. The conch fishery is much larger than the eel fishery along the Atlantic coast (Shuster *et al.*, 2003), but Florida does not have a conch fishery.

Fishermen began using horseshoe crabs for bait in the mid-1970s (Shuster, 2003). Landings data reported here were compiled from each state by the National Marine Fisheries Service (NMFS, in pounds) and ASMFC (in numbers). Until recently, harvesters in most states were not required to report landings of horseshoe crabs; therefore, landings were probably underestimates of the true harvest. From 1970 to 1975, Atlantic-coast landings averaged 49,667 pounds per year (NMFS, 2006); from 1976 through 1993, landings averaged 676,641 pounds per year. Conch fishing increased dramatically in the mid-1990s, and horseshoe crab bait landings on the Atlantic coast peaked at 6,835,305 pounds (2,748,585 animals) in 1998, when a horseshoe crab management plan was implemented (ASMFC, 2000a). After the plan's implementation, landings declined coastwide to 973,425 pounds (681,388 animals; ASMFC, 2005b) in 2004.

In 1999, ASMFC conducted a workshop introducing bait bags that reduce bait usage by up to 50% (ASMFC, 2000a). These bait bags were distributed free to conch fishermen in the mid-Atlantic region; the decline in horseshoe crab landings after this date can be attributed at least partially to the use of the bait bags (ASMFC, 2005b). Researchers in Massachusetts are examining ways to further reduce the amount of bait used by changing the design of the bait bags. A new bait cup preserves the horseshoe crab enough that one animal can be used to bait ten traps (ASMFC, 2005b). All fishermen in Massachusetts voluntarily use these bait cups. Researchers at the University of Delaware are trying to isolate the chemical in horseshoe crabs that attracts eels and conchs (Ferrari and Targett, 2003; Wakefield and Targett, 2005). Characterization of the substance is proving difficult, because the attractant appears to be a mixture of several compounds. If the substance can be replicated, artificial bait could be manufactured.

In Florida, reported landings remained low through 1998, when only 200 horseshoe crabs were reported as landed by the bait fishery (Figure 6; FWC, 2006). However, in 1999, an increase in fishing effort in north

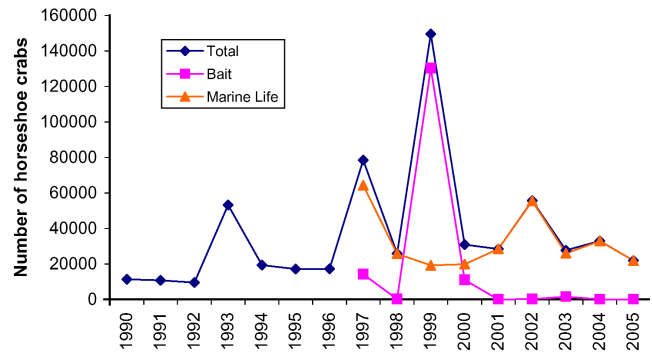


Figure 6 Florida horseshoe crab landings as reported on trip tickets (FWC Marine Information System). Horseshoe crab landings were not recorded before 1990. Bait and marine-life landings were not recorded separately until 1997.

Florida, especially near Port St. Joe in the Panhandle, led to an increase in landings. In that year, fishermen in mid-Atlantic states were experiencing a bait shortage that was due to increased regulation of horseshoe crabs in Delaware Bay. In addition, the St. Joe paper mill near Port St. Joe closed, leaving many people unemployed, and a local company, Raffield Fisheries, encouraged many of the out-of-work people to collect horseshoe crabs to send north for bait. Raffield Fisheries estimated that they sold approximately 99,000 horseshoe crabs in 44 days (Wallace, 2000). By 2001, Florida horseshoe crab bait landings decreased to zero and have remained relatively low since.

THE MARINE-LIFE FISHERY

In Florida, most horseshoe crabs are captured alive for the marine-life fishery. As reported on trip tickets, marine-life harvesters in Florida landed 22,019 horseshoe crabs during 264 trips in 2005 (Figure 6; FWC, 2006). Approximately three-quarters of the harvesters used scuba gear to collect horseshoe crabs; the others collected animals by hand on the beach or while snorkeling. Horseshoe crabs were collected in all months, but the majority were collected during the first half of the year. The highest numbers of horseshoe crabs were harvested in the Florida Keys (49%; Figure 7). The average price of a horseshoe crab sold by the marine-life fishery was \$1.21 in 2005 (FWC, 2006).

In August of 2003, the FWRI Crustacean Fisheries Group asked 40 marine-life harvesters to provide sexes and sizes of a random sample of their catch; only five responded. Most of the animals reported were juveniles that were 1"–2" PW and were sold for aquaria. Other horseshoe crabs collected by marine-life harvesters were used in research and education; these animals were usually adults that were 6"–10" PW (FWRI, unpublished data).

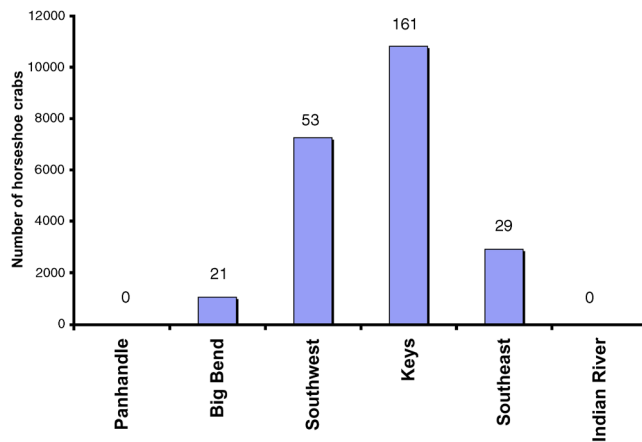


Figure 7 Regional landings of horseshoe crabs by the marine-life fishery in Florida during 2005 as reported on trip tickets (FWC Marine Information System). The numbers over the bars are the number of trips for each area.

Florida is the only state that requires separate reporting of marine-life harvest on trip tickets. In fact, little is known about the collection of live horseshoe crabs for resale outside of Florida. In Delaware, bait harvesters are allowed to resell horseshoe crabs to the marine-life or biomedical industries, but those animals count against the bait quota (S. Michels, personal communication). Most states have a standard scientific collecting permit that allows the collection of restricted species for research and education. These permits are issued on a case-by-case basis and have annual reporting requirements. Delaware, Maryland, Massachusetts, and Virginia allow a small number of horseshoe crabs to be taken for personal use, but they cannot be sold (R. Unsworth, personal communications).

THE BIOMEDICAL FISHERY

Beginning in 1885, scientists noted that horseshoe crab blood clots in the presence of gram-negative bacteria (Novitsky, 1984). Most pathogenic (disease-causing) bacteria are gram-negative and produce endotoxins that cause fever. In the 1950s, Frederik Bang discovered the causative agent for clotting, a compound found in the horseshoe crab amebocyte cells. He and his colleagues isolated this compound by lysing, or breaking, the cells; the resulting substance was thus named *Limulus Amebocyte Lysate* (LAL). At that time, the Food and Drug Administration (FDA) tested drugs for endotoxins by injecting them into rabbits. In 1977, Associates of Cape Cod was the first company licensed by the FDA to make LAL as an alternative test for endotoxins. Currently five companies extract horseshoe crab blood, three of which produce LAL. The LAL test

is 1,000 times more sensitive than any other method to detect endotoxins and is now required by the FDA for testing all injectable drugs and implantable devices sold in the U.S. (Levin *et al.*, 2003).

To obtain LAL, harvesters collect large horseshoe crabs (usually female) and take them to a sterile facility. The animal is flexed at the joint between the cephalothorax and the abdomen, and a needle is inserted into the heart. The blood flows by gravity into a collecting container. Each horseshoe crab is bled for approximately three minutes, and about 30% of the blood volume is removed. Next, the blood is centrifuged to remove the amebocytes, which are then lysed. Other components are added to the solution to improve stability and solubility. To test a product for endotoxin, equal amounts of LAL and test solution are mixed. If endotoxins are present, the solution will gel (Levin *et al.*, 2003). The concentration of endotoxin can be calculated based on how long the solution takes to gel, but the species of bacteria producing the endotoxin cannot be determined. For this reason LAL has limited use in detecting diseases in humans, although it has been used to diagnose spinal meningitis, urinary tract infections, and gonorrhea (Novitsky, 1984).

Bleeding appears to have a minor effect on horseshoe crabs. In studies on survival of bled horseshoe crabs, mortality was 8%–20% (Rudloe, 1983; Kurz and James-Pirri, 2002; Walls and Berksen, 2003). Hurton and Berkson (2004) found no mortality in crabs held under low-stress conditions even when 40% of the blood volume was extracted. They found significantly higher mortality when horseshoe crabs were exposed to external stressors such as high temperature and air exposure, which are typically associated with transport and holding of animals. Bleeding could have indirect effects; bled horseshoe crabs can become disoriented, which may prevent them from finding nesting beaches, which in turn could ultimately reduce reproduction (Kurz and James-Pirri, 2002).

Coastwide, 283,720 horseshoe crabs were used by the biomedical industry in 2005 (ASMFC, 2006c). In Massachusetts, a “rent-a-crab” program reduces overall mortality of harvested horseshoe crabs. Bleeding facilities borrow horseshoe crabs (39,429 animals in 2005) from bait fishermen, remove blood, and then return the animal for use as bait. Thus the mortality associated with bleeding is considered to be part of the bait fishery mortality. No harvesters have reported landing horseshoe crabs in Florida for the biomedical industry. The bleeding facility closest to Florida is in South Carolina, and horseshoe crabs do not appear in large enough numbers in Florida to support a biomedical fishery.

Stock Assessment

The size of a population of marine organisms usually cannot be counted directly; instead, statistical models are used to estimate population size and dynamics. These population models are only as accurate as the data put into them. For horseshoe crabs, much of the data needed is incomplete or is available only for a limited area of the horseshoe crab's range. Also, estimates produced by models are generally compared to some biological reference point that puts changes in context. For horseshoe crabs, a reference point is difficult to determine because historical data is lacking. Therefore, managers must use the best available data to produce stock assessments.

METHODS

The ASMFC horseshoe crab Stock Assessment Subcommittee (SAS) originally did not assess stocks with any models because of a lack of data over a sufficient length of time (ASMFC, 2004a). Because horseshoe crabs live a long time, at least ten years of data are needed to properly use statistical models. Instead, SAS used trend analysis to determine whether populations were increasing or decreasing over the duration of the studies. The trend analysis incorporated data from commercial landings, from surveys of the commercial catch, and from fishery-independent monitoring programs in four regions: the Southeast, Delaware Bay, New York, and New England. In the Southeast region, data came from surveys conducted by the Southeast Area Monitoring and Assessment Program (SEAMAP) and the states of Georgia and South Carolina. Results were mixed: the Southeast region showed a stable population, the Delaware Bay region showed a decline in horseshoe crabs since the 1980s, the New York region showed an increase in horseshoe crabs in the western portion of the area but a decrease in the eastern portion since the 1990s, and the New England region showed a stable or slightly declining population.

The data necessary for a horseshoe crab stock assessment are becoming more complete. Several new studies have started, and older studies continue. The major studies directed at assessing horseshoe crab populations include trawling studies (Delaware Bay, offshore mid-Atlantic), tagging studies (Delaware Bay, Maine, New York), egg surveys (Delaware Bay), and nesting beach surveys (most Atlantic coast states; ASMFC, 2006a). Recently, three groups of researchers have developed models to look at various aspects of horseshoe crab populations in Delaware Bay. These models can be considered intermediate steps to the ultimate goal of a true stock assessment. The first model

is a traditional surplus-production model that gives estimates of biomass and fishing mortality (Davis *et al.*, 2006). The mark-recapture study produces estimates of the spawning population size and harvest rates (Smith *et al.*, 2006). The age-structured population model simulates population dynamics in relation to various parameters; for example, changes in egg mortality produce the greatest changes in adult abundance (Sweeka *et al.*, 2005). The pending publication of these models prompted SAS in early 2006 to review each model by using the most recent data. They determined that each model has strengths and weaknesses, and together the models give a better understanding of the status and trends in Delaware Bay (ASMFC, 2006a). Their general conclusions about the Delaware Bay population were that (1) relative abundance has declined though the 1990s; (2) fishing mortality peaked in 1998 and has declined since; and (3) although harvest rates are less than 10% of the population, they are still in excess of the maximum sustainable harvest level.

ISSUES WITH ASSESSING HORSESHOE CRAB STOCKS

Federal fishery managers showed little interest in horseshoe crab population numbers until recently, when declines in shorebird populations triggered questions about declines in horseshoe crab populations. With so little historical data on population sizes, biological reference points are hard to establish. Models can detect decreases or increases in populations but cannot determine how they compare to "normal" populations levels.

Some researchers have attempted to estimate the sizes or changes in the sizes of stocks. On Cape Cod, the spawning population decreased 83% between 1984 and 1999 (Widener and Barlow, 1999). A study during the six years of recent management showed that spawning populations are either stable or decreasing slightly in Delaware Bay (Smith and Bennett, 2005). Mark-recapture estimates of adult horseshoe crab abundance in Delaware Bay were 19,980,000 in 2003 (Smith *et al.*, 2006) and 13,308,000 in 2004 (ASMFC, 2006a). Estimating numbers of horseshoe crabs when they are not on the beach has additional problems. Most trawling studies have not specifically targeted horseshoe crabs; instead, crabs were simply recorded as by-catch during finfish studies in which gear that was not designed for capturing horseshoe crabs was used. Even when horseshoe crabs are targeted, the gear misses the large number of crabs buried in the sediment (Hata and Berksen, 2004).

The lack of knowledge about horseshoe crab movements makes estimating population sizes even more difficult. Some populations may be resident; adults

may remain relatively close to their natal beaches throughout their lives, as they do in Chesapeake Bay (Pierce *et al.*, 2000), Mashas Sands (Rudloe, 1980), and the IRL (Ehlinger *et al.*, 2003). Other horseshoe crabs show fidelity to a beach during a spawning season but switch beaches between years (Swan, 2005).

The variation shown in population genetics studies suggests that biological information obtained about horseshoe crabs from one area of their range may not be applicable to horseshoe crabs from other areas. The most wide-ranging data necessary for population models deal with reproduction; for example, spawning behavior and fecundity (reproductive output per individual) have been studied throughout the U.S. species' range. Growth rates have been estimated (Rudloe, 1981; Carmichael *et al.*, 2003; Shuster and Sekiguchi, 2003) but can vary greatly with environmental conditions. Natural mortality rates have been calculated to some extent; for example, rates of mortality during early life stages (Carmichael *et al.*, 2003) and of mortality due to stranding (Botton and Loveland, 1989) have been calculated but only within small areas of the species' range. Another aspect of horseshoe crab biology that remains unclear is the age structure of the population. As stated above, size and age at maturity are difficult to calculate, especially for females. The long lives of these animals make them hard to study in the laboratory or in the field.

At this time, we cannot use the models presented above to assess the Florida population because most of the data needed is not available—only certain aspects of reproduction have been studied in Florida to the extent necessary for determining population estimates. The only estimates of population size in Florida were made by Rudloe (1980) for Mashas Sands. She estimated a population of 33,330 horseshoe crabs but concluded that she probably estimated only the male population. She also estimated that the size of the population at Bald Point was three to four times the size of the Mashas Sands population.

CURRENT HORSESHOE CRAB RESEARCH BY THE FISH AND WILDLIFE RESEARCH INSTITUTE

In an effort to identify the prime nesting areas for horseshoe crabs in Florida, FWRI began a public survey in 2002. The survey requests that citizens and visitors report any sightings of horseshoe crabs. Reports can be submitted through a website (research.myfwc.com/horseshoe_crab), on a toll-free phone line (1-866-252-9326), or via a dedicated e-mail (horseshoe@myfwc.com). Reporters are asked to provide the location and time that horseshoe crabs were sighted, state the approximate number of animals present, and

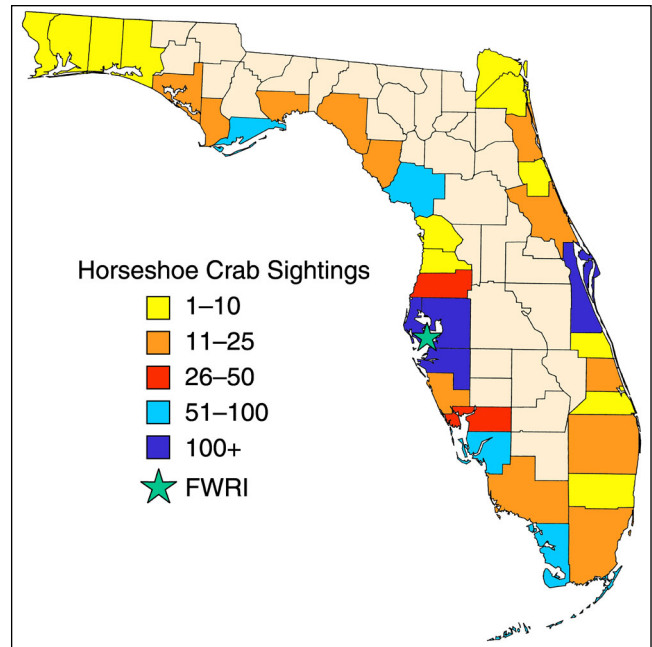


Figure 8 Numbers of reports of horseshoe crab sightings by county as reported to the Florida Horseshoe Crab Spawning Survey as of June 2006.

report if the animals were showing mating behavior. From its inception until June 30, 2006, FWRI has received 1,510 reports from the survey. Despite the vague details often received, this survey has helped locate major areas of horseshoe crab nesting. The highest number of reports has been from Franklin (site of Rudloe's work), Pinellas, Hillsborough, Manatee, and Brevard (site of Ehlinger's work) counties (Figure 8). Very few reports have been submitted from the far western portion of the Panhandle, northeastern Florida, and southeastern Florida. Survey reports are being mapped using GIS in conjunction with habitat maps to determine the characteristics of nesting beaches in Florida. FWRI has also initiated a more structured beach survey in Tampa Bay that is designed to collect data on the timing of reproduction, sex ratios, and sizes of horseshoe crabs on specific beaches in this area. The results will be compared to data collected in other areas of the state. A tagging study in conjunction with the beach survey will give information on site fidelity and other behavioral patterns.

Several studies have identified distinct horseshoe crab populations on the Florida Atlantic and Florida Gulf coasts, but the area where the genetic break between these two populations occurs has not been located. To try to find this area, FWRI began sampling horseshoe crabs on beaches throughout Florida in 2002 (as of December 2005, 560 samples have been analyzed). Sample sites include West Palm Beach, Bis-

cayne Bay, the Lower Keys, the Marquesas Keys, Marco Island, Punta Gorda, Safety Harbor, Cedar Key, and Alligator Point. From each animal, researchers clip a small portion of the pusher leg and return this tissue to the laboratory for genetic analysis. The sex and PW of each animal sampled are recorded. Tissue samples are analyzed using the same 14 microsatellite loci used by King *et al.* (2005).

History of Horseshoe Crab Fisheries Management

PAST MANAGEMENT

No regulations of the horseshoe crab fishery existed before 1991 at the state or federal levels (ASMFC, 1998). In that year, South Carolina lawmakers prohibited harvest of horseshoe crabs except for the biomedical industry. Within five years, New Hampshire, New Jersey, Delaware, Maryland, and Virginia had restrictions on horseshoe crab harvest. In 1997, ASMFC initiated development of a horseshoe crab fishery management plan in response to concerns over increased harvest in the mid-Atlantic states. The Interstate Fishery Management Plan for Horseshoe Crab (FMP) went into effect in December 1998.

The goal of the FMP is to “conserve and protect the horseshoe crab resource to maintain sustainable levels of spawning stock biomass to ensure its continued role in the ecology of the coastal ecosystem, while providing for continued use over time” (ASMFC, 1998). The FMP originally had six monitoring components designed to “collect information to assist in future management decisions”; some of these components applied only to the states where most of the harvest was taking place. The FMP also stated that a limit on landings would be developed and implemented in 2000 but that harvest for biomedical applications and scientific research would be exempt from these limits. The ASMFC reserved the right to take action if mortality from biomedical harvest exceeds 57,000 horseshoe crabs in any year.

Addendum I (ASMFC, 2000b) to the FMP established quotas for each state based on reference-period landings. The reference period varied among states but was within the years of 1995–1999. The cap for each state was set at 25% below the reference-period landings; states are required to close their fishery when the cap is reached. Addendum I defined *de minimis* status for states in which average landings for the previous two years constituted less than one percent of the total coastwide landings. States qualifying for *de minimis* status were exempt from some monitoring and surveying components of the FMP and were not subject to the 25%

decrease in landings. *De minimis* states must still gather commercial-landings data, continue any ongoing sampling programs, evaluate mortality of horseshoe crabs processed by the biomedical industry (if applicable), and identify potential horseshoe crab habitat. Because landings might shift to *de minimis* states from more regulated states, the ASMFC encouraged *de minimis* states to implement one of three management measures: close the horseshoe crab fishery when landings exceed the *de minimis* level, establish a landing permit available only to individuals with previous landings, or limit daily harvest to 25 horseshoe crabs per person per day. Also in Addendum I, ASMFC recommended that NMFS prohibit harvest in federal waters off Delaware Bay. In March 2001, NMFS established the Carl N. Shuster Jr. Horseshoe Crab Reserve, which covers 1,500 square nautical miles off the mouth of Delaware Bay.

Addendum II to the FMP (ASMFC, 2001) allowed transfer of quotas between states, with approval by ASMFC. Addendum III (ASMFC, 2004b) addressed several issues: decreases in the quotas for states in the Delaware Bay region, closure of the fishery in the Delaware Bay region during peak spawning times, and modification of the monitoring components of the original FMP.

In response to public concerns about the harvest of horseshoe crabs and the decline in shorebird populations, ASMFC implemented Addendum IV to the FMP in June 2006 (ASMFC, 2006b). This addendum prohibits harvest of all horseshoe crabs in New Jersey and Delaware before and during the peak spawning period (January 1 through June 7) and prohibits harvest of females at any time. Restrictions were also implemented for Maryland and federal waters off Virginia during the peak spawning period. In addition, the quotas for New Jersey and Delaware were each lowered to 100,000 horseshoe crabs per year. All of these regulations will remain in effect for two years.

The quota for Florida was set at 9,455 horseshoe crabs, based on reported landings in 1997. The total of reference-period landings for all states was 2,999,491 horseshoe crabs, setting the initial *de minimis* level at 29,995 (1%). The first regulatory action by Florida was in response to the 1999 increased harvest in the Panhandle. Concern about the spread of increased fishing to other parts of the state prompted the industry to work voluntarily with regulators to close the fishery until regulations could be initiated. In 2000, rules covering harvest restrictions, license requirements, gear specifications, and daily bag limits were entered into Florida Administrative Code, Chapter 68B-46. These rules were amended in 2002 to establish a biomedical collection permit and to designate horseshoe crabs as

a saltwater product, which requires the reporting of commercial landings on trip tickets. Proposed restrictions that were not passed included closed seasons, closed areas, and a permitting program (Teehan, 1999).

PRESENT MANAGEMENT

The FMP and its addenda are still in effect and are implemented by ASMFC. The Horseshoe Crab Management Board recommends actions on the FMP to the commissioners, based on information provided by several other groups. The Technical Committee includes a representative from each state (usually from the state regulatory agency), plus representatives from federal agencies. They provide a connection between the Management Board and individual states. The SAS assesses horseshoe crab populations; it consists of scientific experts who report to the Technical Committee. The Advisory Panel consists of citizens representing the fishery, environmental organizations, and others concerned with horseshoe crab management. Usually, each of these groups reports to the Management Board through the Plan Review Team. This team provides staff support to the Management Board. The FMP and a list of representatives of each group can be viewed on the ASMFC website at www.asmfc.org.

Florida statutes require a valid saltwater product license (SPL) for harvest, possession, or sale of horseshoe crabs. Any SPL holder may harvest up to 25 horseshoe crabs per day; those with either a marine-life endorsement or a permit to harvest eels may harvest up to 100 horseshoe crabs per day. Horseshoe crabs may be captured only by hand or gig. A biomedical collecting permit allows the holder to possess horseshoe crabs temporarily to extract blood. The holder is exempt from bag limits but must return the animals alive to the area where they were collected. Anyone possessing a biomedical permit must submit annual reports on the number of animals collected, locations of collection, and mortality of animals. The full regulations can be found on the Florida Administrative Code website (<http://fac.dos.state.fl.us/faconline/chapter68.pdf>).

All Florida wholesale dealers, and retailers who collect their own product, must submit a trip ticket for each trip during which saltwater products are collected. Trip tickets are submitted to FWC, and the data are entered into FWC's Marine Fisheries Information System. Required data include SPL number, trip date, time fished, area fished, gear fished, amount of catch, and unit price. Sizes are also requested; however, only 2.5% of trip tickets with horseshoe crab landings submitted in 2005 included size information. Furthermore, sizes are limited to small, medium, and large, which are not officially defined. A large horseshoe crab from the

bait fishery would not necessarily be similar in size to a large horseshoe crab from the marine-life fishery.

FUTURE MANAGEMENT

Management decisions by ASMFC now incorporate information on the interaction between horseshoe crabs and shorebirds. Because declines in migrating shorebird populations coincided with an increase in harvest of horseshoe crabs, many researchers believe that the birds have not been finding enough horseshoe crab eggs to support their energy needs. Castro and Meyers (1993) estimated that migrating shorebirds need approximately 539 metric tons of horseshoe crab eggs to obtain enough energy during their spring stopover in Delaware Bay. The most recent egg surveys show that there are not enough eggs available to supply that energy (ASMFC, 2005c). From the 1997–1998 season to the 2001–2002 season, the proportion of Red Knots leaving Delaware Bay at a healthy body weight decreased by 70% (Baker *et al.*, 2004).

Many migrating shorebird populations have declined, but the decline has been most dramatic in the Red Knot population. The number of Red Knots in their main wintering areas decreased from 67,500 in the mid-1980s to around 30,000 in 2003 (Morrison *et al.*, 2004). Numbers at other sites decreased even more dramatically, showing that the decline did not result from a change in wintering area. Baker *et al.* (2004) calculated predicted population trends based on 56% survival (1999–2001 survival rate) and 85% survival (1994–1998 survival rate). They found that at the lower survival rate, the Red Knot subspecies would become extinct by 2010. Subsequent counts in 2003 and 2004 showed that the populations maintained the lower survival rate. In July 2004, the Pennsylvania, New Jersey, and Delaware chapters of the Audubon Society submitted a petition to the U.S. Fish and Wildlife Service (USFWS, 2006) to list the Red Knot subspecies as an endangered species. Their main concern was the increased harvest of horseshoe crabs, which coincided with the decline in shorebirds. The USFWS began processing the petition in 2005, and in July, several other organizations submitted a petition for an emergency listing while USFWS continued the process. The USFWS determined that an emergency listing was not warranted because ASMFC and individual states were implementing management plans to reduce horseshoe crab harvest. In September 2006, the USFWS designated the Red Knot subspecies as a candidate for listing across its entire range. If the Red Knot is listed as an endangered species, harvest of horseshoe crabs may be restricted beyond the current regulations.

Potential Effects of an Increase in the Marine-Life Bag Limit

Potential Biological Effects

The effects of current harvesting on horseshoe crab populations in Florida are not known because accurate estimates of past and present population sizes are not known. However, we can foresee potential problems based on the information we have. Many reported marine-life landings are from southeastern Florida and the Florida Keys, because these areas have the highest concentration of marine-life collectors. Low numbers of horseshoe crabs in this area might be expected considering the relative dearth of suitable adult and spawning habitat. Some preliminary evidence collected by FWRI also suggests that the numbers of adult horseshoe crabs in these areas are low. Only 5% of reports to the FWRI public survey came from Palm Beach, Broward, Dade or Monroe (Keys portion only) counties, and almost all of those reports were in the lowest number-category of individuals (1–24 horseshoe crabs). In addition, FWRI scientists have had little success in attempts to collect adults from these counties for a genetics project. If the current population abundance is indeed low, extensive removal of individuals could hamper the ability of the population to sustain itself.

Another biological issue involves the age at which horseshoe crabs are collected. Animals of the size collected by marine-life harvesters are first- or second-year juveniles. They are well below the size where they could be mature, so they are removed from the population before contributing to the reproductive output. Removing immature individuals from a population results in fewer adults to replenish the population in future years (Walters and Martell, 2004).

Potential Management Effects

Although marine-life landings are not addressed by the current FMP, the ASMFC Management Board recently expressed concern over the relatively large number of horseshoe crabs landed by this fishery in Florida (B. Spear, personal communication). If ASMFC determines that marine-life landings should be included in the FMP, they could take several different actions.

- Include marine-life landings in the quotas allotted to each state. If this happened, and marine-life landings remained at current levels, Florida would exceed its quota and be out of compliance with the FMP. With the current bag limit of 100 horseshoe crabs per day, the quota could be exceeded after only 95 trips.

- Create a new quota specifically for marine-life

landings. In the 2005 ASMFC Report for Compliance, the Plan Review Team encouraged Florida to set its own limit on marine-life landings to ensure that the harvest would not “get out of control” (ASMFC, 2005a).

- Include a minimum size for harvest of horseshoe crabs in the FMP. Size limits are common in fisheries management to ensure that individuals can reproduce before being removed from the population. Minimum sizes are usually based on the average or minimum size at sexual maturity. For example, the average size of mature females captured during the FWRI beach survey in Tampa Bay was 180 mm PW (± 17 mm, range 125–228 mm) and of mature males was 136 mm PW (± 10 mm, range 108–170 mm).

Even if horseshoe crab landings stayed below any quotas imposed, the level might exceed that for *de minimis* status. Addendum IV does not directly affect the Florida fishery, but it will reduce the total Atlantic coast landings; this in turn will lower the level for *de minimis* status. Based on preliminary landings reports, the *de minimis* for 2005 will be 7,309 (73 trips at the current marine-life and bait bag limits). If Florida exceeds the *de minimis* level, FWC will be required to submit monthly reports on horseshoe crab harvests and to implement additional monitoring of the fishery. If Florida landings exceed 5% of total coastwide landings, annual reports must incorporate a detailed characterization of the fishery, including information on the sex composition and sexual maturity of the catch, as well as sizes of harvested horseshoe crabs. To collect this data, FWC could require all horseshoe crab harvesters to submit detailed catch reports that include sex, maturity, and size of each animal harvested. This would provide the best data with which to characterize the fishery, but funding would be required for personnel to enter and collate data. Alternatively, FWC personnel could conduct fishery-dependent data sampling, but funding for this type of data collection is not available in the current budget.

Conclusions

Much is known about certain aspects of horseshoe crab biology, but much more is unknown. Because Florida horseshoe crabs differ from those in other areas, many of the conclusions from studies elsewhere do not apply to Florida populations. The lack of data makes assessing horseshoe crab stocks difficult. The Florida horseshoe crab fishery is also different from the horseshoe crab fisheries in other states; the majority of Florida animals are harvested for the marine-life industry, rather than for bait or biomedical purposes.

The potential effects of the request for an increase

in the daily limit of horseshoe crabs taken by marine-life harvesters must be acknowledged. The concentration of marine-life landings in an area of low horseshoe crab abundance and the prereproductive age of animals harvested combine to magnify the potential for disrupting the dynamics of this population. Management impacts could be far-reaching: increased marine-life harvest could trigger additional action from ASMFC, which in most cases would result in less take for marine-life harvesters than they have now.

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