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PROCEEDINGS OF THE HORSESHOE CRAB FORUM

Status of the Resource

FEBRUARY 23, 1996

University of Delaware
Hugh R. Sharp Campus
Lewes, Delaware

Sponsored by the
University of Delaware
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Edited by

Joseph Farrell and Colleen Martin

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PREFACE

The horseshoe crab, ***Limulus polyphemus***, is of economic, scientific, and ecological importance. Its blood has important biomedical applications, and it is used as bait in several fisheries in the Mid-Atlantic region. Horseshoe crab eggs are a primary food source for migratory shorebirds along the eastern flyway.

Census and trawl surveys suggest that the Delaware Bay population has declined in recent years. The decline may be related to fishing pressure, but the population dynamics are not well understood. Currently, there is no coordinated effort to conduct stock assessment, and inaction may lead to further stock reductions.

On February 23, 1996, ***The Horseshoe Crab Forum — Status of the Resource*** was held at the Virden Center of the University of Delaware's Hugh R. Sharp Campus in Lewes. Organized by the University of Delaware Sea Grant College Program, the forum's goals were to develop a consensus on the status of the horseshoe crab and to identify short-term research priorities.

The forum was unique because it brought together for the first time all of the groups who have an interest in horseshoe crabs — state and regional fish and wildlife managers, scientists, and representatives of key stakeholder groups, including the pharmaceutical industry, fishing industry, and environmental groups. Eighty-one invited participants attended.

The objectives of the forum were to (1) develop consensus on the status of the horseshoe crab in the Mid-Atlantic region, (2) determine information needs to better manage the resource, (3) identify research priorities for the University of Delaware Sea Grant College Program, and (4) build partnerships among resource agencies, research institutions, industry, and environmental groups.

Forum presentations focused on the life history, population dynamics, and distribution of ***Limulus;*** shorebird predation on horseshoe crab eggs; an overview and trends of horseshoe crabs in the Mid-Atlantic fishery; pharmacology opportunities; and stock assessments for Delaware, New Jersey, and Maryland. Work groups met separately to address forum objectives. Their reports, which are included in this volume, draw conclusions on the status of the resource, outline what we still need to know, and identify the next steps that need to be taken.

The luncheon speaker, Dr. James F. Cooper, President of Endosafe, Inc., Charleston, South Carolina, provided a brief overview of the ***Limulus*** Amoebocyte Lysate (LAL) industry and related the importance of the ***Limulus*** base assay to the biomedical industry. Endosafe, Associates of Cape Cod, and BioWhittaker, the three major manufacturers of LAL in the United States (each company was represented at the forum) harvest horseshoe crabs from three major areas along the Atlantic coast — Cape Cod, the Virginia coast from Chincoteague to Wachapreague, and from Charleston to Beaufort, South Carolina. ***Limulus*** Amoebocyte Lysate is obtained from the blood cells of the horseshoe crab. The animals are bled (approximately 20% of blood volume) and returned unharmed to the ocean, as prescribed by Food and Drug Administration regulations.

Growth of the LAL industry is about 5% per year, but improved efficiency of testing methods has kept harvest levels at less than 200,000 animals annually. The LAL ***in vitro*** test, which provides great simplicity, sensitivity, and specificity, replaced a difficult animal assay. The test is used to detect endotoxins associated with gram-negative bacteria and is accepted worldwide as one of the key methods to test acceptability of a drug product for injection drug therapy.

I am grateful to Dr. Carl Shuster for preparing the introductory chapter to this volume, which is a consolidation of data on the abundance and distribution of adult horseshoe crabs in Delaware Bay and nearby offshore waters from 1850–1990. Dr. Shuster is a world-renowned expert on horseshoe crabs, having observed, pursued, counted, and studied ***Limulus polyphemus*** since he was first introduced to them in 1949. On behalf of all forum participants, I would like to thank Carl, not only for his considerable contribution to this volume, but for his willingness to share, with all who inquire, the invaluable data on horseshoe crabs that he has compiled so meticulously for so many years. His work has aided us all in our understanding of ***Limulus polyphemus***.

The active participation and valuable input of our audience added immeasurably to the success of this forum.

Joseph G. Farrell
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University of Delaware Sea Grant Marine Advisory Service

Abundance of Adult Horseshoe Crabs, *Limulus polyphemus*, in Delaware Bay, 1850–1990

by Carl N. Shuster, Jr.,
Virginia Institute of Marine Science

Introduction

Historically, Delaware Bay has been the site of the largest spawning population of horseshoe crabs, *Limulus polyphemus,* along the Atlantic coast of North America. Beyond death due to old age and other natural events, such as an occasional storm (especially during the winter) casting tons of horseshoe crabs onto ocean and bay beaches, the major cause of horseshoe crab death has been their harvest for a variety of human uses. Native Americans used horseshoe crabs and fish for fertilizer, a practice that the English colonists followed. By the middle of the nineteenth century, millions of horseshoe crabs were being harvested annually from the shores of Delaware Bay and elsewhere for fertilizer, with some being used as food for livestock and poultry.

This paper consolidates information on the abundance and distribution of adult horseshoe crabs, *Limulus polyphemus,* in Delaware Bay and nearby offshore waters from 1850–1990. The earliest reports, beginning in the 1850s, are based on the quantities harvested from the bay shores. Even in the 1870s, at least 4 million adults were collected each year. More recently, from about 1949 onward, data have been accumulating on the abundance and distribution of horseshoe crabs on the continental shelf.

Except for Cook (1857) and Smith (1891), commercial fisheries harvest data recorded by U.S. fisheries agencies provide most of the information on the former abundance of horseshoe crabs in the bay. From harvests of over 4 million adult crabs per season in the 1870s, the population remained at around 1.5 million from the 1880s through the 1920s. Then, from the 1930s, the population declined steadily each decade until the 1960s (Table 1).

The next published account of the abundance of horseshoe crabs was based on their spawning intensity in the late 1970s (Shuster and Botton 1985). Studies by volunteers and state agencies since 1989 are reported elsewhere in this volume. Unpublished information collected by the author during the 1950s is included in this paper.

Current interest in the size of the horseshoe crab population in the Delaware Bay area arises from the following: (1) the fact that *Limulus* eggs attract migratory shorebirds; (2) a decrease in the spawning population due to increasing harvests of the crabs, especially of the egg-laden females; (3) changes in the shoreline and attendant decreases in prime spawning habitat, especially the sandy beaches, due to erosion and counter measures such as the construction of groins and bulkheads; and (4) an extensive bait fishery.

It has been the use of horseshoe crabs as bait in the eel and conch fisheries, along with the resurgence of the crab population since the 1960s, that has led to increasingly heavy annual harvests of these crabs from Delaware Bay and the continental shelf. In addition to resident fishermen that dredge in the bay, fishermen from several states have arrived in increasing numbers on the shores of Delaware Bay during spawning season to collect horseshoe crabs. Since the egg-laden females are the target of these fishermen, questions have been raised on the effect of the sex-biased fishery on

TABLE 1

Estimates of Abundance of Adult Horseshoe Crabs in Delaware Bay Based on Harvest and Spawning Data

Decade	Years of Data	New Jersey	Delaware	Total
1871	1	3,400	900	4,300
1881	4	1,333	360	1,693
1891	4	819	412	1,231
1901	3	1,098	728	1,826
1911	0	–	–	–
1921	4	1,309	254	1,563
1931	8	681	110	791
1941	8	258	28	286
1951	6	115	–	115
1961	2	42	–	42
1971	1	225	49	274
1981	1	748	175	923
1991	5	155	267	422

Notes: Average annual harvest per decade, 1871–1961 (compiled by Shuster and Botton 1985; based on data from *Fisheries Statistics of the United States).* Average annual peak spawning per decade, 1971–1991 (based on Shuster and Botton 1985; Finn et al. 1991; and Swan et al. 1992, 1993, 1994, this volume). Although the data sets are estimates of two different entities — harvest and spawning peaks — the link between them is spawning since most of the crabs were hand-harvested from the beaches while spawning or were captured in pound nets while coming inshore to spawn. Also, the harvest data represent catches for an entire spawning season, but the spawning data are only estimates of peak spawning activity. Nevertheless, it can be argued that the two data sets are representative of the same magnitude of crabs since the spawning surveys (1971, and 1990–1995) were baywide, while crabs were not harvested from all spawning areas (decades of 1871–1961). Thus, this table probably roughly represents trends in horseshoe crab abundance in Delaware Bay from the 1870s to the 1990s.

the Delaware Bay horseshoe crab population. Just when horseshoe crabs were first used in the eel fishery is not clear, but it has been known, at least from Warwell (1897), that eels feed upon *Limulus* eggs even as they are being laid; this was probably already known to watermen. This writer learned firsthand in the 1950s of the use of horseshoe crabs to catch eels in the Navesink River (Raritan Bay), New Jersey; the Miles River (Chesapeake Bay), Maryland; and the Barrington River (Narragansett Bay), Rhode Island.

Abundance Records (1850s–1960s)

By the middle of the nineteenth century, at least 4 million horseshoe crabs were being harvested annually during their spawning season on the Delaware Bay shoreline. At first, harvesting occurred directly from beaches; pound nets were introduced in New Jersey in 1870. The crabs then were fed to livestock or stored in pens (Figure 1) or stacked like cordwood until utilized for fertilizer (Figure 2). The lack of extensive intertidal flats in Delaware prohibited the use of pound nets; all harvests there were by hand-collecting, which may explain, at least partly, the lesser numbers of horseshoe crabs captured by Delawareans (Table 1).

The use of dried, ground *Limulus polyphemus* for fertilizer was reported by Cook (1857). His observations on harvesting are the oldest known records of the abundance of adult horseshoe crabs in Delaware Bay (repeated by Rathbun 1887; Fowler 1908): "The Bay-shore of this county [Cape May] is remarkable for the immense numbers of this animal (*Polyphemus occidentalis*, or *Limulus polyphemus* of the naturalists) which frequent it. At the season for depositing their eggs, which is in the latter part of May and in June, they come on shore in almost incredible numbers. The whole strand for many miles is covered with them — sometimes two or three deep. Mr. Thos. Hughes, of Town Bank, says that on his shore of one hundred rods [503 m] he could get 100,000 in a week; 750,000 were taken on about a half mile [0.8 km] of the strand a year since (1855), and this year (1856) 1,200,000 were taken on about a mile [1.6 km]."

Within 30 years, however, Richard Rathbun (1884) wrote that the horseshoe crabs in Delaware Bay were "very much less abundant now than formerly, on account of so many having been caught from year to year for use as fertilizer. It would appear as though a few years more of indiscriminate capture would result in their being entirely exterminated from the region." By 1887, Rathbun again reported ever-decreasing numbers: "Horseshoe crabs are becoming constantly less abundant in Delaware Bay, owing to the practice of capturing, so far as possible, every individual that comes upon the shore."

Shortly thereafter, Smith (1891) speculated that "it seems probable that before long the decimation will become so pronounced that the profitable prosecution of the fishery will be impossible; then it is hoped that the employment of the destructive forms of apparatus will be discontinued and the crabs given an opportunity to multiply unrestrictedly for a few years at least." He also observed that the diminution in the abundance of the crabs was due chiefly to the capture of the crabs during the spawning season, usually before they reached the beaches to spawn. The "apparatus of destruction" was the pound net. According to Earll (1887), the pound net was introduced in about 1870, and by 1880, nine of them were in operation in New Jersey. By 1890, there were 108 pound nets and weirs (Smith 1891). A survey of the coastline of Cape May County in the 1930s recorded 19 pound nets (Works Progress Administration, 1935–36). Only a few pound nets were still constructed in the 1960s (Shuster MS). Although pound nets had to be built annually, mainly due to removal by ice floes, their utility over hand-collecting lay in the longer period of time they caught horseshoe crabs and, then, could be tended during daytime low tides.

Smith (1891) identified the fishing centers of the Delaware Bay horseshoe crab fishery (see Figure 3). His list of

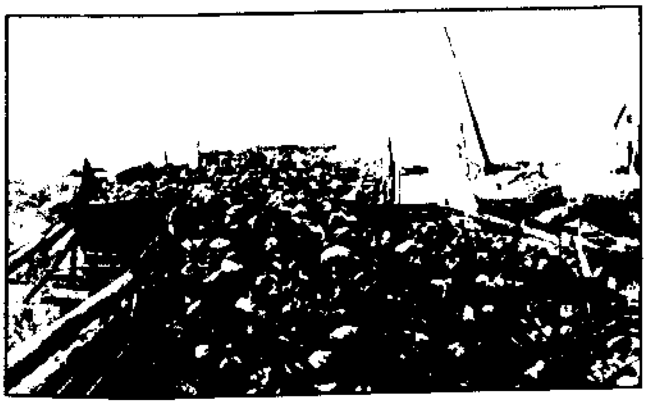

Figure 1. View of a large holding pen for horseshoe crabs on the Delaware Bay shore of New Jersey (from Fowler 1908). This pen, estimated as possibly 1.8 m high by 3 m wide by 24 m long, could hold over 18,500 adult horseshoe crabs. Harvested horseshoe crabs were stored in many such pens, of all sizes, until ready for processing into fertilizer.

Figure 2. Horseshoe crabs harvested from Bowers Beach, Delaware, were stacked on a marsh bank until taken to a fertilizer factory, possibly at Barkers Landing. The number of horseshoe crabs can almost be counted. This scene may have been on the St. Jones River; neither the actual site nor the men have been identified. Photograph courtesy of Delaware State Archives, June 1924.

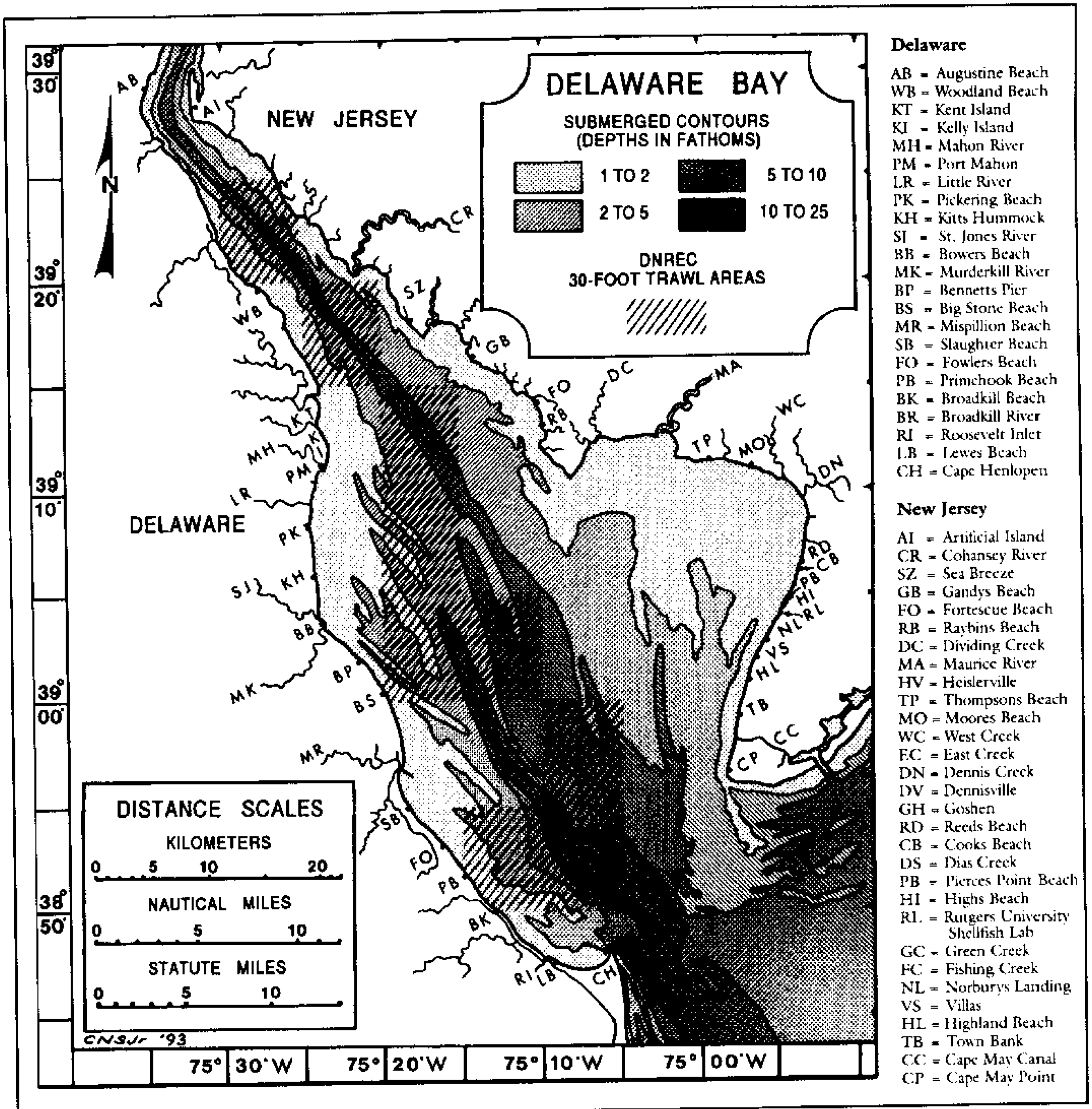

Figure 3. Delaware Bay and the continental shelf at the mouth of the bay. Shaded areas show four ranges of submerged contours (i.e., water depths) in fathoms. For convenience, due to the size of the map, the names of beaches and rivers are reduced to two letters and read north to south.

"centers" is confusing at first, because he named natural landmarks and the inland towns from which the fishermen came rather than the harvest sites. His northernmost point on the New Jersey side of the bay was the town of Heislerville about 2 miles due north of Thompsons Beach. The major "centers" between there and Cape May Point were Ewing Neck, West Creek, East Creek, Dennisville, Goshen, Dias Creek, Green Creek, Fishing Creek, and Town Bank.

About seven-eighths of the entire catch was taken between Dennisville and Fishing Creek, inclusive. In 1890, about three-fourths of the yield was taken in the vicinity of Goshen, Dias Creek, and Green Creek — 335,000; 410,000; and 411,000 crabs, respectively. The catch at the extremities, Heislerville and Town Bank, were much smaller, varying from 10,000 to 30,000. Horseshoe crabs were gathered by hand at Bowers Beach and vicinity in Delaware; the

TABLE 2
Horseshoe Crab Spawning Activity from 21 May through 11 August 1951 on the Cape May Shore in the Vicinity of Highs Beach, New Jersey

Date	Pairs	Single Crabs Males	Single Crabs Females	Location
21 May	11	8	2	tidal flats
	0	8	6	tidal flats
22 May	6	3	0	BEACH
23 May	7	0	4	tidal flats
7 June	17	6	2	tidal flats
8 June	11	4	2	tidal flats
9 June	4	4	2	tidal flats
13 June	3	0	1	tidal flats
	14	2	5	tidal flats
	2	5	1	tidal flats
14 June	11	9	4	BEACH
16 June	10	32	1	BEACH
	34	163	1	BEACH
20 June	0	1	2	tidal flats
	0	0	2	tidal flats
21 June	0	3	2	tidal flats
22 June	0	4	2	tidal flats
	11	3	0	tidal flats
	1	3	1	tidal flats
	1	5	0	BEACH
	24	101	4	BEACH
23 June	1	1	6	tidal flats
27 June	7	47	6	BEACH
29 June	23	63	0	BEACH
	9	14	14	tidal flats
5 July	1	3	3	tidal flats
6 July	3	10	3	BEACH
7 July	1	0	0	BEACH
11 July	5	12	3	BEACH
	4	0	8	tidal flats
12 July	0	7	3	BEACH
	8	37	3	tidal flats
13 July	2	1	0	BEACH
	7	24	2	BEACH
14 July	1	4	1	BEACH
18 July	0	4	1	tidal flats
	2	5	3	tidal flats
19 July	14	17	3	tidal flats
	6	7	0	tidal flats
20 July	0	5	0	BEACH
	29	41	3	tidal flats
21 July	17	20	15	tidal flats
24 July	11	17	2	tidal flats
27 July	1	3	1	BEACH
	13	44	8	tidal flats
4 August	4	4	1	BEACH
7 August	1	5	5	tidal flats
11 August	1	5	1	tidal flats
SUMMARY				
30 trips	198	271	117	tidal flats
18 trips	140	493	30	BEACH
48 trips	338	764	147	total horseshoe crabs

Total males = 1,102 (on BEACH = 633; on tidal flats = 469)
Total females = 485 (on BEACH = 170; on tidal flats =315)

Notes: Counts were made during walks from a cottage just off Highs Beach Road to the New Jersey Oyster Research Laboratory, some 600 m, often two round trips a day. Spawning (BEACH) and tidal flat counts were possible on only 48 of those trips, when the water level was either near or at high tide or low tide.

1890 catch was 275,000 crabs. Even as late as 1924, large numbers of horseshoe crabs still were being taken at Bowers Beach, Delaware.

Nadir of Abundance (1940s – 1970)

Exactly when the horseshoe crab population spawning on Delaware Bay shores was at its lowest level, between the 1850s and today, is not known. It appears, however, that the nadir in spawning was reached between the years 1940 and 1970, probably during the 1950s and 1960s. The commercial-scale harvesting of horseshoe crabs (which were also known as "king crabs") ceased in the 1960s when the last plant using king crabs in fertilizer products for the home owner stopped using horseshoe crabs in favor of blue crabs. The main reason to switch from a meal made from horseshoe crabs to one made from blue crabs (made elsewhere from shucking-house offal) was because of the complaints from new inhabitants in the vicinity of the fertilizer plant. The complaints were due to the awful stench that emanated from decaying horseshoe crabs. In the beginning, the plant had been in a remote, rural area where the stench had not been that much of a public problem. Since the U.S. Bureau of Commercial Fisheries stopped collecting horseshoe crab harvest data in the 1960s, almost concurrently with the cessation of the use of horseshoe crabs in fertilizers, the harvest data cannot be interpreted strictly as an indication of a lack of crabs.

There are only scattered bits of information (from the beaches and the benthic zone inside and outside Delaware Bay) during this period, but altogether they provide a rough idea of the abundance and distribution of horseshoe crabs.

On the Beaches

- Milne and Milne (1947) reported that a stretch of Cape May beach yielding only 150,000 crabs annually was the same area where 500,000 crabs were harvested annually only a decade before.
- In 1949, when Dr. Thurlow C. Nelson of Rutgers University introduced me to the horseshoe crabs of Delaware Bay, I jotted down a few notes on *Limulus* activity in the vicinity of Highs Beach, New Jersey. On 7 May 1949, 437 crabs were on a 600-m strand in the early morning, near dawn (high water at 0355 hours; full moon on May 12): 79 single males, 267 males in mating groups with 91 females.
- In 1951, on 5 May, during high tide in the vicinity of Highs Beach, just before midnight, some 429 horseshoe crabs were counted on a 600-m strand just south of the 1949 sighting: 71 single males and 230 males in mating groups with 128 females. The incidence of horseshoe crabs in this same area, from 21 May to 11 August, is given in Table 2. These observations (Shuster, unpublished), the only known data from that period at a specific site, are indicative of the low numbers of crabs spawning in the area. They are cited for comparison with more recent data (Table 3).

TABLE 3

Peak Numbers of Horseshoe Crabs Observed During Surveys of Spawning Activity, 1949–1995, at Highs Beach, Cape May, New Jersey

Year	Number of Horseshoe Crabs	Data Source
1949	7	Shuster (unpublished)
1951	7	Shuster (unpublished)
1977	150–250	Shuster & Botton (1985)
1990	440	Finn et al. (1991)
1991	28	Swan et al. (1992
1992	162	Swan et al. (1993)
1993	70	Swan et al. (1994)
1994	76	Swan et al. (unpublished)
1995	86	Swan et al. (this volume)

Note: Because the length of the beach strand surveyed varied from year to year, all data have been transformed to numbers of crabs per 10 m of beach strand for easier comparison.

- On 26 and 27 June 1953 and in 1954, Shuster (1955) measured the prosomal widths of 102 males (range = 178–258 mm; mean = 218 mm) and 56 females (range = 243–351 mm; mean = 291 mm) in the vicinity of Highs Beach, New Jersey.
- On 2 and 4 May 1955, Richard A. Booth reported that large numbers of horseshoe crabs were taken by beach haul seines at Slaughter Beach, Delaware. Seining was conducted between 2200 to 2400 hours under a full moon. Booth noted that hundreds of horseshoe crabs were spawning in a half-mile stretch, mostly in pairs, but that there were some groups with two or three males per female. The fishermen told him that the greater concentration of horseshoe crabs was along the southern side of the Mispillion River Inlet where a sandy beach had accumulated against the jetty.
- On 29 May 1961, Shuster et al. (1961 MS) collected 100 mated pairs from Slaughter Beach, Delaware, between 2200 and 2400 hours during a full-moon high tide. Prosomal width measurements were as follows: females (range = 245–350 mm; mean = 285.6 mm); and males (range = 190–260 mm; mean = 219.6 mm). The beach strand from which the crabs were collected was about 100 m long and had a total of about 1,000 spawning horseshoe crabs.

Benthic Zone of Delaware Bay

- On 14 March 1955, Booth recorded horseshoe crabs caught by Capt. Parsons on the *Thelma Dale* in the lower portion of the bay during three dredge tows for blue crabs: several immature specimens and 18 adult males (prosomal widths from 15.0 – 23.0 cm, average = 19.0 cm), 7 immature males (14.0 – 16.5 cm, average = 15.5 cm), and 12 females (widths from 15.0 – 24.0 cm; average = 20.5 cm; some of the smaller females probably were immature but that is not always easy to determine).
- On 16 September 1955, four males and two females and three or four exuvia were taken in a small, hand-operated trawl from the University of Delaware boat, *Acartia*, from Old Bare Shoal directly east of Mispillion River Inlet.
- On 13 December 1955, Booth was on the *American Beauty*, which caught only one female horseshoe crab in a total of five tows between Bare Shoal and Hawks Nest (a shoal east of Bowers Beach, Delaware).
- On 7 August 1957, Booth was on Capt. Petersen's boat dredging for conch (location not given, but most probably in the lower part of the bay). During the day, 147 horseshoe crabs were caught and Booth measured their prosomal widths: 115 were females (ranging 214–357 mm in width; average = 277 mm) and 32 males (201–254 mm; average = 228 mm).

Continental Shelf

- On 10 October 1955, Richard A. Booth reported that adult horseshoe crabs up to 12 in. (30.5 cm) wide were abundant in 50–60 ft. (15.2–18.3 m) of water southeast of the then Overfalls Lightship and had been so for at least the prior week.
- On 26 October, Booth reported one to two dozen horseshoe crabs in each of two tows at 50 – 65 ft. (15.2–19.8 m), southeast of Overfalls Lightship; only one was taken in another tow made at a depth of 80 ft. (24.4 m).
- On 6 November 1956, the prosomal widths of 18 males and 18 females were measured by Booth on the *American Beauty*, some 4 miles southeast of the Overfalls Lightship: females (range 21.5–33.0 cm; average = 26.5 cm); males (range 20.0–26.5 cm; average = 22.0 cm).
- On 10 November 1955, Booth reported approximately 4, 5, 15, and 15 horseshoe crabs were taken in four tows (by otter trawl) on Hen and Chicken Shoal. Capt. Tom White, skipper of the *American Beauty*, told Booth that during fall fishing and winter crabbing (for blue crabs) in the early 1950s, he encountered horseshoe crabs on the flats of the shoals at all times and in "the hole" situated about four miles southeast of the Overfalls Lightship (as on 6 November 1956).
- During the week of 1 August 1956, Booth reported that the trawler *Faith* (working outside the bay from a Delaware port) got a "split" on horseshoe crabs (i.e., caught so many horseshoe crabs that the net had to be hauled in in sections, by tying a rope around the middle of the bag to help haul in the net). In the 1950s, the vessels operating out of Delaware ports considered the horseshoe crabs to be a nuisance and dumped them overboard.

Resurgence in Abundance (1970s)

By 1977, when David Attenborough and his BBC TV crew filmed the spawning of *Limulus* on the Cape May shore for his acclaimed series "Life on Earth," horseshoe crabs were again abundant in Delaware Bay. The increase in numbers of crabs between the 1950s and the 1970s, from a few dozen to thousands within a 100-m strand of beach, was so startling that it was deemed worthy of study. Shuster and Botton (1985) estimated that in 1977 the peak spawning population in Delaware Bay comprised about 222,000 males and 51,000 females. This number, probably comparable to the population prior to the 1940s, suggests, tentatively, that a decade or more is needed to evaluate changes in numbers of horseshoe crabs.

Botton and Haskin (1984) gathered a considerable amount of data on horseshoe crabs caught during hydraulic dredge surveys of surf clams in the inshore 5.5 km (3 nautical miles) of the continental shelf, off the coast of New Jersey, from 1976 through 1979. There were 19 survey areas from Cape May Canal Inlet to Shark River Inlet. The standard tow (ST) was a five-minute haul using a dredge 152 cm wide; this ST covered an area of about 418 m^2. The mean number of crabs taken per ST increased each year: 3.34 in 1976, 4.00 in 1977, 9.18 in 1978, and 11.46 in 1979. The frequency of occurrence and abundance of the horseshoe crabs, higher off the southern half of the state, was presumed to be a function of the proximity of the region to Delaware Bay. Horseshoe crabs were more abundant inshore in the late spring and early summer than in late summer and fall. Some of their data are given in Table 4, but Botton and Haskin (1984) should be consulted for more extensive data. The horseshoe crabs on the shelf have supported, and still support, several local trawl fisheries that operate out of ports from New Jersey to Virginia (Figure 4).

John W. Ropes, National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NMFS), Woods Hole, Massachusetts, and I developed the sampling/measuring methodology used to record data on horseshoe crabs. Analyses of two sets of data, obtained during NMFS benthic fisheries surveys (groundfish and clam) from 1975 to 1983 along the continental shelf, from Cape Cod to off South Carolina, were reported by Botton and Ropes (1987a, b). During groundfish surveys, 7,035 horseshoe crabs were taken at 983 stations distributed from off New Jersey to South Carolina (Figure 5, Table 5). Fewer crabs were taken during ocean clam surveys (probably due to the difference in fishing gear used), from 35° N to 40° N, but the data mirrored the groundfish survey: 1,640 horseshoe crabs at 535 stations, primarily from the shelf off Virginia through New Jersey. The two data sets — groundfish and ocean clam — show the same patterns of latitudinal

TABLE 4

Horseshoe Crabs along the New Jersey Coast: A Partial Recounting of Survey Results, 1976–1979

Area Year	Number of Stations	% with Crabs	Mean	Coefficient of Variation	Maximum
1 (1976)	27	85.2	7.7	0.81	25.7
1 (1977)	34	94.1	11.3	1.41	87.0
1 (1978)	32	96.9	16.7	0.79	54.0
1 (1979)	30	96.7	20.2	1.20	107.8
2 (1976)	12	66.7	4.1	1.27	10.7
2 (1977)	10	70.0	2.8	1.29	12.0
2 (1978)	10	90.0	12.2	0.71	24.0
2 (1979)	11	100.0	9.6	0.70	18.3
3 (1976)	21	90.5	6.0	0.65	15.0
3 (1977)	16	93.8	7.0	0.83	20.6
3 (1978)	21	90.5	10.4	0.70	28.0
3 (1979)	21	100.0	15.5	0.63	33.3
4 (1976)	7	71.4	11.2	1.14	35.3
4 (1977)	17	100.0	6.1	0.68	14.2
4 (1978)	14	100.0	13.4	0.46	24.0
4 (1979)	20	100.0	20.6	0.96	92.5

Notes: From Botton and Haskin 1984; their report, especially Tables 2–5, should be consulted in its entirety to examine the entire matrix of abundance data versus distribution (seasonal, latitudinal, and distance from the shoreline). Only four areas are recounted here (those nearest to the mouth of Delaware Bay, along Cape May): 1 = Cape May Inlet to Hereford Inlet; 2 = Hereford Inlet to Stone Harbor; 3 = Stone Harbor to Townsends Inlet; and 4 = Townsends Inlet to Corson Inlet (note also the 13 June 1988 entry in Table 6). The distance offshore was from the shoreline to 1.8 km. Area means are expressed as the number of crabs per standard tow. The standard tow (ST) was a 5-minute haul using a dredge 152 cm wide; the ST covered an area of about 418 m^2. In 1976, sampling commenced in mid-July and was most extensive in late August and early September; in 1977–1979, most sampling was in June and July.

Figure 4. A deck load of horseshoe crabs on the FV Elizabeth C *in 1978. The crabs were caught with a Yankee 36 net (the number of tows represented by this catch was not recorded, but each tow was for 15 minutes); location on the continental shelf was not recorded. Photograph courtesy of Thomas Azarovitz (Northeast Fisheries Center, NMFS/NOAA, Woods Hole, MA).*

and bathymetric distribution as well as seasonal abundance. All the data (Tables 4 and 5; Figure 5) are consistent with the observation that the shores of Delaware Bay are the major spawning area for *Limulus*.

- *Latitudinal Evidence.* The highest abundance and frequency of occurrence is on the shelf nearest to the mouth of Delaware Bay, with the average number per tow generally decreasing with distance from the shore.
- *Bathymetric Evidence.* Horseshoe crabs were abundant, well within their migratory range, in reference to the mouth of Delaware Bay. They were taken, from the inshore sampling limit of 9 m to 290 m depth, with 74% of the total from stations shallower than 20 m and 92% from stations less than 30 m.
- *Seasonal Evidence.* The data show that more horseshoe crabs were taken inshore during the spring survey, well within their migratory range to spawning areas in Delaware Bay.

The question of whether horseshoe crabs on the continental shelf can make it back to Delaware Bay is answered by tagging data that demonstrate that *Limulus* is capable of migrating relatively long distances (Shuster 1950 = 13.5 statute miles in Cape Cod Bay; Baptist et al. 1957 = about 15 statute miles, Plum Island area, Massachusetts; Swan, Limuli Laboratories, unpublished data = 100+ statute miles — see Table 6). I believe the differences in distances traveled is a function of the number of animals competing for ***lebensraum*** (the space required for life). The first two populations, noted above, had markedly fewer horseshoe crabs than in the Delaware Bay area, which may have been reflected in their lesser migrations.

Recent Abundance (1990 – 1995)

The decline of the horseshoe crab population in the Delaware Bay area since 1990 is suggested by three independently

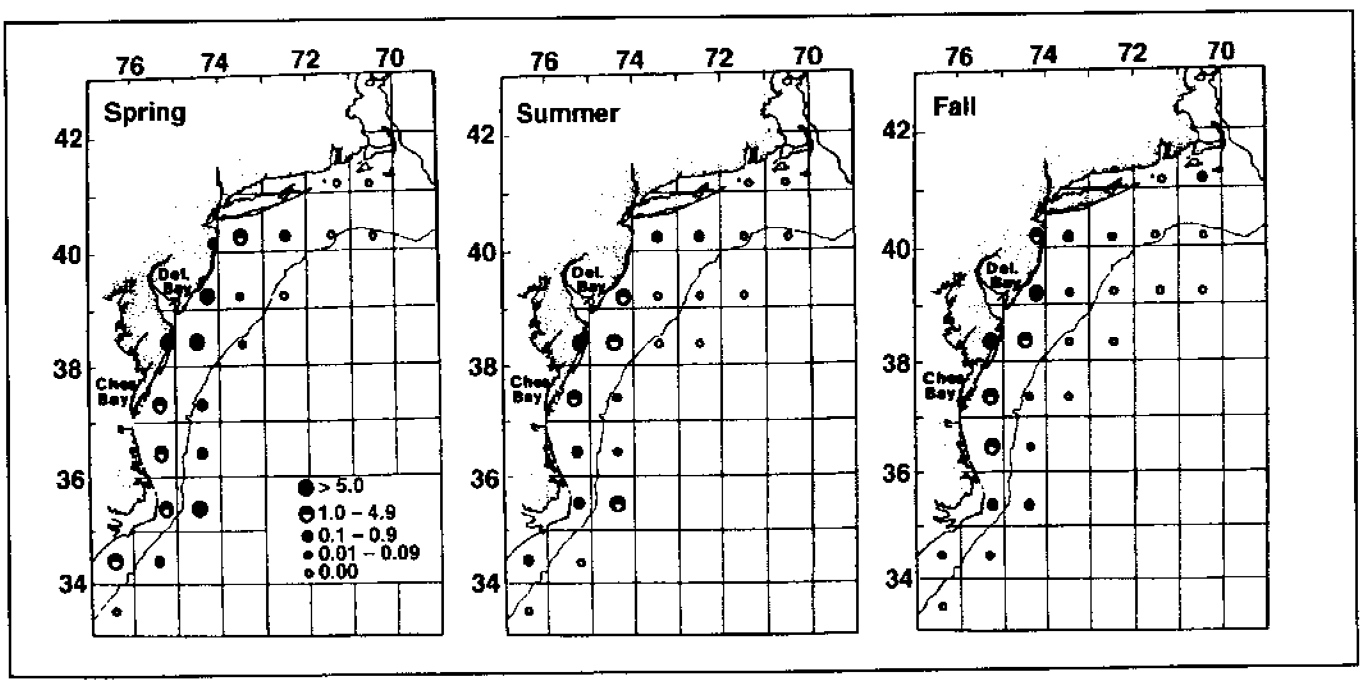

Figure 5. Mean number of horseshoe crabs per 30-minute tow, in each 1° latitude and longitude block, based on Northeast Fisheries Center, National Marine Fisheries Service/NOAA groundfish trawl data from 1975 to 1983 (from Botton and Ropes 1987b). The symbols for the number of crabs per tow is in the lower right corner of the "Spring" chart. The meandering line offshore is the 200-m depth contour.

developed data sets: (1) estimates of abundance during peak spawning (volunteer survey); (2) benthic trawl information within Delaware Bay (Delaware Division of Fish and Wildlife); and (3) benthic trawl data on the continental shelf (New Jersey Division of Fish, Game and Wildlife, Bureau of Marine Fisheries). A fourth related data set resulted from tagging (sponsored by Finn-Tech Industries, Inc., and Limuli Laboratories). These four surveys are cited here to complete the references to known data sets; the results of the first three of these independent surveys were reported separately at this forum (see Swan; Michels; Himchak; this volume).

Local tagging data are sparse but the recapture of nine tagged horseshoe crabs (Table 6), along with the distances from shore established by the fisheries surveys (see Figure 5), help to delineate the range of their migrations. The results are consistent with the observation that horseshoe crabs move between Delaware Bay and the shelf.

Summary

Decreases and resurgences in the Delaware Bay horseshoe crab spawning population can be tracked roughly from the accumulated data, sparse as it may be, for almost 145 years (1850–1995). From that data and life cycle information (see Loveland et al., this volume), certain conclusions can be drawn:

- For as long as records have been kept, since at least the 1850s, the Delaware Bay shoreline has been and continues to be the major spawning area of *Limulus polyphemus*.

TABLE 5

Average of Seasonal Variation in Horseshoe Crab Abundance and Biomass on the Continental Shelf, Northern New Jersey to Southern Virginia, Based on Groundfish Surveys from 1975 to 1983

	Winter	Spring	Summer	Autumn
Inshore				
Mean number (per trawl)	0.41	7.44	3.26	4.54
% occurrence	56	76	61	78
Population (x 10^6)	0.410	3.103	1.258	1.881
Biomass (in metric tons)	93	3,626	2,075	2,969
Offshore				
Mean number (per trawl)	–	1.03	0.10	0.42
% occurrence	–	29	30	22
Population (x 10^6)	–	1.445	0.129	0.530
Biomass (in metric tons)	–	1,975	231	972

Notes: From Botton and Ropes, 1987b. Strata shallower than 27 m were defined as inshore; strata deeper than 27 m were defined as offshore.

TABLE 6

Distribution of Nine Adult Horseshoe Crabs (Specimens "A" through "I") Tagged in the Vicinity of Delaware Bay

Date Tagged	Location	Sex	Date Recovered	Location
5 June 1987 A	NJORL, Cape May, NJ	female	8 July 1987	By trawl, off Ocean City, MD
13 June 1988 B	Corson Inlet, NJ	female	14 Sept. 1988	Trawl, mouth of Delaware Bay
23 June 1989 C	Cape Henlopen, DE	female	31 July 1989	Boat, Indian River Inlet, DE
9 June 1990 D	Cape Henlopen, DE	male	10 Aug. 1990	Trawl, 5 miles off Ocean City, MD
9 June 1990 E	Cape Henlopen, DE	female	10 Oct. 1990	Trawl, 5 miles off Ocean City, MD
10 June 1993 F	Pickering Beach, DE	female[a]	4 Sept. 1993	By trawl, south of Ocean City, MD
10 June 1993 G	Pickering Beach, DE	male[a]	4 Sept. 1993	By trawl south of Ocean City, MD
10 June 1994 H	East Point, NJ	female	4 January 1995	Trawl, off Ocean City, MD
27 May 1995 I	Big Stone Beach, DE	female	— Aug. 1995	Boat, Indian River Inlet, DE

Notes: The individuals tagged at Pickering Beach, Delaware, and East Point, New Jersey, migrated at least 62 statute miles (100 km) in straight-line water distances. Assuming that these horseshoe crabs actually traveled these distances, then the "fastest" (A) moved some 55 statute miles (89 km) within 33 days.

- The spawning season within Delaware Bay usually extends over several months, within the months from April to August, with peak spawnings usually coincident with the full- and new-moon phases. Why this is so may be due to two or more factors: (1) Shuster and Botton (1985) speculated that, due to the distances the adults had to travel to reach the spawning beaches, several spawning cohorts might arrive at different times throughout the season, depending primarily upon the distances they traveled. (2) Most of the year, and certainly during the spawning season, all mature females appear to contain at least two clutches of eggs: those that are mature (average volume of 0.0057 cc) and those that are immature (average volume of 0.0010 cc) (Shuster 1955; Baptist et al. 1957; Shuster and Botton 1985). This situation raises the question of whether some of the females might spawn twice a year — early and late in the season.
- Horseshoe crabs may remain in the mated condition (i.e., in ***amplexus)*** for days and even weeks to months. It is not unusual, therefore, to observe mated pairs in the bay and on the continental shelf during the spawning season, or at other times of the year than the spawning season. Amplexus by itself, however, does not necessarily indicate that spawning is occurring; spawning occurs on beaches. Everything that is known about the survival, development, and hatching of ***Limulus*** eggs is that environmental conditions in the intertidal zone on beaches are prerequisites (including at least certain degrees of warmth, moisture, and aeration).
- The normal sex ratio of the adult horseshoe crab is one male per female (Shuster, unpublished observations based on studies in the Cape Cod area, summers of 1949 and 1950; Shuster 1950). A change in that ratio toward more males can be used as an indicator of the bias due to collecting the egg-laden females for bait. The ratio, however, can not be ascertained readily from beach counts of the spawners because the mating behavior of the males is normally that of concentrating along the shoreline whereas the females generally move into deeper water after spawning. On the spawning beaches, males commonly outnumber females. Due to an apparent tendency for the females and males to have different migration patterns, sufficient numbers must be sampled over a large area to ascertain the sex ratio. A difference in the migratory patterns or distribution of the adults is suggested by data from an area just north of the mouth of Chesapeake Bay (Shuster 1982). There, Dr. Paul A. Haefner, Jr. (pers. comm. 1979, Virginia Institute of Marine Science) recorded no males and 53 females in water depths from 17 to 39 m in early June 1973 and 17 males and 96 females in depths from 23 to 45 m in mid-November 1974.
- The Delaware Bay spawning population is far-ranging. Its numbers have been so great that a significant portion of the total population ranges out onto the continental shelf. Undoubtedly, in decades of sparse spawning on the bay shores, adults were less numerous on the shelf, as some commercial fishermen attest.
- Horseshoe crabs move freely between the bay and shelf.
- Species in the diet of horseshoe crabs are available within the bay (Botton 1984) and on the shelf (Botton and Haskin 1984).
- Horseshoe crabs have been harvested heavily in the Delaware Bay region, from the bay shores and bottom and from the continental shelf. Despite over 145 recorded years of harvests, the population remains the largest for the species.
- Impacts upon the spawning population are not readily apparent, and the recovery of the population takes several years after heavy harvesting has ceased. This is due to the long life cycle of horseshoe crabs, upwards of 20 years, half of which is in the adult stage, which mutes rapid changes in abundance (as compared to the blue crab, ***Callinectes sapidus,*** and its much shorter life cycle and its sometimes great annual swings in abundance).

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Life History of the American Horseshoe Crab (*Limulus polyphemus* L.) in Delaware Bay and Its Importance as a Commercial Resource

by Robert E. Loveland, Rutgers University;
Mark L. Botton, Fordham University; and
Carl N. Shuster, Jr., Virginia Institute of Marine Science

Abstract

We review those aspects of the natural history of *Limulus polyphemus* L., the American horseshoe crab, that are important in understanding the long-term stability of this species. Mating behavior, age and growth, natural mortality, and habitat selection are emphasized. Spawning migrations involve seasonal, lunar, and tidal rhythms. Mating is random with respect to body size. Females deposit batches of about 4,000 eggs at sediment depths between 10 and 25 cm on open sandy beaches of the New Jersey and Delaware shores of Delaware Bay. Horseshoe crab eggs are recognized as an essential food for migratory shorebirds in Delaware Bay. Eggs that are eaten by birds probably are dislodged from their initial position by the burrowing action of other crabs or by wave turbulence. Horseshoe crabs are very slow growing, requiring about nine years to attain sexual maturity. Mortality is extensive among the eggs and larvae, but probably rare in subtidal adults. Beach stranding is the most significant natural cause of adult mortality in Delaware Bay.

The distribution and abundance of horseshoe crabs in lower Delaware Bay are governed by availability of sandy beaches for spawning. This, in turn, is influenced by geological factors, as well as human development of the shoreline. Presently, most of the principal horseshoe crab spawning habitat occurs in the lower bay, although small patches of sandy beach farther up the bay may have very high densities of crabs. Sea-level rise and beach erosion associated with global warming appear to be diminishing the extent of sandy beaches. The commercial utilization of horseshoe crabs for bait has increased since the late 1980s. The results of several horseshoe crab survey programs suggest a declining stock size and the need for a coordinated regional management strategy for this species.

Introduction

The spectacular migration of shorebirds in Delaware Bay coincides with the equally impressive mass spawning of the horseshoe crab, *Limulus polyphemus* L., whose eggs are a vital food source for the birds. This paper reviews the factors that influence the life history and abundance of horseshoe crabs in Delaware Bay, and discusses the past and present commercial utilization of this species. We argue for the importance of an appropriate time frame for this discussion. Both short-term (ecological) and long-term (geological) perspectives must be scrutinized to understand why horseshoe crabs spawn where they do, and whether they will continue to be present on the same beaches and in the same numbers in the future. This information is important for the management of the horseshoe crab itself and for the migratory shorebirds that rely on horseshoe crab eggs during their spring migration.

Life Cycle of the American Horseshoe Crab

The horseshoe crab, *Limulus polyphemus*, is one of four extant species of Xiphosurans and is the only North American representative of this group of ancient Chelicerates. The fossil record suggests that *Limulus* may have its origins in the Cretaceous, at least 60 million years ago (Reeside and Harris 1952; Fisher 1984; Sekiguchi 1988). The distribution of this species currently is limited to the east coast of North America. *Limulus polyphemus* ranges discontinuously from the Gulf of Maine in the north to the Yucatán Peninsula in the south (Shuster 1979). The epicenter of this species, based on the abundance of spawning adults in the spring, is Delaware Bay. The high density of *Limulus* in this region is also reflected by the concentration of crabs on the continental shelf located off the mouth of Delaware Bay (Botton and Haskin 1984; Botton and Ropes 1987a).

The horseshoe crab is usually an epibenthonic creature, which spends most of the year dispersed over the bay bottom and the continental shelf; adults begin to migrate toward the coast in the spring. They enter the shallow waters of embayments in the early spring, where they remain until the temperature and/or day length triggers an inshore movement. Barlow et al. (1986) have determined that the mass movement of spawning crabs onto the beaches of Cape Cod has a lunar component; that is, the peak in numbers of crabs occurs at the time of spring tide at either the full or new moon. Although horseshoe crab spawning in Delaware Bay is of greater intensity at the time of spring tide, the overwhelming numbers of crabs here, in comparison to Cape Cod, tend to dampen the lunar rhythmicity observed by Barlow et al. (1986). During the first spring tide in May, there is an initial burst of spawning activity; however, large numbers of crabs will come ashore on any night, especially if there is little wave action (Botton and Loveland 1989).

By late April or early May, many males are coupled to females, a phenomenon known as ***amplexus***. There is pronounced sexual size dimorphism; on average, males are only about 80% of the carapace width of females (Pomerat 1933; Loveland and Botton 1992). There is some evidence that males locate females visually. Barlow, Ireland, and Kass (1982) have shown that wandering subtidal males are attracted to shapes that resemble the dome-like carapace of the female, and this has been shown to be visually, as opposed to chemically, mediated. Not all males manage to amplex with a female; in Delaware Bay, free-roving suitor males are very abundant, relative to the number of females, resulting in an imbalanced operational sex ratio of about three males to every female. A particular female may be amplexed by males of any size (Botton and Loveland 1992; Loveland and Botton 1992), which suggests that there is neither selection by the female for larger males, nor a large male advantage in any male-to-male interactions. Cohen and Brockmann (1983) have reported a few instances on a Florida beach in which larger males displaced smaller males already in amplexus. However, Loveland and Botton (1992) showed that male displacement was quite rare in the Delaware Bay population and played no role in mate selection among horseshoe crabs. The composition of a cluster of spawning crabs, consisting of a mated pair and up to 15 suitor males, is entirely random with respect to the prosoma width of the participants. More than one male can potentially contribute sperm to the female during egg deposition because horseshoe crabs possess external fertilization, unlike other aquatic arthropods.

Sometime in early spring, horseshoe crabs will emerge from deeper portions of the bay and lie in wait in the shallows. By the spring tides in late April or early May, some mated pairs can be seen in the intertidal zone. As the water begins to rise, the crabs begin to make their way to the beaches. The female generally will begin to burrow in the wave-washed soft sand about 45 minutes before high tide. After the female digs a "nest," which requires her to nearly bury herself completely in the sand, she will extrude about 4,000 eggs that are shaped into a clutch, a mix of eggs and sand several centimeters across (Shuster and Botton 1985). At this time, the amplexed male will milt sperm, which is pulled down into the sand, probably with the aid of currents created by the female's book gills, to a depth up to 20–25 cm below the surface, thus fertilizing the eggs. Suitor males appear to be attracted to the mated pair just as the female begins to extrude eggs and may milt along with the amplexed male (Brockmann 1990; Loveland and Botton 1992). Shortly after forming a clutch of eggs, the female pulls up out of the sand, moves forward, and begins to deposit another clutch of eggs. This process may be repeated a number of times for every visit a female makes to the beach. Shuster and Botton (1985) have estimated that, on average, an individual female may approach the beach on at least three separate occasions for purposes of spawning throughout the spring.

Once fertilized, the bright green eggs begin to develop within the warm, moist sand of the beach. The majority of horseshoe crabs nest across 3 m within the mid-tide region. Most egg clutches are deposited 15–25 cm beneath the surface. After approximately two weeks, the outer membrane of the developing egg is shed, the inner membrane swells up, and a tiny embryonic crab can be seen moving around and around inside the egg. After two more weeks, the clear membrane splits and a miniature horseshoe crab escapes. This larval stage is so reminiscent of trilobites in superficial appearance that they are so named. This first free-living stage has molted within the egg membranes several times, but still lacks a jointed tail.

The trilobite larvae remain within the sediments of the beach for varying lengths of time. Densities over 100,000 combined eggs, developing larvae, and trilobites per square meter occur on some Delaware Bay beaches during the late spring (Botton, Loveland, and Jacobsen 1994). Most of the larvae emerge from the sand within a month of hatching (Rudloe 1979); they most likely enter the water at high tide, swim a short distance, and enter the sediments of the flats off the beach. However, Botton, Loveland, and Jacobsen (1992) found that about 1,000 to 10,000 live trilobite larvae per square meter remain in the mid-beach sediments throughout fall and winter, only to emerge in April. Although no proximate reasons for this phenomenon have been studied, these authors have suggested that the ultimate reason for overwintering by the trilobite larvae may be a hedge against predation by gulls and shorebirds.

The growth rate and longevity of horseshoe crabs have been studied by a number of investigators. Most studies have inferred values for the growth schedule because it is nearly impossible to (1) age this species with certainty because of the lack of any permanent structures that reflect growth increments, and (2) track individual crabs over their life span because tags would be lost upon molting. Shuster (1982) has estimated that *Limulus polyphemus* in the northern part of its range matures in 9–11 years and molts at least 16 times before reaching sexual maturity. Sekiguchi, Seshimo, and Sugita (1988) and Sekiguchi (1988) actually have reared *Limulus polyphemus* in the laboratory through 14 molts. They estimated that at least an additional four to five molts would be necessary for the crab to reach its terminal growth stage. However, since Sekiguchi projected the growth schedule of animals from North Carolina onto the adult sizes of New England crabs, it is possible that more than 19 molts are necessary for horseshoe crabs from Delaware Bay to reach their terminal molt. Using a clever approach to indirectly estimate age in horseshoe crabs, Botton and Ropes (1988) estimated the age of large slipper limpets, *Crepidula fornicata*, that live on the carapace of horseshoe crabs. Reasoning that these sedentary snails were attached to the crab since it last molted, they determined that horseshoe crabs can live for at least eight years after they reach sexual maturity. If Shuster correctly assumed crabs to be at least nine years old when they mature, then a conservative estimate of the total life span of ***Limulus polyphemus*** is 17 years. Both Riska (1981) and Sekiguchi, Seshimo, and Sugita (1988) have found that growth schedules for ***Limulus polyphemus*** indicate both positive and negative allometry when specific dimensions of the exoskeleton were compared to the width of the prosoma. The growth "curve" of the prosoma itself indicated a saltatory exponential form for ***Limulus polyphemus*** (Sekiguchi 1988).

Natural Mortality

Natural mortality among adult horseshoe crabs probably is very low while they are dispersed on the continental shelf. Few direct observations of predation on these large arthropods have been reported (Shuster 1982). However, in Chesapeake Bay, horseshoe crabs are an important component of the diet of loggerhead turtles (Keinath, Musick, and Byles 1987). Once the crabs reach the spawning beaches, however, mortality increases considerably. The single greatest cause of mortality among adult horseshoe crabs is due to beach stranding. On days when the wind is onshore, wave action along the beaches of Delaware Bay can be substantial. Horseshoe crabs that spawn on windy days risk being turned over and washed farther up the beach. Once on their back, especially above the highest reach of the waves, horseshoe crabs find it difficult to right themselves; this is especially true for crabs with a short or damaged telson. After the tide recedes, stranded crabs may begin to desiccate and eventually die after a few hours when exposed to direct sun (Botton and Loveland 1989). Many stranded crabs also are attacked by great black-backed and herring gulls, which devour the gills of the crabs, causing death (Botton and Loveland 1993). In 1986, we estimated that approximately 190,000 crabs, or about 10% of the adult spawning population, was lost to stranding along the New Jersey shore of Delaware Bay (Botton and Loveland 1989).

Adult mortality also occurs when mated pairs attempt to spawn on beaches that have very little slope. Crabs may become very disoriented after emerging on the flat part of a beach. On typical Delaware Bay beaches with a slope of approximately 6°, crabs can return to the bay, even when temporarily blinded, presumably by detecting slope (Botton and Loveland 1987). On flat beaches, however, the crabs wander randomly in search of the bay. If by chance they do not find the water, these crabs become stranded right side up. They may burrow to conserve moisture and return to the bay on the next tide. Some, however, die of heat exposure or desiccation before the tide returns and thus are lost to the population.

Another cause of mortality in the adult population involves attempts to spawn in inappropriate places, such as along vegetated tidal creeks, among rubble used to stabilize beaches, in boat slips, behind bulkheads, on roads during extreme storm tides, etc. It is our impression that animals becoming stranded under these conditions rarely return to the bay. Finally, another factor contributing to adult mortality is disease. Although older, "worn" crabs may be covered with fouling organisms (Shuster 1982; Botton and Ropes 1988), only a few epizootic species cause direct weakening of the animal. Algal infestations of the carapace (Leibovitz 1986; Leibovitz and Lewbart 1987), and a disease known as gill ballooning, which erodes the surface of the book gills (Bang 1979), may cause mortality among an unknown number of adult crabs.

The enormous fecundity of horseshoe crabs has one unavoidable consequence: many of the eggs, developing embryos, and trilobite larvae are prey items for a variety of invertebrates and vertebrates. Possible predators on eggs include nematodes, ghost crabs, killifish, and most notably, several species of gulls and shorebirds. Bird predation on ***Limulus*** eggs in Delaware Bay was first noted in May 1948 by Harold Gibbs (pers. comm., cited in Shuster 1955), who recorded the presence of the semipalmated plover, black-bellied plover, red knot, pectoral sandpiper, least sandpiper, dunlin, sanderling, dowitcher, ruddy turnstone, and laughing gull. Shuster (1953) reported that "shorebirds follow along after mated pairs or dig in the sand to feed upon the newly laid eggs or the larvae." However, the importance of Delaware Bay as a stopover site for migratory shorebirds was not known widely until the late 1970s (e.g., Myers 1986).

Most of the horseshoe crab egg clutches in the sand are deposited at depths below 10–15 cm, where they initially are unavailable to bird predators. However, successive waves of spawning females cause large numbers of eggs to be brought to the surface by the digging and burrowing action of the depositing females. These surface eggs are carried by waves and ultimately collect in windrows on the beach. It has been suggested that most of the eggs available to predators, especially shorebirds, are eggs that have been displaced from their normal horizons in the sand. The numerical impact of bird predation on the total number of eggs is unknown, but probably is not significant (Botton, Loveland, and Jacobsen 1994). Once at the surface, most eggs desiccate and cease development, and are lost to the population even if they are not eaten by shorebirds. Desiccated or decaying eggs may provide food for such detritivorous crustaceans as ghost crabs *(Ocypode* sp.) and beach fleas *(**Talorchestia*** sp.).

Developing horseshoe crab larvae found within the beach sediments are unavailable to surface-feeding predators. However, shortly after hatching in mid-summer, the trilobite larvae emerge from the sediments and make their way to the water. At this time, because shorebirds mostly have migrated away from Delaware Bay, trilobites are preyed upon by gulls. The mortality rate among trilobites probably is substantial during their summer emergence. L. Wagner (pers. comm.) has observed laughing gull parents feeding chicks a diet of nearly pure trilobites. Little is known about the early life history of post-hatch horseshoe crabs; they rarely are found in samples of the benthic community on the tidal flats (Botton 1984). Trilobite larvae are not important as a dispersal stage because they seldom are found in plankton samples (C. Epifanio, pers. comm.). Those larvae that escape gull predation and make it to the offshore waters without being eaten by fish most likely immediately burrow into the sediments of the flats and metamorphose within a short time. Those trilobites that overwinter and emerge in the early spring of the following year can begin their aquatic existence in the relative absence of bird predation (Botton, Loveland, and Jacobsen 1992).

Influence of Shoreline Topography and Beach Erosion on *Limulus* Distribution

The shoreline characteristics in Delaware Bay are products of the interactions among wave energy, tides, shoreline configuration, and, over geological time, the rise in sea level (Phillips 1986; Knebel, Fletcher, and Kraft 1988; Fletcher, Knebel, and Kraft 1990, 1992; Jackson and Nordstrom, 1992). Along the Cape May peninsula, narrow sandy beaches predominate up to Reeds Beach. North of Reeds Beach is a major break in shoreline orientation. Exposed peat banks with patches of active salt marsh *(Spartina)* predominate up to the Maurice River Cove. North of Egg Island Point is another break in shoreline orientation, and the bay narrows considerably. Salt marshes with pockets of sandy beaches are found along the shoreline. The salt marshes eventually give way to brackish and freshwater marshes in the tidal freshwater portion of the estuary (Orson, Simpson, and Good 1992) and lie upstream of any horseshoe crab activities. A similar gradient in beach topography exists along the Delaware shoreline.

Beaches in lower Delaware Bay are exposed to greater wave energies because of longer fetch distances and proximity to oceanic swell (Jackson and Nordstrom 1992). These factors prevent the establishment of salt marshes in the lower bay except where there are minor coves or embayments. Conversely, although most of the Cumberland County (New Jersey) shoreline consists of salt marsh and peat, patches of sandy beach are interspersed (Shuster and Botton 1985; Botton, Loveland, and Jacobsen 1988).

Shuster and Botton (1985) and Botton, Loveland, and Jacobsen (1988) established that the broad distribution of spawning horseshoe crabs correlated with the availability of sandy beaches. Some of the most dense concentrations of crabs occur on small, isolated sandy beaches (e.g., at the southern end of Fortescue) that are surrounded by salt marshes or bulkheaded areas. The requirement for sandy substrate is a consequence of the reproductive behavior of females because they often bury themselves completely as they deposit their eggs. Moreover, porous, well-oxygenated sandy beaches probably are most suitable for egg survival and development. The importance of sediment geochemistry in determining the fine-scale patchiness of spawning horseshoe crabs was shown by Botton, Loveland, and Jacobsen (1988).

Intertidal geomorphology is an important variable in beach selection by horseshoe crabs. However, some sandy beaches south of the Cape May Canal have little breeding activity in spite of the large crab population just offshore of this area (Botton and Haskin 1984). The extensive intertidal sand flats characteristic of the central Cape May peninsula, which are not found south of the Cape May Canal, may be linked to the distributional patterns of spawning horseshoe crabs within Delaware Bay.

Concentrations of mated pairs have been seen within salt-marsh creeks, e.g., in the vicinity of Moores Beach, New Jersey, and the Mahon River in Delaware. Fine anaerobic muds and dense *Spartina* stems would seem to constitute a suboptimal spawning habitat. However, we do not know yet whether these crabs are actually depositing eggs, or if they have somehow become disoriented and cannot find their way out of the marsh system. We also have observed mating activity on severely disturbed beaches with rubble or oyster and clam shell debris; on boat ramps on the Maurice River at Bivalve, New Jersey; and on small sandy patches below or behind bulkheads. We believe it is important to assess the survival of eggs in these kinds of disturbed or marginal habitats to gain an understanding of their value to *Limulus* reproduction.

The quality of beaches for horseshoe crabs can be compromised by human activities that alter the shoreline. Groins (oriented perpendicular to the shoreline) and bulkheads (parallel to the shoreline) constructed of wood, cinder block, and sheet steel are in use to protect Delaware Bay shore properties. Bulkheads are especially destructive to horseshoe crabs because access to the intertidal spawning beaches is completely blocked. On a local level, bulkheads tend to funnel the crabs into smaller and smaller areas.

Global warming is a consequence of increased emissions of CO_2, CH_4, and other atmospheric gases (e.g., Hansen and Lacis 1990). Although the magnitude of global warming remains debatable and goes beyond the scope of this paper, an emerging consensus is that sea level will rise by about 50 cm^{-1} m by the year 2100 (Hoffman 1984; Oerlemans 1989; Titus et al. 1991). This global effect will result from the melting of ice from the poles and from glaciers, and from thermal expansion of ocean water (Oerlemans 1989). Because of subsidence of the east coast of the United States, Hull and Titus (1986) predicted that the relative rise in sea level in Delaware Bay would be approximately 25 – 30 cm greater than the global average. Although New Jersey's barrier islands have received much of the public attention and governmental support for erosion control (e.g., attempts at beach replenishment or stabilization), Nordstrom (1989) provided a thorough documentation of the reasons why erosion of bay and estuarine shorelines may be even more severe.

Global warming and sea-level rise will pose a variety of environmental challenges to coastal biota (Reid and Trexler 1992) and must be factored into any discussion about the future abundance and distribution of horseshoe crabs and migratory shorebirds in Delaware Bay. In terms of potential impacts on horseshoe crabs, we would anticipate few directly detrimental effects from rising temperature per se, or from saltwater intrusion (Hull and Titus 1986), because *Limulus* has extremely broad temperature and salinity tolerances (Shuster 1982). Lester and Myers (1991) point out, however, that a temporal shift of horseshoe crab spawning to earlier in the spring would result in migratory shorebirds arriving at a time when fewer eggs are present.

Accelerated coastal erosion associated with global warming could have major repercussions on the abundance and distribution of horseshoe crabs in Delaware Bay. In the short term, erosion of sand could expose peat sediments, which may reduce the suitability of a beach for spawning (Botton, Loveland, and Jacobsen 1988). Under natural conditions, beaches simply retreat landward as sea level rises (e.g., Titus 1990; Titus et al. 1991). However, it is clear that coastal development (e.g., groins and bulkheads) impedes the natural cycle of beach migration. A 1-m vertical rise in sea level could cause the transverse erosion of about 50–100 m of beach along the northeast coast (Titus et al. 1991). Even without any additional development along the Delaware Bay shore, we would predict a significant loss of optimal horseshoe crab spawning habitat over the next few centuries. At least 8 km of sandy beach along the New Jersey bay shore has been extensively bulkheaded by the addition of cinder blocks and other solid material and is now unsuitable for egg laying; this type of material does not degrade very rapidly. If sea level does rise by 50–100 cm in the next century, then it is likely that properties and roadways located well inland of the present bay shore may be threatened and may require some type of protection. Currently, elevation differs little between Delaware Bay and the "upland" forests; some of these forests are beginning to exhibit effects of saltwater intrusion (e.g., along Moores Beach Road near Route 47, Cumberland County, New Jersey).

Impacts of Commercial Fishing

In the late nineteenth and early twentieth centuries, horseshoe crabs from Delaware Bay were processed in huge numbers for fertilizer and animal feed (Smith 1889; Fowler 1907; Shuster and Botton 1985). Between the 1870s and 1920s, annual harvests from Delaware Bay averaged over 1 million crabs (Shuster and Botton 1985). Crabs were collected by hand, in pound nets, or stake weirs set out on tidal flats (Smith 1889). The industry declined because of competition with chemical fertilizers, public complaints about odors, and possibly declining horseshoe crab abundance. Between the 1950s and 1980s, few horseshoe crabs were taken from Delaware Bay (Shuster and Botton 1985).

On a 0.47-km stretch of Highs Beach, New Jersey, Shuster counted a daily maximum of 232 spawning adults during the 1950 breeding season (= 494 per km). In contrast, Botton, Loveland, and Jacobsen (1988) routinely counted over 100 crabs per 15 m on this beach during the 1986 breeding season (= 6,667 per km). This indicates at least a thirteen-fold increase in the peak size of the spawning population during a time in which commercial fishing pressure was minimal.

Limulus presently is used for bait, primarily in eel and whelk (*Busycon* sp.) fisheries, and for the extraction of blood in the production of *Limulus* amoebocyte lysate (LAL) (Botton and Ropes 1987b). Biomedical applications of LAL are based on its exquisite sensitivity to gram-negative bacterial endotoxin (Novitsky 1984). Mortality from LAL operations is minimized as a result of a U.S. Food and Drug Administration mandate that all bled crabs must be returned to their habitat within 72 hours after capture. After bled crabs are released, about 90% survive (Rudloe 1983). Thus, we do not consider the LAL industry a major cause of mortality of the Delaware Bay crab population.

Botton and Ropes (1987b) estimated that the bait fishery in the early 1980s harvested at least 350,000 adult horseshoe crabs annually from the Middle Atlantic states during the early 1980s, and an annual catch of only 10,000–15,000 horseshoe crabs from New Jersey. However, this fishery grew dramatically beginning around 1990. It must be emphasized that the bait fishery selects for egg-bearing females (Botton and Ropes 1987b), which has obvious consequences for the stability of the population. For example, we (Botton and Loveland) observed a major shore-based bait-collecting operation at Moores Beach, New Jersey, in May 1992. We counted at least 150 large burlap sacks filled with horseshoe crabs; at (conservatively) 10 crabs per sack, this group removed 1,500 crabs in one day. These fishermen reportedly were catching crabs for about ten days. Shuster also saw a large truckload of horseshoe crabs, taken from the Cape May shore of Delaware Bay, aboard the Cape May-Lewes ferry in summer 1992. Swan (pers. comm.) and Loveland observed a dredge boat collecting large numbers of horseshoe crabs off the Cape Shore flats in spring 1995. Trawlers based in Delaware and New Jersey ports take tens of thousands of horseshoe crabs each year from the continental shelf; the majority of these animals undoubtedly contribute to the Delaware Bay spawning population (Botton and Haskin 1984; Botton and Ropes 1987a).

Based on data provided to the authors by the New Jersey Department of Environmental Protection, horseshoe crab landings in New Jersey were 252,239 in 1994 and 307,446 in 1995. Fifty-six percent of the catch came from the Atlantic coast and 43% from Delaware Bay. Overall, coastwise horseshoe crab landings averaged over 1 million animals between 1989 and 1992, and exceeded 2 million animals in 1993 (S. Michels, pers.

comm.). Current harvest rates, therefore, have reached the same order of magnitude as those recorded during the height of the fertilizer/animal feed fishery of the early twentieth century.

Summary and Conclusions

Limulus polyphemus is an ecological generalist in the subtidal environment, in terms of its food and habitat requirements. Delaware Bay is the population epicenter for this species, suggesting that environmental conditions are ideal for reproduction. Within the Delaware Estuary, spawning and egg development are optimal on sandy beaches, which occur mainly in the lower bay. Extensively bulkheaded beaches are unsuitable for horseshoe crabs. However, further investigations are needed to assess the importance of marginal habitats, such as salt-marsh banks and partially disturbed beaches.

The availability of sandy beaches may limit the reproductive success of horseshoe crabs. At present, undisturbed sandy beaches comprise only about 10% of the New Jersey shore of Delaware Bay, and this habitat will probably decrease in the near future. Sea level may rise by about 0.5–1 m over the next 100 years as a consequence of global warming. As beach erosion continues, additional pressures to stabilize bay shore properties and roads by using bulkheads and groins will result, much to the detriment of horseshoe crabs and shorebirds using the intertidal zone.

The abundance and distribution of horseshoe crabs in Delaware Bay also are influenced by commercial fishing. Horseshoe crabs are used as bait for various fisheries, and also for the extraction of blood in the production of *Limulus* amoebocyte lysate. The bait industry selects for pre-spawning female crabs, a practice that is especially destabilizing for any fishery. The slow maturation rate of horseshoe crabs suggests that a heavily exploited population will be slow to recover. Indeed, this has been confirmed in an earlier case history: the Delaware Bay population took many decades to rebound from the extensive fertilizer/animal feed industry of the early twentieth century, when millions of horseshoe crabs were harvested. The recent expansion of the bait fishery has led to annual crab harvests of magnitude comparable to the historic peaks.

In our opinion, coordinated regulation of the *Limulus* fishery is urgently needed. The wide-ranging migration of the Delaware Bay population over the mid-Atlantic continental shelf (Botton and Haskin 1984; Botton and Ropes 1987a) suggests that a regional approach to management is warranted. Recent regulations of the commercial bait fishery have focused on *Limulus* and its relationship to foraging shorebirds. Furthermore, the preservation of sandy beaches in Delaware Bay must be prioritized to maintain the population of horseshoe crabs into the twenty-first century, when sea-level rise will be an ever-growing concern of coastal managers.

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Horseshoe Crabs and the Shorebird Connection

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Introduction

This forum brought participants together to discuss horseshoe crabs and their population trends in Delaware Bay. One of the important aspects of horseshoe crabs, which is making them a subject of wider attention today, is their significance as a resource for migrating shorebirds.

Shorebird Migration

Spring shorebird migration through Delaware Bay has received attention since the early 1980s when the New Jersey Audubon Society began surveys along the bay beaches. Before that, few ornithologists mentioned it as the impressive phenomenon we recognize today. This is a bit of a mystery, but it may be that shorebird numbers were actually reduced in Delaware Bay because of low horseshoe crab populations at the turn of the century, when crabs were being heavily harvested for fertilizer. Regardless, the shorebird migration through the bay today is significant for hemispheric shorebirds and is supported by horseshoe crab eggs.

Nearly everyone recognizes that shorebirds eat horseshoe crab eggs. Crabs lay billions of eggs along Delaware Bay beach strips in May. The peak of shorebird migration through the bay tends to occur in the third or fourth week of May, usually near the peak of crab spawning. Shorebirds crowd onto these strips of beach and make a very visible, dense scene as they forage in the intertidal wet sand for eggs. This amazing phenomenon occurs because foods that shorebirds eat are at very low levels in early spring. For shorebirds to make their 3,000- to 4,000-mile migration north, they need to feed wherever food is available. Their migration north is time-constricted — they need to reach the Arctic just as snow is melting, lay their eggs, and hatch them in time for the insect hatch (on which young shorebirds feed). Adults begin the southbound migration shortly after that. Given these factors — that food is relatively scarce, their need for food is great, and they have limited time in which to complete migration and begin nesting — Delaware Bay is an essential, unequaled stopover in the eastern United States to meet the needs of shorebirds for food and rest (Clark, Niles, and Burger 1993). The numbers of shorebirds reflect its importance: Delaware Bay hosts the second largest number of migrating shorebirds in spring in the Western Hemisphere (only Copper River Delta in Alaska is larger).

In the early years of our research, we focused on the beaches as the primary and most critical habitat for shorebirds. For several species, the beaches are critical habitat: red knots, ruddy turnstones, and sanderlings feed heavily on the bay beaches where eggs provide an abundance of food. In recent years, however, we have surveyed marsh habitats on Delaware Bay and the nearby Atlantic marshes and found heavy use by birds. Shorebirds use a complex of habitats based on their needs (food or rest), time of day, and the tides that make habitats available or unavailable. Although shorebirds are found in the marshes in much lower density than on beaches, the vast area of the marsh more than makes up for it. On average, twice as many shorebirds may occupy marshes than beaches alone. (Marsh habitats include mud flats and tidal ponds, nontidal ponds, creek edges, and generally nonvegetated marsh.)

The marshes also are critical habitat because shorebirds augment their diet of horseshoe crab eggs with invertebrates. Some species rely on invertebrates more than others (e.g., dunlins and dowitchers are found primarily in the marsh), but it is speculated that many birds consume invertebrates in addition to crab eggs. Castro, Myers, and Place (1989) found that horseshoe crab eggs were not very digestible and that 72% of eggs passed unbroken through sanderlings. Eggs remain important, however, because the portion that is digested provides necessary fats that help the birds gain weight quickly. Above all, the sheer volume of eggs available and consumed by shorebirds makes up for the low digestibility. Castro, Myers, and Place (1989) concluded that sanderlings compensated for the low digestibility by consuming three times more than they would of a similar invertebrate diet. Myers (1986) estimated the number of horseshoe crab eggs consumed by a single sanderling during a two-week period at 135,000. Using that estimate, 25,000 migrating sanderlings alone may consume about 3 billion eggs (based on a diet of 100% eggs). Sanderlings, which probably rely on horseshoe crab eggs more than other species that may feed some portion on marsh invertebrates, also feed on Atlantic beach invertebrates.

Niles et al. (in prep.) estimate the number of shorebirds coming through on spring migration between 900,000 and 1.5 million birds of six species. Some may presume, therefore, that shorebirds have an impact on horseshoe crab numbers. Although it is possible that shorebirds remove some viable eggs, it is likely they do not have a significant impact. Most eggs consumed are not viable, having been disturbed from the "nest" or cluster of eggs.

Among the shorebirds found in high numbers, red knots and sanderlings have the longest bills, 3.5 cm and 2.5 cm, respectively (from tip to base near the eyes). They forage in moist sand where their reach is not much deeper than their bills. Ruddy turnstones may be the exception; they are known to excavate holes in the sand to find eggs and may be reaching eggs at slightly deeper depths (5–10 cm). Most shorebirds, however, are taking eggs that have been disturbed from crab nests. Tides make these eggs available throughout the sand column for use by small birds.

This aspect of shorebird use of horseshoe crab eggs is important in the discussion of horseshoe crab population trends in the Delaware Bay. The minimum population required for crabs to remain a functioning part of the shorebird-crab relationship may be higher than the minimum level for other parts of the ecosystem. It may be that shorebirds are using crab eggs that are made available in the sand when crabs spawn at a density such that they disturb previously laid nests and disperse the eggs. This happens when crab spawning is above some minimum level (below which nests are laid and not disturbed by later spawning). We do not know yet what that level is, but we are continuing a study using egg density within the sand as an index to the crab population.

The link between horseshoe crab populations in Delaware Bay and migrating shorebirds is critical. To deter threats to shorebirds, we must maintain horseshoe crabs at or above minimal functioning levels. Shorebirds face other potential threats in Delaware Bay, including disturbance, habitat degradation and loss, and oil or chemical spills. These and other topics were addressed by the 1993 workshop that produced the Comprehensive Management Plan for Shorebirds on Delaware Bay (Niles, Clark, and Paul 1993) and formed the Delaware Bay Shorebird Working Group.

Disturbance

Early research showed the impact that human activities have on shorebird feeding and resting on Delaware Bay beaches. Even someone walking down the beach causes flocks to fly. More severe disturbances cause birds to fly and leave the beach, stopping them from feeding at what may be the best foraging location and forcing them to move to less optimal habitat. Ultimately, this may prolong their stay until they can restore their body condition to resume migrating. How to reduce disturbance has become the top priority for shorebird management in New Jersey. We have established a system of viewing areas on the bay shore to which we direct visitors. Local cooperators and/or volunteers maintain these sites. Volunteers, trained as "warden-educators," encourage visitors to view birds from one location and discourage random beach entries or walking too close to feeding birds. This system recently expanded to include a consortium of conservation groups who own land on the bay and who want to manage for both shorebirds and visitors. The "Shorebird Outreach Team," a product of the Shorebird Working Group, is working to promote sound ecotourism around the shorebird-horseshoe crab phenomenon.

Habitat

Shorebirds require a number of habitats while stopping over in the Delaware Bay region. Beaches provide the area used most heavily by the greatest number of shorebirds. Our research showed that knots and turnstones will feed on bay beaches whenever tidal conditions make that possible. Only on evenings when the tide is high on the bay beaches do most birds move into bay and Atlantic salt marshes. At high tide, most birds cluster in and around nontidal ponds, where the tide does not affect water levels except about twice a month. Sanderlings tend to use only sandy beaches found in the lower Delaware Bay and on the Atlantic Ocean; they are not found often in the marsh. Semipalmated sandpipers are found mostly in the upper bay beaches and marshes where marshes are vast. They use mud flats heavily when available at receding tides. Dunlins and short-billed dowitchers usually are found in marsh habitats, but use the upper bay beaches also. These habitats mostly are protected under New Jersey state wetlands regulations. Habitat losses have occurred (and may continue) to Delaware Bay beaches where bulkheads have been built to protect houses and roads. Marsh habitats that were diked decades ago for salt-hay farming are now being restored, either through neglect or by active marsh restoration (such as the current Estuary Enhancement Program by Public Service Electric and Gas). The natural system of marsh ecosystem change generally has worked to provide alternating habitats for shorebirds. All habitats are subject to degradation by pollution or a catastrophic spill.

Oil Spills

Delaware Bay is among the largest shipping ports in the world, especially for oil products. It also is one of the most dangerous bays, with a narrow channel and frequent occurrence of treacherous wind and tide conditions. Ford et al. (1992) examined the risk to migrating shorebirds from various sized spills at several locations in the bay. They found that large spills upriver or moderate spills in the upper bay have the potential to contact a significant portion of the shorebird concentration areas. Although the migration period is short when crabs and shorebirds are present, a large spill could affect beach quality for many years. Both New Jersey and Delaware officials work continuously with Emergency Response managers and the U.S. Coast Guard in planning for such an occurrence. Last year, the New Jersey Division of Fish, Game and Wildlife co-hosted an Oil Spill Response Workshop during which we worked through two spill scenarios with emergency response managers and biologists. The results were used to modify the Area Contingency Plan for Delaware Bay to make it more effective in protecting key habitats. Some aspects remain to be discussed, such as the pros and cons of using dispersants and the impact they would have on benthic fauna. Participants of this forum perhaps should consider these aspects.

Delaware Bay has both international and local significance. South American countries with shorebird concentrations consider what we do here to protect animal and habitat resources as important, because it helps them enact site protection and garner political support. Protection in Delaware Bay is important locally to maintain a complex ecosystem of shorebirds, horseshoe crabs, and countless other species. Additionally, the migration phenomenon is important to the economies of local communities in the Delaware Bay region, and it provides reasons for people to protect open space and biological resources. This is a very real example of conservation that has many benefits: biological, social, and economical.

Demand is great right now for sound information on the magnitude of the crab population and the relative impact of harvesting and other mortality. We need such data to make proper regulations to sustain the crab population in the long term for both their economic value and ecological role.

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Summary of Trends in Horseshoe Crab Abundance in Delaware

by Stewart F. Michels,
Delaware Division of Fish and Wildlife

Introduction

The Delaware Division of Fish and Wildlife (DE DFW) collects both fisheries-dependent and fisheries-independent data on horseshoe crabs. Fisheries-independent data are collected from Delaware's commercial harvesters as part of a mandatory reporting system.

Adult Trawl Survey

In 1990, recognizing the importance of the species to the estuary, the DE DFW began collecting data on horseshoe crabs as part of its adult finfish trawl survey. The survey used a 30-ft. (9.1 m) (headrope) bottom otter trawl with 2-in. (5.1 cm) stretch mesh in the wings and body and a 2-in. (5.1 cm) stretch mesh cod end. Sampling was conducted monthly, from March through December, at nine fixed stations (Figure 1) in the Delaware Bay. Crabs taken in the survey were counted, measured for prosomal width, and sexed. Specimens measuring 160 mm or less were classified as immature.

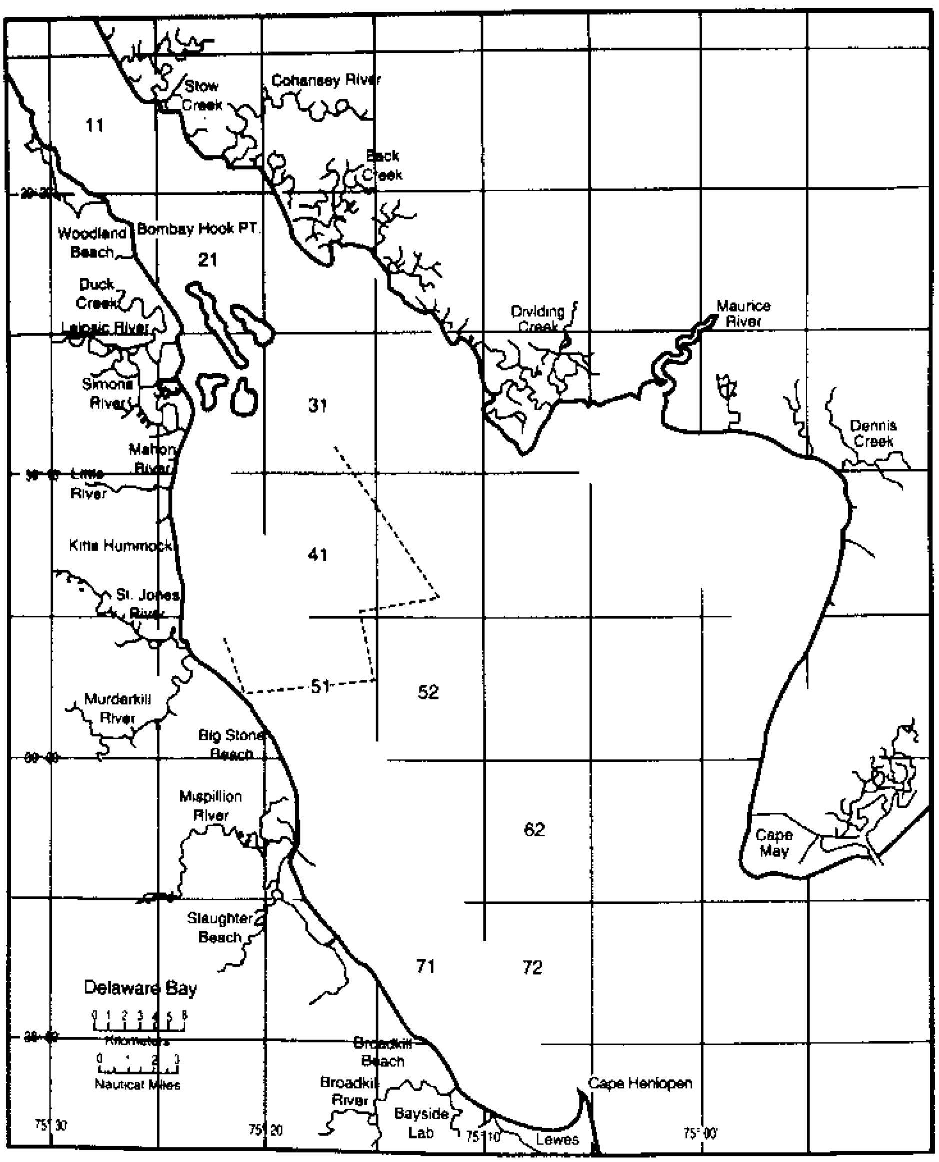

Figure 1. Delaware Bay sampling stations — adult finfish trawl survey, 1990.

Annual catch rates, expressed as the geometric mean catch per tow, from Delaware's adult trawl survey showed a significant decline since 1990 (Figure 2). Comparisons of the adult trawl survey catch rates to the annual horseshoe crab spawning survey estimates (B. L. Swan, pers. comm.) showed a highly significant correlation (Table 1).

Sex ratios obtained from the survey were not significantly different from 1:1 in the years 1990–1992 (Table 2). Sex ratios were significantly different from the 1:1 ratio in 1993 and 1994, favoring males (60%). This caused some concern as it was thought that the shift in sex ratios may be attributed to the selected harvest of females. The sex ratio in 1995, however, was not significantly different from 1:1.

Juvenile Trawl Survey

In 1992, the DE DFW began collecting catch statistics on juvenile horseshoe crabs (< 160 mm) taken in its 16-ft. (17-ft. headrope) trawl survey. The net was constructed of 1.5-in. (3.8 cm) stretch mesh, with a knotless 0.5-in. (1.3 cm) stretch mesh liner inserted in the cod. Sampling was conducted from April through October at 34 fixed stations (Figure 3) in the Delaware Bay. Immature crabs

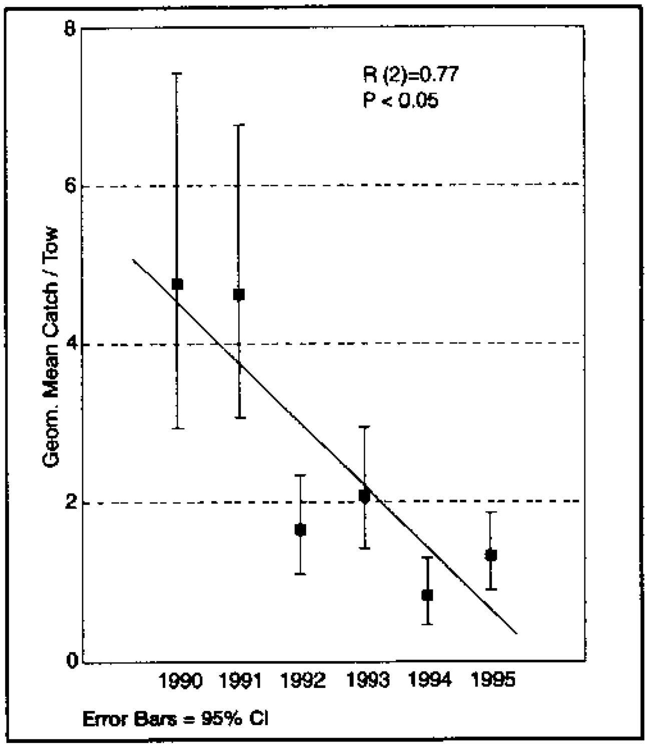

Figure 2. Horseshoe crab geometric mean catch per tow – Delaware.

TABLE 1

Comparison of Adult Trawl Survey Catch Rates and Annual Spawning Survey Estimates— Delaware Division of Fish and Wildlife

	Adult Trawl Survey Geometric Mean Catch Per Tow	Spawning Census
1990	4.75	1,240,679
1991	4.64	1,224,771
1992	1.66	399,147
1993	2.10	394,039
1994	0.84	104,000
1995	1.34	87,652

Adult vs. Census
Regression Output:

Constant	-205169
Std. Err. of Y Est.	83312.97
R Squared	**0.980002**
No. of Observations	6
Degrees of Freedom	4
X Coefficient(s)	305368.6
Std. Err. of Coef.	21810.91
	t = 14.001
Critical Value of t	(0.05) = 2.776
	P < 0.001

TABLE 2

Horseshoe Crab Sex Ratios

	Male (%)	Female (%)	Chi-square*
1990	53.7	46.3	0.5476
1991	47.9	52.1	0.1764
1992	50.1	49.9	0.0004
1993	61.7	38.3	5.4756**
1994	61.6	38.4	5.3824**
1995	50.8	49.2	0.0604

*Chi-square values assume a 1:1 sex ratio.
**Indicates significantly different P = .05; critical value of chi-square = 3.841.

(<160 mm) taken in this survey were counted and measured for prosomal width.

The utility of this survey was limited due to the short time series. The survey showed an increase in juvenile catch rates (geometric mean catch per tow) since 1992 (Figure 4); however, no significant (P = .05) trend was evident. The absence of long-term, length-frequency data prevented the extraction of an accurate young-of-the-year index.

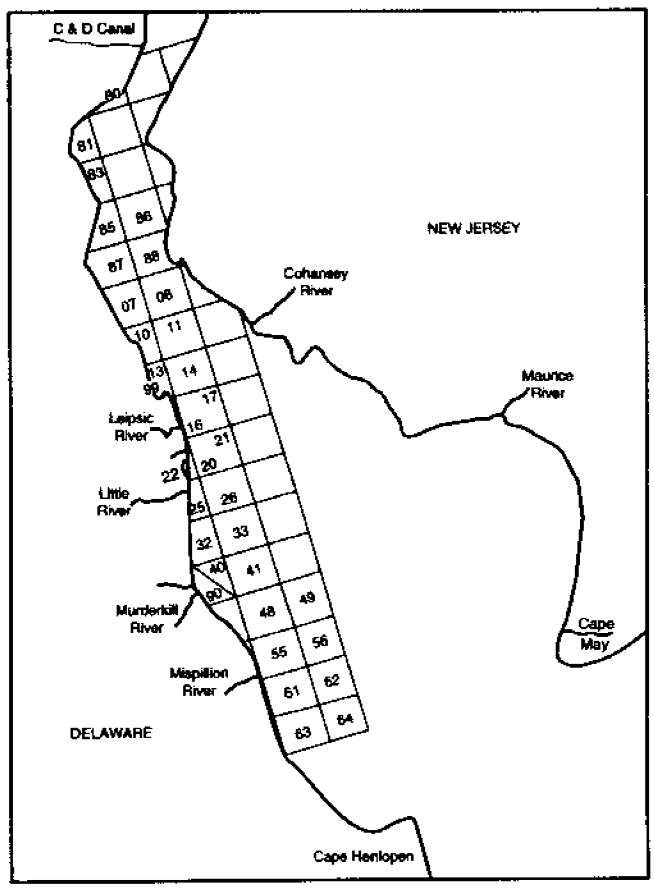

Figure 3. Sampling stations – juvenile horseshoe crab trawl survey, Delaware Bay, 1992.

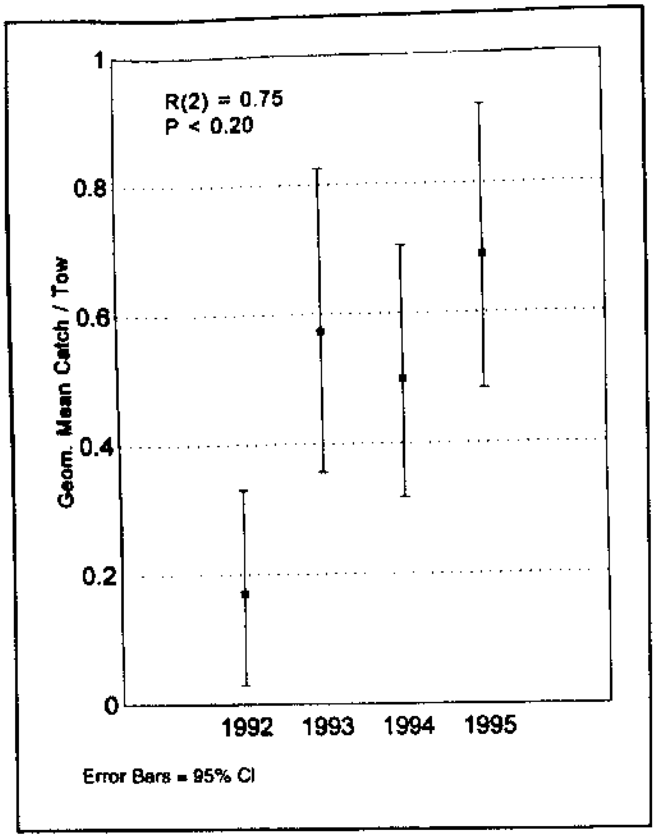

Figure 4. Horseshoe crab juvenile index.

The most significant use of these data to date was in determining juvenile horseshoe crab distribution (Figure 5). Catch rates (1992 - 95 pooled) plotted by station showed that juveniles were most abundant near the mouth of the St. Jones River with high concentrations occurring from the Little River to the Mispillion River.

Commercial Landings

Commercial harvesters have been required to report their monthly horseshoe crab landings to the DE DFW since 1990. All reports must be received before a harvest permit for the following year is issued. Prior to 1990, landings were collected solely by the National Marine Fisheries Service (NMFS).

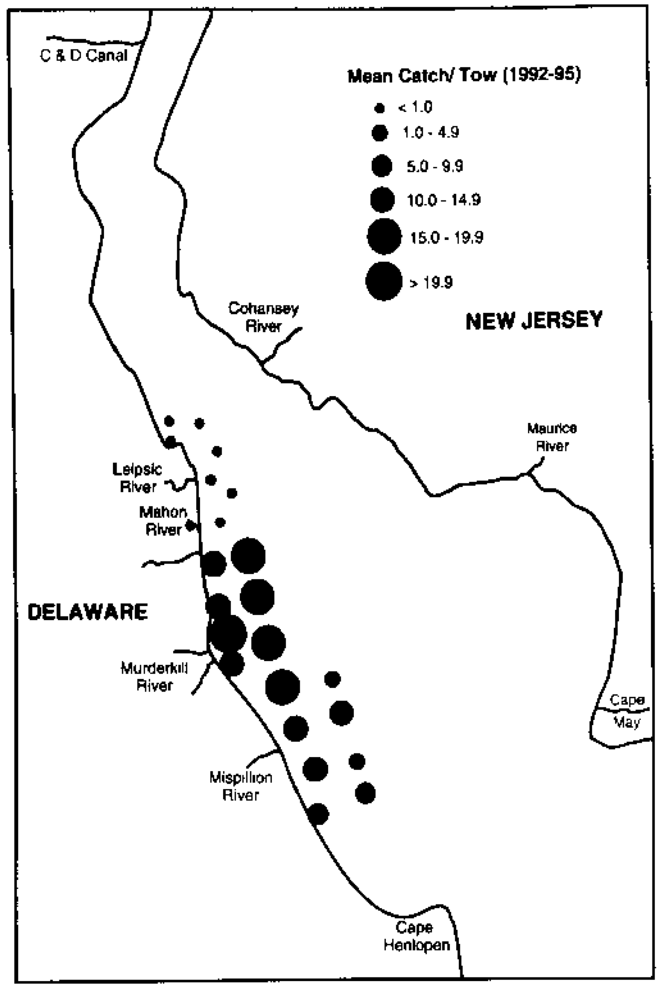

Figure 5. Juvenile horseshoe crab mean catch rates by station.

Horseshoe crab landings in Delaware have been highly variable since 1929 with the highest landings occurring in 1976 at 2 million pounds (Figure 6). The NMFS and the DE DFW horseshoe crab landings for the years 1983 through 1994 showed that Delaware accounts for approximately 12% of the annual coastwide take (Figure 7). While most of the coastwide landings (1983 – 94) were taken in the trawl fishery (Figure 8), approximately 60% of Delaware's landings were taken by hand collection (Figure 9); the remainder were taken by dredge.

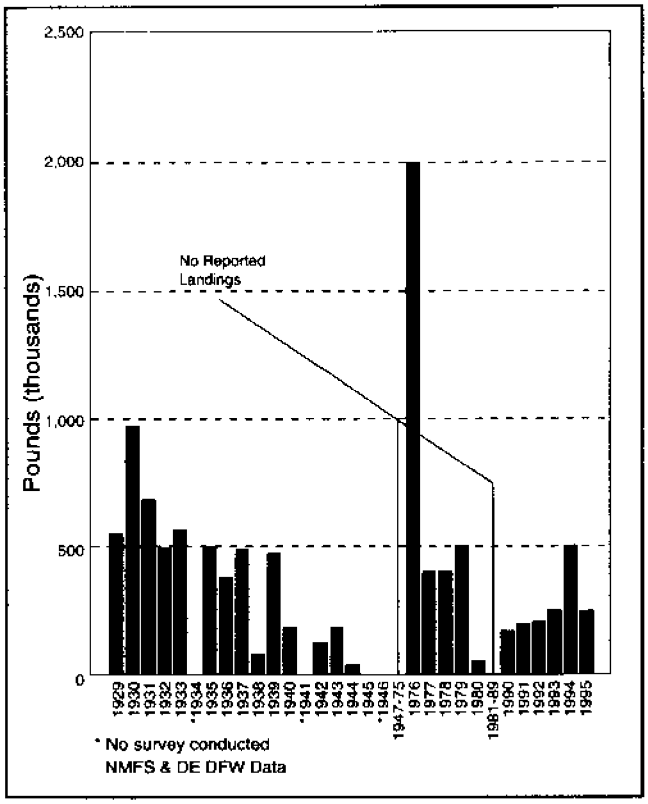

Figure 6. Delaware commercial horseshoe crab landings.

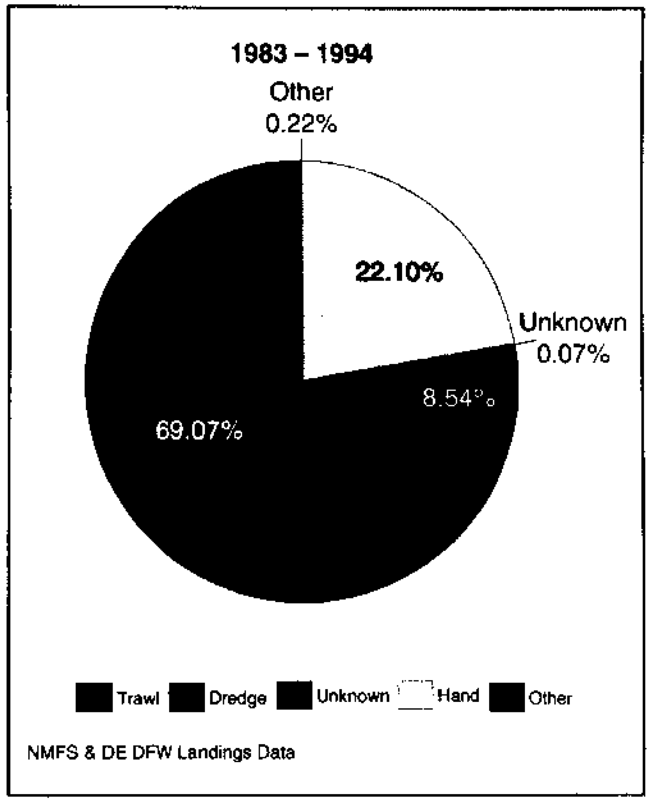

Figure 8. Coastwide horseshoe crab landings by gear type.

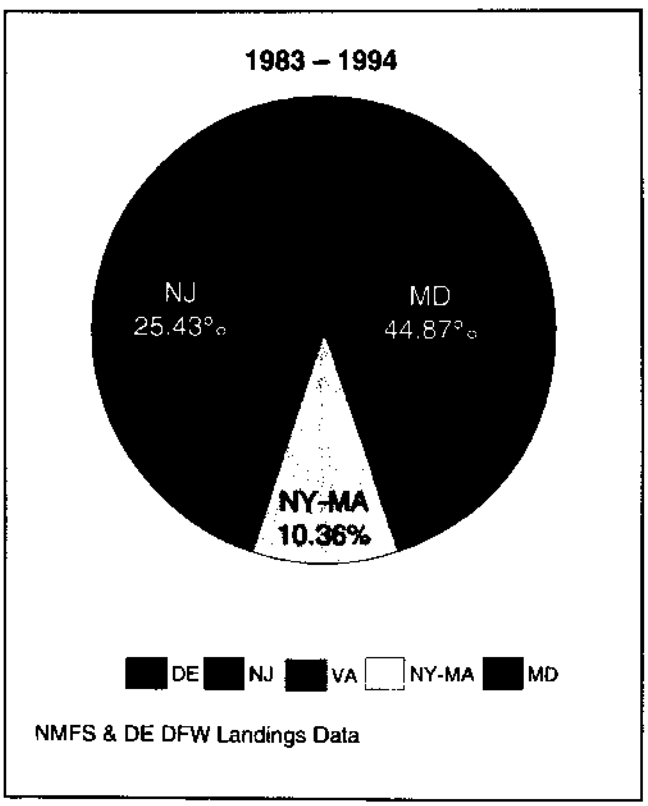

Figure 7. Coastwide horseshoe crab landings by state.

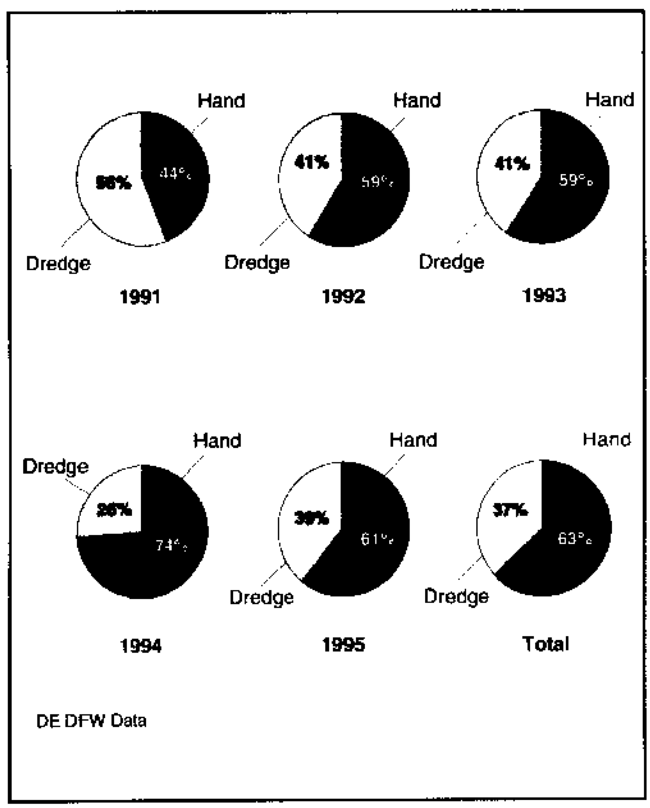

Figure 9. Delaware horseshoe crab landings by gear type.

Summary of Maryland's Horseshoe Crab Fishery, Management, and Research

by Thomas J. O'Connell,
Maryland Department of Natural Resources

Effort recently has increased in the whelk, eel, and catfish fisheries due to the decline of traditional fisheries. Horseshoe crabs, particularly egg-bearing females, are preferred bait for these fish, thus increasing the bait market for horseshoe crabs. Average commercial landings have increased from 180,000 pounds during 1975–1984 to 600,000 pounds during 1985–1994. Landings in 1994 exceeded 1.5 million pounds (National Marine Fisheries Service [NMFS] data). Reported landings by NMFS for the years 1983 through 1994 showed that Maryland accounts for 45% of the annual coastwide harvest. The majority of landings were taken in the trawl fishery with the remainder being taken from the surf-clam dredge fishery, Chesapeake Bay pound- and fyke-net fishery, and from a few hand collectors. (See Appendix B for Maryland regulations.)

Maryland, recognizing the importance of the species, adopted the Chesapeake Bay and Atlantic Coast Horseshoe Crab Fishery Management Plan (FMP) in 1994. The goal of the FMP is to protect the horseshoe crab resource in the Chesapeake Bay and along the Atlantic Coast to insure its continued role in the ecology of coastal ecosystems while providing the opportunity for commercial, recreational, and medical usage over time. The FMP identifies areas of concern (ecological value, stock status, fishery, habitat), and recommends management strategies. In addition, the FMP gives the Maryland Department of Natural Resources (MDNR) authority to regulate the fishery.

One strategy of the FMP is to delineate and protect horseshoe crab spawning habitat. Spawning areas have not been well documented in Maryland because spawning does not occur in easily observed areas or in large concentrations. In 1994, the MDNR developed a horseshoe crab hotline and volunteer spawning beach survey to delineate spawning areas. Reports indicate that spawning areas consist of narrow stretches of sandy beaches usually less than 200 meters long and a few meters wide. Spawning occurs throughout Maryland's Chesapeake and coastal bays but is restricted from parts of the upper Chesapeake Bay (north of the Bay Bridge) and its tributaries. The northern extent of their distribution varied considerably in 1994 and 1995. The annual variation appears to be related to salinity, with crabs being restricted to areas greater than 5–7 ppt. Almost all spawning occurs during the "darker" of the two daily high tides. Sex ratios vary seasonally, with 2.0 and 1.8 males per female during peak spawning activity in 1994 and 1995, respectively. Peak spawning activity varies annually and appears to be related to water temperature. During 1994 and 1995, peak activity occurred during the full-moon phase on 23 June and new-moon phase on 29 May, respectively. Spawning densities are higher in the coastal bays but remain low at less than 4.0 crabs per meter. Few nests are disturbed at these densities, resulting in few eggs being available to shorebirds. This may explain why there were no reports of shorebirds consuming horseshoe crab eggs, and why Maryland attracts only a small number of migratory shorebirds. Furthermore, the MDNR has identified problems with certain sampling and estimating procedures, and in 1994 initiated a tagging program.

The spawning survey has led to many interesting questions, which need to be answered if anyone is to use the spawning beach survey to monitor the annual abundance of spawning crabs. As the MDNR works with the University of Maryland Eastern Shore to answer these questions, the MDNR will continue to delineate spawning habitat and monitor the horseshoe crab fishery.

Resource Monitoring of Horseshoe Crabs in New Jersey

by Peter J. Himchak,
New Jersey Division of Fish, Game and Wildlife

Coastal Trawl Survey

The New Jersey Ocean Stock Assessment Program is a coastal trawl survey designed to develop comprehensive baseline data for recreational fishes and their forage items. The survey area consists of New Jersey coastal waters from the entrance to New York Harbor south to the entrance to Delaware Bay (Figure 1). Samples are collected by trawls of 20 minutes' tow duration. Trawl specifications include an 82-ft. (25.0 m) headrope, and a 100-ft. (30.5 m) footrope covered with 2 ⅜-in. (6.0 cm) rubber cookies. Five sampling surveys are completed each year (January, April, June, August, and October). Sampling stations for each survey are selected randomly for each stratum.

The New Jersey ocean trawl survey provides a relatively long-term (1988–1995), continuous resource monitoring data base (Table 1, Figure 2), which has been used to estimate the relative abundance of horseshoe crabs in New Jersey coastal waters.

With all samples from each year pooled, the number of horseshoe crabs per tow shows a precipitous decline from 1990 through 1994, with a slight rebound in 1995. Standard deviations around mean catch per unit effort (CPUE) estimates each year are noticeably large. Horseshoe crab catches are highly variable, influenced by season and sampling stratum. An analysis of 1994 trawl survey data shows that of the 186 tows successfully completed, no horseshoe crabs were taken in 118 tows. In other tows, the following horseshoe crabs were taken: 1 in each of 24 tows; 2 in each of 9 tows; 3 in each of 4 tows; 4 through 10 in each of 13 tows; and 11 or more in each of only 18 tows.

The 18 tows that took 11 or more horseshoe crabs per tow in 1994 accounted for 683 horseshoe crabs, 83.7% of the yearly horseshoe crab catch. The remaining 16.3% of the yearly horseshoe crab catch, 133 crabs, was taken in 168 tows. Inshore strata (numbers 18, 21, and 24), as well as strata nearest Delaware Bay (numbers 22, 23, 25, and 26), during April, August, and October surveys account for most of the crabs taken throughout the year (Figure 1). Thus, pooling all sampling strata for all seasons for a yearly mean CPUE may not provide the best estimate of horseshoe crab relative abundance from year to year. The New Jersey trawl survey data will be analyzed more closely, both spatially and temporally, to detect trends in horseshoe crab relative abundance.

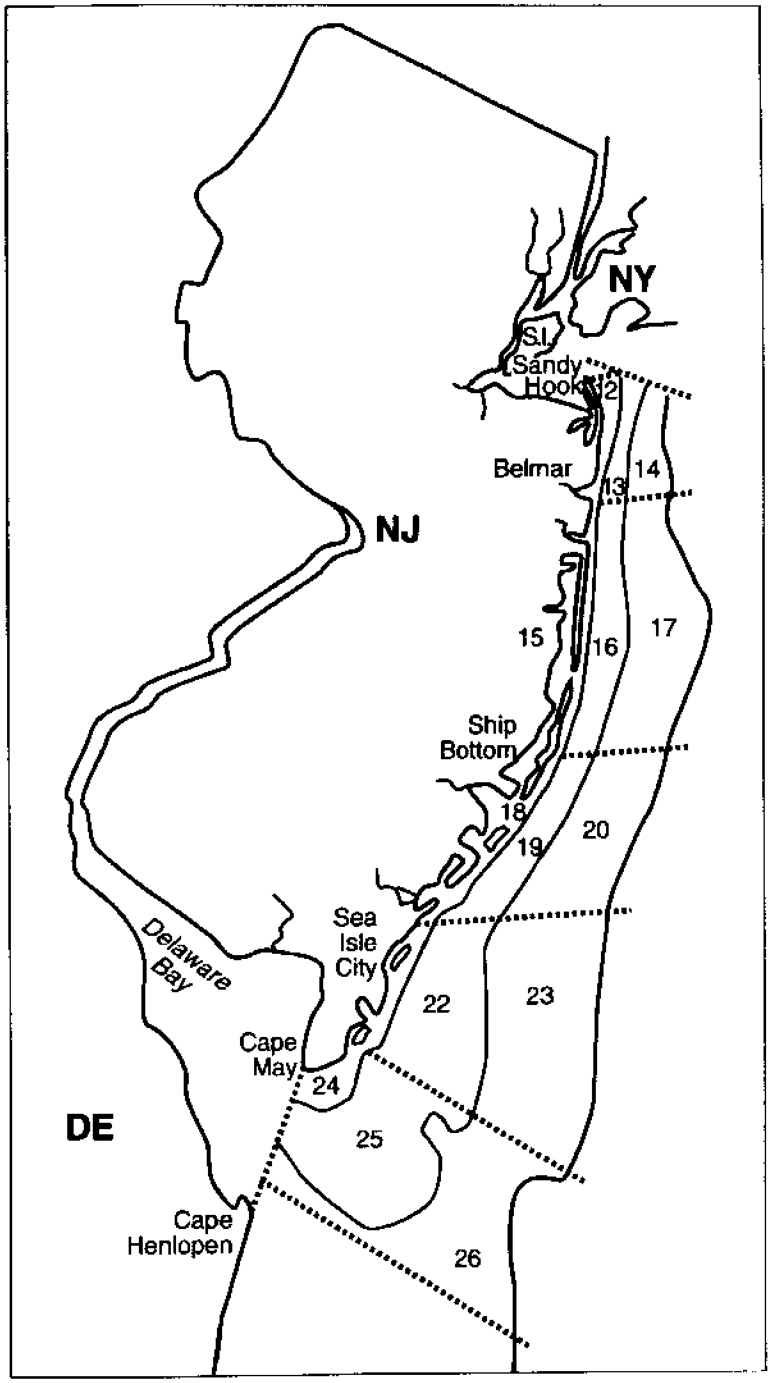

Figure 1. Survey area of New Jersey ocean stock assessment program. Strata correspond to those of the National Marine Fisheries Service's spring and fall groundfish surveys except at Sandy Hook and Cape Henlopen, where they are truncated. Longitudinal boundaries approximate 9.1 m, 18.3 m, and 27.4 m.

TABLE 1
New Jersey Horseshoe Crab Trawl Survey Data, 1988–1995

Year	No. of Crabs	No. of Tows	Mean Catch per Unit Effort	Standard Deviation
1988	518	65	8	30
1989	1,562	191	8.2	29.9
1990	2,823	163	17.3	63.7
1991	1,150	188	6.1	20.4
1992	1,316	193	6.8	17.2
1993	1,014	189	5.4	16.4
1994	816	186	4.4	13.8
1995	918	187	4.9	15.2

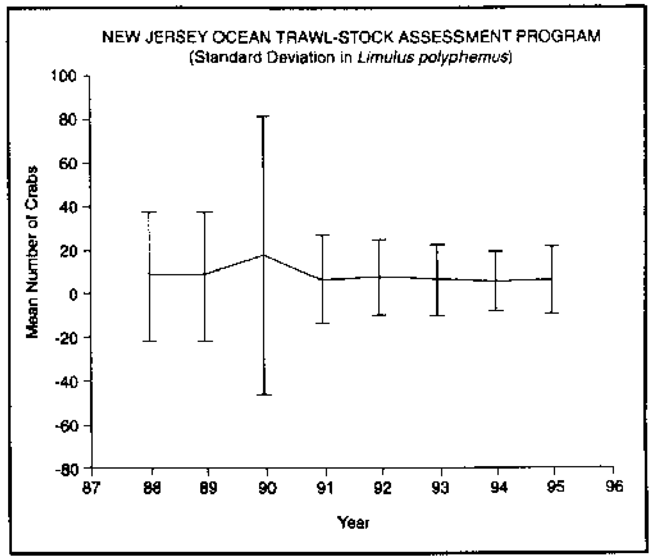

Figure 2. New Jersey ocean trawl stock assessment program.

Horseshoe Crab Management in New Jersey

by Peter J. Himchak,
New Jersey Division of Fish, Game and Wildlife

Horseshoe Crab Rule

In response to escalating confrontations between shorebird conservationists and horseshoe crab harvesters on Delaware Bay beaches, the New Jersey Division of Fish, Game and Wildlife (Division) developed and implemented Horseshoe Crab Rule N. J. A. C. 7:25–18.16 effective 3 May 1993. The rule, which minimizes the disturbance of migratory shorebirds while they are feeding on Delaware Bay beaches in New Jersey, also established the Horseshoe Crab Permit, whereby any person harvesting horseshoe crabs is required to possess a permit and to provide monthly reports that include the number of horseshoe crabs harvested, the area of collection, the gear utilized, and other information. The Horseshoe Crab Rule did not restrict the number of horseshoe crabs harvested, but it did restrict times from 1 May through 7 June when horseshoe crab harvesting could take place along the Delaware Bay shoreline. Harvesting was allowed on Monday, Wednesday, and Friday during nighttime hours only.

Although the horseshoe crab harvesting season was under way when the permit system became effective, 141 permits were issued, and the reported harvest was 252,239 horseshoe crabs. Only 30% of those who obtained permits complied with reporting requirements, but many permits were obtained by individuals who subsequently did not harvest horseshoe crabs. The Horseshoe Crab Permit is free, but both residents and non-residents are charged a two-dollar administrative fee to obtain the permit.

The reported total harvest of horseshoe crabs for 1994 was 307,446. Table 1 identifies the two predominant horseshoe crab fisheries: hand harvesting on Delaware Bay beaches in the springtime, and an offshore trawl fishery during the late summer and fall. In 1994, non-residents harvested 42,810 horseshoe crabs (13.9% of the total); all were harvested by hand on Delaware Bay beaches.

The number of horseshoe crab permits issued in 1995 (Table 2) increased substantially as the public became aware of an amendment to the Horseshoe Crab Rule that was being developed (discussed below).

Reported estimates of the 1995 horseshoe crab harvest are still preliminary (Table 3). No harvest has been reported by non-residents. In 1995, two major groups of non-residents from Virginia and Massachusetts who had permits in previous years were able to obtain their horseshoe crabs without harvesting in New Jersey.

Amendment to N. J. A. C. 7:25–18.16

In response to increased concern over the biological condition of the horseshoe crab resource, an amendment to N. J. A. C. 7:25–18.16 was developed to provide added protection to spawning horseshoe crabs and to reduce the disturbance to migratory shorebirds feeding on the Delaware Bay waterfront beaches. The amendment was

TABLE 2
Horseshoe Crab Permits Issued, 1993–1995

Year	Residents	Non-Residents	Total
1993	109	32	141
1994	128	23	151
1995	272	13	301

TABLE 1
1994 Horseshoe Crab Harvest

	HAND		TRAWL				OTHER	
	No.	%	No.	%	No.	%	No.	%
Delaware Bay and Beaches	94,738	30.8	31,386	10.2	4,722	1.5	130,846	42.6
Atlantic Coast	963	.3	175,637	57.1	–	–	176,600	57.4
Total	95,701	31.1	207,023	67.3	4,722	1.5	307,446	100

Table 3

Reported Estimates of 1995 Horseshoe Crab Harvest

	HAND		TRAWL		OTHER		TOTAL	
	No.	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
Delaware Bay and Beaches	98,093	26.6	–	10.2	28,674	7.8	126,767	34.3
Atlantic Coast	500	.1	237,070	64.2	4,919	1.3	242,489	65.7
Total	98,593	26.7	237,070	64.2	33,593	9.1	369,256	100

developed by the New Jersey Marine Fisheries Council in coordination with the Endangered and Non-Game Species Advisory Committee, bird conservationists, and commercial fishermen.

Adoption of the amendment to the horseshoe crab rule will prohibit harvest of horseshoe crabs on the Delaware Bay waterfront at any time. Hand harvesting will be permitted only in back bays and tidal creeks of New Jersey (minimum of 1,000 ft. from bayfront) on Tuesdays and Thursdays. The amendment does not restrict the use of legal gear (net or other means used) in the prescribed manner in the bay or Atlantic coastal waters except from 1 May through 31 May when all horseshoe crab harvesting is limited to two days a week by hand only. This provision will provide protection to crabs during the peak spawning period. The amendment further authorizes the Division to suspend or revoke a horseshoe crab permit for failure to comply with the specified reporting requirements.

Annual Survey of Horseshoe Crab Spawning Activity Along the Shores of Delaware Bay: 1990–1995 Summary

by Benjie Lynn Swan, Limuli Laboratories;
William R. Hall, Jr., University of Delaware Sea Grant College Program;
and Carl N. Shuster, Jr., Virginia Institute of Marine Science

Abstract

Hundreds of volunteers devoted several thousands of hours to document the numbers of horseshoe crabs spawning on Delaware Bay shores from 1990 to 1995. The resulting data lead to several tentative conclusions: (1) the number of spawners shows a steady decline; (2) the majority of the spawners occur on the "middle" stretch of beaches along the bay shore; (3) during spawning, males tend to congregate on the beaches in greater numbers, but at other times of the year, the male-female ratio usually is 1:1; (4) spawning activity usually is greatest during the hours of darkness; (5) the loss of spawning habitat should be a concern; (6) the age composition of the spawners should be determined as a further indicator of the "health" of the spawning population; (7) the impact of climate and weather on the occurrence and distribution of the spawners should be studied; (8) a massive tagging program to define better the geographical range and abundance of the populations spawning in Delaware Bay should be considered; and (9) the survey is an important factor in emphasizing the importance of horseshoe crabs and the need for data collection to protect and manage the species.

Discussion

The easiest way to survey the adult component of a horseshoe crab population is to count the number of spawners during their peak activity on beaches. This occurs, usually in the hours of darkness, during one or more periods of full- and new-moon high tides, sometime in the months of May and June; lesser spawning has occurred in April, July, and August. Climate and weather, especially cold winters and local storms, have an obvious but unmeasured impact upon the arrival of the spawners. As a prerequisite to organizing a volunteer group to make counts of the spawners, a planning board met each winter from 1990 to 1995 to select the most probable forthcoming spawning peak activity; in actuality, the Saturday nearest the predicted peak was chosen because of the logistics of assembling volunteers. Spawners are generally of equivalent abundance at least two days before and after a full-moon high tide; this is usually a suitable "window" of time within which to observe peak spawning. On some years (1990 and 1991), the predicted dates of peak spawning were accurate; on other dates the horseshoe crabs knew better than the forecasters when to come in.

Initially, the survey (popularly called a "census") was designed to cover all the beaches along the shores of Delaware and New Jersey where spawning might occur during the pre-selected survey date (based on the study by Shuster and Botton 1985). Subsequently, through experience, greater emphasis has been placed on obtaining data from selected beaches of known high densities of spawners and for all full- and new-moon high tides during the period when horseshoe crabs are active on the beaches. This affords a greater concentration of effort to limited areas over long periods of time. As such, the present approach to the annual survey is believed to yield a better indicator of the "health" of the population than the previous one-day, baywide survey. We do not have, however, an index to the age composition of the spawning population. Since recruitment into the spawning population occurs each year and each adult has the potential for spawning upwards of at least eight years (Botton and Ropes 1988), the relative percentages of young, middle-aged, and old adults would be an additional indicator of the "health" of the population.

Briefly, the survey procedure was based on a random method. On the selected date, each group of volunteers counted all the male and female crabs within six 5-m segments along the water's edge, 1 m wide, on a beach. If no crabs were seen, this also was reported. The volunteers placed a base stake on the beach two hours before high tide. A 100-m string, marked off with three 5-m segments before arriving at the beach, was stretched along the beach to the left and then to the right of the base stake. The string was used to locate the six 5-m segments.

The results over the past six years, on the selected "census" date, indicate a steady decline in the spawning numbers of horseshoe crabs. Spawning estimates were about 1.2 million crabs in both 1990 (Finn, Shuster, and Swan 1991) and 1991 (Swan, Hall, and Shuster 1992). The 1992 and 1993 estimates were approximately 400,000 crabs each year (Swan, Hall, and Shuster 1993, 1994). By 1994, and again in 1995, only 100,000 crabs were estimated to be spawning during their peak activity on Delaware Bay shores (unpublished data).

The data show relatively wide shifts, however, due to factors either not clearly understood or measured. In 1992, for example, the survey was conducted after three weeks of stormy weather; the crabs did not come in in any numbers during this survey. After that survey, the observation period was lengthened to all full- and new-moon tides during the spawning season. On 11 June 1994, the number of spawners was about 343,000 compared to 104,000 on the day of the survey, 21 May. The majority of the June spawners were at Big Stone Beach (207,900). These data also illustrate the wide shifts in numbers and locations. In 1990 and 1992 (no count was made in 1991), spawning estimates for Big Stone Beach were 9,120 and 3,040, respectively. These estimates were questionable (due to lack of firm numbers on extent of the spawning area) and aberrant at best. During the first three years (1990–92), the majority of spawners were found on New Jersey beaches, but shifted to Delaware beaches from 1993 to 1995. Also, not all the estimates of the lengths of the spawning strands at each survey location have been walked off during actual spawning. Originally, as a first cut, the distances were ascertained from examination of U.S. Geological Survey topographic maps and then "ground tested." Not all locations, however, have been measured accurately. The strand at Big Stone Beach, for example, continues to be estimated at 7.6 km.

The number of beaches surveyed over the past six years ranged from 15 to 8 on the New Jersey side; 21 to 5 on the Delaware side. In recent years, in part because of the logistics involved in assembling and assigning the volunteers, and to the attention to proven "centers" of spawning activity, the tendency has been to concentrate on fewer beaches. These beaches are probably the best indicators of overall spawning activity. When the data are arrayed on a south-to-north axis (mouth of Delaware Bay to upstream), the most important aspect of location is that the numbers of spawners create a bell-shaped curve, with the majority of the spawners coming into the middle beaches. This is another reason for concentrating the annual survey on the "middle" beaches. There also have been beach "problems." Some beaches are virtually inaccessible (except by boat), as at Kent Island off Bombay Hook, Delaware. No crabs were seen at Woodland Beach, Delaware, from 1990 to 1992. Also, viable spawning beaches have been lost over the years, as at Moores and Thompsons beaches in New Jersey. Loss of spawning habitat, particularly in the "middle" beach area, will have an impact on spawning success on Delaware Bay shores because sandy beaches are the prime, most favorable, spawning areas.

The annual spawning and resource management surveys by Delaware and New Jersey state agencies contribute to understanding the horseshoe crab population in the vicinity of Delaware Bay. Altogether, however, the actual geographic range and abundance of this horseshoe crab population have not been defined, if it is indeed a single population.

A summary of the data supporting these remarks is given in Tables 1 through 4 and in Figure 1.

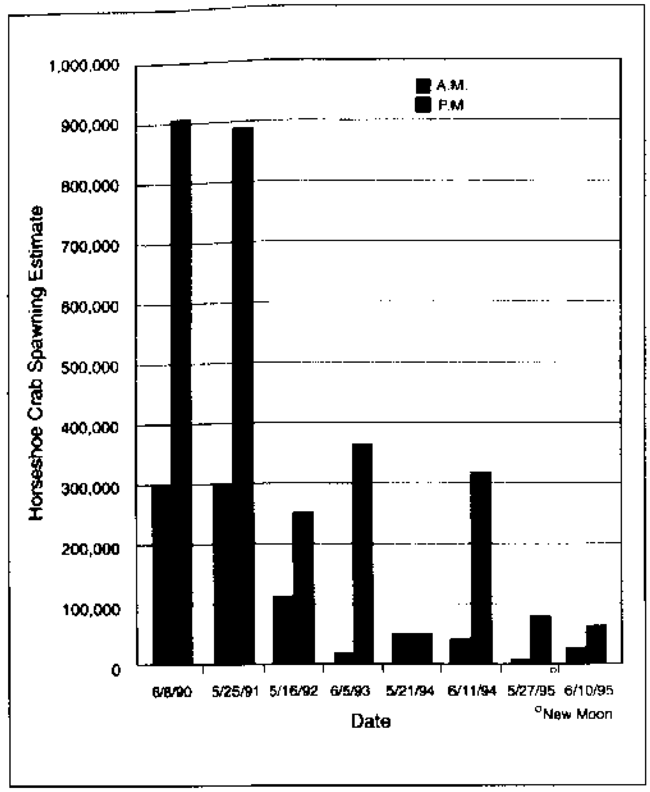

Figure 1. Yearly horseshoe crab spawning estimates.

Acknowledgments

The idea of an annual census of the peak spawning activity of horseshoe crabs within Delaware Bay was advanced by the late James J. Finn, who also initiated a tagging program and organized a 1988 symposium on horseshoe crabs. The census has been successful over the years because of strong public support; as many as 100 volunteers have participated (many every year) from the general public, including state, federal, and private agency employees; beach property owners; bird enthusiasts; teachers and pupils; scouts; and scientists. The census also plays an important educational role, emphasizing the importance of horseshoe crabs and the need for data collection to protect and manage the horseshoe crab population.

Each year from 1990 to 1995, a planning session, under the aegis of the Sea Grant College Program, was held at the University of Delaware. Many of the planners of those annual surveys are also participants in this 1996 Horseshoe Crab Forum: Dr. Mark L. Botton (Department of Natural Science, Fordham University); Pearl Burbage (Delaware Department of Natural Resources and Environmental Control); Nancy H. Butowski and Tom O'Connell, Maryland Tidal Fisheries Division; the late Pete Churchill, editor, *Delaware Estuary News*; Karen Sullivan Day (Endangered Species Program, U.S. Fish and Wildlife Service); the late Dr. Norman H. Dill (Delaware State University); Lisa Gelvin-Innvaer (Nongame and Endangered Species Program, Delaware Division of Fish and

Table 1

Horseshoe Crab Spawning Data on Delaware Bay Shore for Pre-Selected Dates [a]

Census Dates	Estimate of Spawners	Percentage of DE Spawners	Percentage of NJ Spawners	DE Beaches Surveyed	NJ Beaches Surveyed	Ratio Male to Female
8 June 90	1,240,679	19	81	21	13	2.19
25 May 91	1,224,771	43	57	13	8	2.64
16 May 92	399,147	28	72	13	11	3.13
5 June 93	394,039	88	12	9	9	2.49
21 May 94	104,000	74	26	8	15	2.46
11 June 94[b]	342,884	91	9	4	3	3.74
27 May 95[b]	91,864	97	3	7	3	
10 June 95	112,912	90	10	7	10	2.65

[a]Each year, at least two months prior to the expected spawning season, a "census" date is selected.
[b]Additional new-moon date.

Table 2

Delaware Beaches Surveyed, 1990–1995

1990	1991	1992	1993	1994	1995
21	**13**	**13**	**9**	**8**	7
Cape Henlopen – 3	Cape Henlopen – 3	Cape Henlopen – 3			
Lewes	Lewes				
Roosevelt Inlet	Roosevelt Inlet				
Broadkill			Broadkill		
	Prime Hook	Prime Hook	Prime Hook	Prime Hook	
	Fowler	Fowler		Fowler	Fowler
	Slaughter	Slaughter		Slaughter	Slaughter
Cedar Beach					
Big Stone		Big Stone	Big Stone	Big Stone	Big Stone
Bennett's Pier		Bennett's Pier			
South Bowers	South Bowers	South Bowers	South Bowers		South Bowers
North Bowers	North Bowers	North Bowers	North Bowers	North Bowers	North Bowers
Kitts Hummock	Kitts Hummock	Kitts Hummock	Kitts Hummock	Kitts Hummock	Kitts Hummock
Pickering	Pickering	Pickering	Pickering	Pickering	Pickering
Port Mahon	Port Mahon – 3	Port Mahon	Port Mahon	Port Mahon	
Kelly Island	Kelly Island	Kelly Island	Kelly Island		
Kent Island					
Bombay Hook Is.					
Woodland Beach	Woodland Beach	Woodland Beach			
Collins Beach					
Augustine Beach					
Atlantic Coast					

Note: Beaches are listed from south to north.

Table 3
New Jersey Beaches Surveyed, 1990–1995

1990 (13)[a]	1991 (8)	1992 (11)	1993 (9)	1994 (15)	1995 (10)
Sunset Beach[b]				Sunset Beach	
					Higbees
			North Cape May	North Cape May	North Cape May
Cox Hall Creek					
Villas	Villas	Villas		Villas	
Norburys Landing	Norburys Landing		Norburys Landing	Norburys Landing	
South CSL		South CSL	South CSL	South CSL	South CSL
Highs Beach	Highs Beach	Highs Beach	Highs Beach	Highs Beach	Highs Beach
				Pierces Point	Pierces Point
		Kimbles	Kimbles	Kimbles	Kimbles
Cooks		Cooks	Cooks	Cooks	Cooks
	Reeds	Reeds (2)	Reeds (2)	Reeds (2)	Reeds (2)
Moores Beach	Moores Beach	Moores Beach		Moores Beach	
Thompsons					
East Point	East Point	East Point		East Point	East Point
				Raybins	
Fortescue	Fortescue	Fortescue	Fortescue	Fortescue	
Gandys	Gandys	Gandys		Gandys	
Sea Breeze		Sea Breeze	Sea Breeze		Sea Breeze

[a] Number in parentheses following date indicates total number of beaches surveyed that year.
[b] Beaches are listed from south to north.

Wildlife); Dr. John Kraeuter (Haskin Shellfish Research Laboratory, Rutgers University); Dr. Timothy E. Jacobsen (Cumberland County College, New Jersey); Dr. Robert F. Loveland (Department of Biological Sciences, Rutgers University); Stewart F. Michels and Jeff C. Tinsman, Delaware Division of Fish and Wildlife); Marian J. Pohlman (Bombay Hook National Wildlife Refuge); Dr. Carl N. Shuster, Jr. (Virginia Institute of Marine Science, The College of William and Mary).

From 1992 to 1994, partial support was provided by a grant from the Delaware Estuary Program, principally for the vital function of collating the data and issuing an annual summary. William R. Hall, Jr., coordinated the survey conducted along the shores of Delaware each year; Benjie Lynn Swan coordinated the New Jersey side as well as the tabulation and summary of the baywide data. The late Dr. Norman Dill was an early protagonist of the survey and arranged workshops at Delaware State University.

Literature Cited

Botton, M. L., and J. W. Ropes. 1988. An indirect method for estimating longevity of the horseshoe crab *(Limulus polyphemus)* based on epifaunal slipper shells *(Crepidula fornicata)*. *J. Shellfish Res.* 7(4):407–12.

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Shuster, C. N., Jr., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.) in Delaware Bay. *Estuaries* 8(4):363–72.

Swan, B. L., W. R. Hall, Jr., and C. N. Shuster, Jr. 1992. *Limulus* spawning activity on Delaware Bay shores 25 May 1991. Fact Sheet of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

Table 4

Census-Day Comparisons, 1990–1995

Census Dates	Full Moon Date	Spawners Estimate	Time A.M.	Tidal Height	Time P.M.	Tidal Height	Weather Conditions
8 June 90	8 June 90	1,240,679	9:25	3.5 ft.	9:40	4.9 ft.	Calm, no wind, no rain, thunder, warm
25 May 91	28 May 91	1,224,771	7:17	3.8 ft.	7:40	4.8 ft.	Calm, no wind, no rain, thunder, warm
16 May 92	16 May 92	399,147	9:10	4.0 ft.	9:29	5.3 ft.	Cold, wind, low water temp., high waves
5 June 93	4 June 93	394,039	9:09	4.0 ft.	9:31	5.5 ft.	Warm, rainy, thunder, rough on DE side
21 May 94	24 May 94	104,000	8:28	4.3 ft.	8:54	5.7 ft.	Clear, slight wind, cool
11 June 94[a]	9 June 94[b]	342,884	10:46	3.8 ft.	11:01	4.9 ft.	Cloudy, calm
27 May 95[a]	29 May 95[b]	91,864	8:14	3.8 ft.	8:31	4.8 ft.	Cloudy, light wind
10 June 95	12 June 95	112,912	6:29	4.0 ft.	7:03	5.3 ft.	Clear, slight wind, mild

[a] Additional date [b] New moon

———. 1993. ***Limulus*** spawning activity on Delaware Bay shores, 16 May 1992. Fact Sheet of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

———. 1994. ***Limulus*** spawning activity on Delaware Bay shores on June 5, 1993. ***Estuary News*** 4(4):7. Newsletter of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

Group Discussions: Summaries of Forum Objectives

The afternoon session of the Horseshoe Crab Forum focused on the forum's four major objectives:

1. Develop consensus on the status of the horseshoe crab in the Mid-Atlantic Bight.
2. Determine information needs to better manage the resource.
3. Identify research priorities.
4. Build partnerships among resource agencies, research institutions, industry, and environmental groups.

Participants were divided into four groups, and each group was assigned a forum objective for discussion. The summaries prepared from those discussions are presented below.

Objective 1

Develop Consensus on the Status of the Mid-Atlantic Bight Resource

*Group Leaders: **John Field**,* Atlantic States Marine Fisheries Commission, and *Robert Loveland,* Rutgers University

Stock Assessment Data

Both fishery-dependent and fishery-independent data are scanty; no reliable and lengthy time series of catch and effort data exists.

The information in hand, however, shows some disturbing trends. Landings from Maine to Virginia doubled from 1989–1993, from 1 million pounds to 2 million pounds, with an assumed increase in effort (anecdotal reports, New Jersey permit data). Population indices derived from National Marine Fisheries Service (NMFS) trawl data vary without trend from 1975–1983, while post-1983 data have not been analyzed yet. Botton and Ropes' study showed similar population stability prior to 1983. However, Delaware Department of Natural Resources and Environmental Control (DNREC) trawl studies and Limuli Laboratories' beach surveys inside Delaware Bay showed drastic declines in catch per unit effort (CPUE) of ***Limulus*** from 1990–1994. Also, sex ratio in the DNREC study became skewed to favor males 3:1 by 1993. This could be because the commercial fishery targets the females, which are larger.

Recommendations

- Obtain and analyze post-1983 NMFS trawl data for *Limulus* abundance indices.
- Request states to begin implementing mandatory effort/landings reports in horseshoe crab fisheries.
- Initiate tagging studies of sufficient size to determine coastwide survivorship.

Objective 2

Determine Information Needs to Better Manage the Resource

Group Leaders: George LaPointe, Atlantic States Marine Fisheries Commission, and *Mark Botton,* Fordham University

As we determine how to better manage the horseshoe crab population, the following perspectives need to be considered:

- The need for resources (people, funds) to conduct assessment.
- Should management measures be voluntary or mandatory?
- The variability of regulatory programs in states needs to be addressed:
  - *Virginia:* Lewis Gillingham, (804) 247-2243
  - *Maryland:* Harley Speir, (410) 974-2241
  - *Delaware:* Rick Cole, (302) 739-4782
  - *New Jersey:* Peter Himchak, (609) 748-2020
  - *South Carolina:* Paul Sandifer, (803) 695-6350
- Rigor of data and plan:
  - — research/information needs for management
  - — quantitative stock assessment to determine whether horseshoe crabs should be managed
  - — movement along coast
  - — include biological reference points (fishing mortality rate, definition of overfishing)
- Economic impacts of management decisions on:
  - — fisheries
  - — bird-watchers
  - — lysate industry
- Are there effective, economical alternatives to the horseshoe crab for eel and conch pot bait (artificial bait)?

- Identify deficiencies in data sets to improve data quality.
- What are the best means of sampling?
  - — beach census
  - — fishery-dependent data
- Spring and fall trawl data on horseshoe crabs (from NMFS) should be analyzed through 1995.

Objective 3

Identify Research Priorities

Group Leaders: Carl Shuster, Virginia Institute of Marine Science, and
Joan Walsh, New Jersey Audubon Society

Research Priorities

- How many horseshoe crabs are there?
- How many adults can we take?
- Where are the horseshoe crabs spawning bay-wise, and what is the quality of the beaches?
- What is an optimum spawning habitat?
- What stage of their life cycle is most critical?
- How important are horseshoe crabs to the economy and ecology of the bay?

Three major research areas and the need for education/extension services were discussed, as described separately below. Stock assessment was identified as the ultimate objective necessary to conduct a horseshoe crab resource management program. More detailed information is needed on population dynamics and habitat, which also were identified as important research areas. The central question may be: Will a massive tagging program be the single-most effective step toward stock assessment and an understanding of population dynamics?

Stock Assessment

From a resource management viewpoint, the top priority is stock assessment, the stock under consideration being the adult fraction of the total horseshoe crab population. For this reason, as an aid in the evaluation of stock assessments, more must be known about population dynamics. Since a single research entity may not have sufficient resources to mount a complete assessment, coordination of stock assessment programs may be essential. Indeed, a joint "interagency" research effort may be the most feasible approach. Related research areas discussed included:

- What stock assessment approaches should be undertaken? Biological parameter estimates? Surplus-production and yield per recruit? Collection and evaluation and extensive data on commercial landings, catch-per-unit effort, biological sampling, trends in abundance, etc.?
- What do we know about maximum sustainable yield?
- What is the minimum population of horseshoe crabs required to sustain each of several uses/needs for the migratory shorebirds, for commercial harvests, for production of lysate and other medical products, and other uses?
- Validation of the current spawning survey ("census") techniques.
- Can spawning areas be identified from satellite photographs?
- Development of a synthetic bait substitute for eels, whelks, and catfish.
- Application of results of population dynamics research to stock assessment.

Population Dynamics

Certain aspects of population dynamics run parallel with stock assessment. Some of the research areas that are needed to better understand the "Delaware Bay" horseshoe crab population include the following:

- A life history model and a longevity table including all instars. (Loveland)
- The most critical stage of the life cycle of horseshoe crabs. It is obvious that large quantities of eggs are lost, but what percentage of the total laid? Is this crucial? Is it possible that the first instar, the so-called "trilobite" larva, is the most critical stage; is it most vulnerable because it is exposed on the intertidal flats at low tide to migratory shorebirds and/or to small fish in the shallow water?
- The spawning magnitude per female per year. Are one or two clutches of eggs matured and spawned each year?
- Development of visual or other criteria of the age of adult horseshoe crabs. Will the age of adults better define the overall "health" of the spawning population? Can the percentage of the adult-age classes being harvested be assessed by aging techniques?
- Tagging is a tool for ascertaining longevity, abundance, and distribution of individuals. What percentage of the presumed/estimated population must be tagged to obtain meaningful results? What percentage of the "Delaware Bay" population of horseshoe crabs spawn in the coastal embayments of New Jersey and the Delmarva Peninsula?
- Research on population identification. Can biochemical definition of populations be a useful tool in defining populations? Can biochemical "fingerprinting" be useful in ascertaining abundance and distribution? (Pierce)

Habitat "Needs" vs. Loss of Spawning Habitat

Discussion of habitat centered on beach replenishment programs and what could or should be done regarding horseshoe crabs, especially in relation to spawning habitat. Ancillary questions that should be answered included the following:

- Effects of management plans?
- Beach replenishment plans and quality of beaches (for spawning)?
- How do horseshoe crabs "use" beaches — selectivity, distribution of nests, etc.?

Education

Research results need to be transmitted to the general public. Potential venues include the following:

- Workshops for fishermen and the general public
- Participation in horseshoe crab events/fairs, such as the Wildwood Crest Horseshoe Crab Festival held the last weekend in May in Lower Township, Cape May County, New Jersey
- Ecotourism

Objective 4

Build Partnerships Among Resource Agencies, Research Institutions, Industry, and Environmental Groups

Group Leaders: Karen Day, U.S. Fish and Wildlife Service, and *Joseph Farrell,* University of Delaware Sea Grant Marine Advisory Service

With a trend toward belt-tightening in resource agency budgets, partnerships are seen as an important way of sharing talent and financial resources.

Partnerships are a method of resolving resource issues. The group emphasized the importance of capitalizing on existing partnerships that are involved in different aspects of the horseshoe crab resource.

The Delaware Estuary Program's Comprehensive Conservation and Management Plan and the New Jersey Department of Environmental Protection's Shorebird Management Plan are examples of existing multi-party partnerships that can be built on.

Functional partnerships, built around identified needs, include the following:

- outreach/education
- data collection/sharing
- research/monitoring
- regulation/consistency
- resource use/management

Partners may include traditional, as well as nontraditional ones:

- a new Delaware Bay foundation, a possible mechanism for funding outreach work groups (such as participants from this forum)
- LAL labs
- fishermen
- pharmaceutical industry
- medical community
- environmental groups
- volunteers
- media
- Internet

Examples of questions that could be addressed with partnerships include the following:

1. What is the critical level of horseshoe crabs necessary to sustain the shorebird population?
2. How much beach do spawners need?
3. How do we get fishermen involved in conserving the resource?

Other Considerations

We need to inventory what we already have in such things as outreach education and source material. We need to determine funding mechanisms for partnerships and criteria for getting funding. And most important, we need to keep in mind opportunities for integration/networking/communication.

EPILOGUE

Much has happened since this forum. New reporting requirements, data analysis, and new and continuing research projects are contributing information to help us manage the horseshoe crab resource wisely in the future. The following is a roundup of horseshoe crab-related activities in the Mid-Atlantic area that have taken place since the forum.

Research

Patrick Gaffney (University of Delaware College of Marine Studies) provided a summary of results from a pilot research project undertaken in his lab in the summer of 1996. His group examined mitochondrial DNA of Atlantic coast horseshoe crabs from New Hampshire to Georgia using high-resolution denaturing electrophoresis. The data suggest that the New Hampshire horseshoe crab population is genetically distinct from the rest, and there is a chance that the Delaware Bay population also may be. More samples from all sites are necessary to confirm initial impressions, but it appears that Cape Cod acts as a barrier to gene flow in *Limulus*. This could have important ramifications as resource management decisions are made.

Nancy Targett (University of Delaware College of Marine Studies) and Joe Farrell (University of Delaware Sea Grant Marine Advisory Service) received funding support from Delaware Sea Grant for their proposal, "Mimicking Horseshoe Crab Eggs: In Search of an Artificial Bait." The goal of this project first is to identify the attractant in the horseshoe crab and then to devise a method to artificially duplicate it. Once the bait works successfully in laboratory tests, local eel and whelk fishermen will field-test the bait. This project began in early 1997, and first-year results are very encouraging.

Dave Carter (Coastal Management Program, Delaware Department of Natural Resources and Environmental Control) is coordinating a collaborative effort to "Evaluate the Ecological Benefits of Delaware Bay Community Beach Replenishment Projects." Quantitative data are being collected to test the hypothesis that Delaware Bay beach replenishment projects in the bay reach (extending from Kelly Island to Beach Plum Island) are beneficial for horseshoe crab spawning as well as for shorebirds by increasing their staging areas.

In a 1990–91 survey, Mark Botton and Bob Loveland surveyed beaches on the New Jersey side of Delaware Bay ("Site Selection by Migratory Shorebirds in Delaware Bay and Its Relationship to Beach Characteristics," *Auk* 111:605–616). With funding support from the New Jersey Department of Environmental Protection, the New Jersey Audubon Society, and the Nature Conservancy, Drs. Botton and Loveland resurveyed these beaches in 1996 using the same sampling approach as in their 1990–91 survey.

During the summer of 1996, Carl Shuster pursued leads on the early "king crab fishery and cancerine industry" as the horseshoe crab fertilizer business was once known. The ensuing manuscript is a historical review of some of the key players in the king crab fishery and fertilizer industry of Delaware Bay and the sites of operation.

Management

Several states promulgated new regulations related to horseshoe crab harvest. New Jersey closed Delaware Bay waterfront beaches during the horseshoe crab spawning period to maximize horseshoe crab eggs as a food source for migrating shorebirds, and in September 1997 adopted new regulations that established eligibility criteria for fishermen, eliminated the trawl fishery and dredge by-catch, and modified the harvest season.

In Delaware, the Department of Natural Resources and Environmental Control (DNREC) has proposed regulations for the 1998 season (going through the public hearing process now) that define the criteria for eligibility for a horseshoe crab commercial collecting permit; control the time and areas where horseshoe crabs may be harvested; limit the number of horseshoe crabs that may be dredged in one day; define the equipment that may be used to store and/or transport horseshoe crabs; and require monthly reporting of the harvest of horseshoe crabs.

Stewart Michels (DNREC, Division of Fish and Wildlife) is looking at the post-1983 National Marine Fisheries Service trawl survey and New Jersey/Delaware spawning survey data to see how well the indices are tracking each other. Stew also reports that Delaware's Division of Fish and Wildlife is continuing to collect data on horseshoe crabs as part of their annual adult and juvenile trawl surveys.

While Virginia established licensing requirements for harvesting horseshoe crabs by hand in 1996, Maryland initiated new reporting requirements in January 1996 and is considering the adoption of emergency regulations before the 1998 season. Tom O'Connell, Maryland Department of Natural Resources, also reported that horseshoe crab tagging studies were conducted in Maryland's coastal bays and in the Chesapeake Bay. The Maryland Department of Natural Resources' Fisheries Service also recently published a very informative "Horseshoe Crab Newsletter." Contact Tom for a copy.

Education

On the education front, the University of Delaware Sea Grant College Program coordinated a special horseshoe crab exhibit in conjunction with Coast Day 1996. Collaborators on the interactive multi-station exhibit included BioWhittaker, Inc., and the Delaware Department of Natural Resources and Environmental Control's Division of Fish and Wildlife Aquatic Resources Education Center and the Non-Game and Endangered Species Program. Approximately 11,000 visitors attended Coast Day, and judging from the large crowds in the horseshoe crab exhibit all day, most of them passed through the horseshoe crab exhibit area.

Conclusion

The University of Delaware Sea Grant College Program is committed to a collaborative approach in identifying and addressing important marine resource management issues. We welcome future opportunities to sponsor additional forums that will further clarify research or management questions related to horseshoe crabs.

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Appendix A: Annotated Bibliography of Horseshoe Crab Information

Compiled by Carl N. Shuster, Jr.

Sources of Information on the Historical Abundance of Horseshoe Crabs in the Delaware Bay Area

U.S. Commission of Fish and Fisheries (and successor agencies):

Rathbun, R. 1884. The Xiphosura. The horseshoe crab, *Limulus polyphemus* Latreille. In *The fisheries and fishery industries of the United States,* ed. G. B. Goode, Section I, Vol. 1, 829–30. Washington, DC: U.S. Commission of Fish and Fisheries.

"During the winter they [horseshoe crabs] are often taken out in Delaware Bay by the oyster dredgers. They are very much less abundant now than formerly, on account of so many having been caught from year to year for use as fertilizer. It would appear as though a few years more of indiscriminate capture would result in their being entirely exterminated from the region. The men catch them mainly in their hands, as they come upon the beaches, but they are also captured in pounds and weirs."

Rathbun, R. 1887. The commercial importance of the horseshoe crab. In *The fisheries and fishery industries of the United States,* ed. G. B. Goode, Section V, Vol. 2, 652–57. Washington, DC: U.S. Commission of Fish and Fisheries.

Rathbun reported ever-decreasing numbers of horseshoe crabs: "Horseshoe crabs are becoming constantly less abundant in Delaware Bay, owing to the practice of capturing, so far as possible, every individual that comes upon the shore."

Smith, H. M. 1891. Notes on the king-crab fishery of Delaware Bay. *Bull. U.S. Fish. Comm.* 9(19):363–70.

Of all the fisheries for horseshoe crabs along the Atlantic coast, only in Delaware Bay was harvesting "a well-defined industry." The extent of the fishing season varied from two to three months (May through July); the fishing centers were from Town Bank to Heislerville [probably Thompsons Beach], with about seven-eighths of the catch being made between the area off Dennisville and Fishing Creek. In 1890, about three-fourths of the yield was taken in the vicinity of Goshen, Dias Creek, and Green Creek: 335,000; 410,000; and 411,000 horseshoe crabs, respectively. While considerable numbers were caught by hand on the spawning beaches, the use of pound nets was becoming more extensive each year.

Smith cited Rathbun's (1880) warning about the decrease in horseshoe crab abundance and noted that the yield in 1880 (4.3 million horseshoe crabs) was more than double that in each of the years 1887–1890. The horseshoe crab fertilizer factory in New Jersey, at West Creek, handled about 1.3 million horseshoe crabs (almost the entire catch of the state) each year in 1887 and 1888 and produced an average of 800 tons of horseshoe crab fertilizer in each of those years. Then, Smith speculated, "It seems probable that before long the decimation will become so pronounced that the profitable prosecution of the fishery will be impossible; then it is hoped that the employment of the destructive forms of apparatus [pound nets] will be discontinued and the crabs given an opportunity to multiply unrestrictedly for a few years at least." He also observed that the diminution of the abundance of the crabs was chiefly due to the capture of the crabs during the spawning season, usually before they reached the beaches to spawn.

Shuster, C. N., Jr., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries* 8:363–72.

Summarized fisheries statistics of the United States, 1870s through 1980s. The Delaware Bay fishery, mainly for fertilizer and livestock food, showed a gradual decline over the years from an average of 4,300,000 horseshoe crabs harvested each year in the 1870s to 42,000 in the 1960s, followed by no reportable harvests in the 1970s and 1980s. Estimated 222,000 males and 51,000 females at the peak of the 1977 spawning season.

National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NMFS):

Botton, Mark L., and John W. Ropes. 1987. Populations of horseshoe crabs, *Limulus polyphemus,* on the northwestern Atlantic continental shelf. *Fish. Bull.* 85(4):805–12.

The highest abundance of horseshoe crabs, collected by bottom trawl and ocean clam surveys, 1975 through 1983, from 9 m and deeper, was from Virginia to New Jersey. Thus, large numbers of horseshoe crabs are in the proximity of the principal spawning area, Delaware Bay, and nearby coastal embayments. Approximately 90% of the minimum estimated standing stock in that area, 2.3–4.5 million individuals, were located at depths less than 30 m. Fewer horseshoe crabs were taken on the shelf during those months when spawning occurred in the estuaries.

Botton, Mark L., and John W. Ropes. 1987. The horseshoe crab, *Limulus polyphemus*, fishery and resource in the United States. *Mar. Fish. Rev.* 49(3):57–61.

Fishing-related mortality in the United States was estimated minimally at 350,000 horseshoe crabs per year, mostly in the Middle Atlantic and southern New England states. Bait operations at the time apparently killed 10 to 20 times the number of animals killed when bled to obtain medical materials. According to the NMFS surveys, the mid-Atlantic continental shelf population of horseshoe crabs remained relatively constant from 1964 through 1977 at 2.3–4.1 million.

Virginia Institute of Marine Science (VIMS):

Shuster, C. N., Jr. 1982. A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus*, with reference to other Limulidae. In *Physiology and biology of horseshoe crabs*, eds. J. Bonaventura, C. Bonaventura, and S. Tesh, 1–52. New York: Alan R. Liss, Inc.

Page 26: Paul A. Haefner, Jr. (VIMS, personal communication, 1979), reported more females than males (53 F: 0 M) at depths of 17–39 m on the continental shelf off Virginia in early June 1973, and 96 F:17 M in mid-November 1974 at depths of 23–45 m.

Shuster, C. N., Jr. 1985. Introductory remarks on the distribution and abundance of the American horseshoe crab, *Limulus polyphemus*, spawning in the Chesapeake Bay area. In *The Chesapeake Bay—prologue to the future*, 34–38. Proceedings of the Chesapeake Bay Symposium, National Marine Educators Conference.

Delaware Bay and Chesapeake Bay populations of horseshoe crabs may overlap along the Delmarva coast.

Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife:

1990–present, unpublished: fishery resource data obtained within Delaware Bay by a 30-ft. otter trawl.

Includes abundance and sex-ratio data of adult horseshoe crabs for 10 months at 9 fixed stations each year in the Delaware portion of the bay. Over the years, abundance has decreased and the sex ratio has shifted from a 1-to-1 ratio toward a decrease in females:

- Abundance information (376 tows from 1990 through 1994; total of 3,117 horseshoe crabs collected)—annual catch rates ranged from 18.6 adult horseshoe crabs per nautical mile in 1990 to 2.4 in 1994.
- Sex ratios for the years 1990 through 1994, expressed as a percentage: 1990 (53.7M, 46.3F); 1991 (47.9M, 52.1F); 1992 (50.1M, 49.9F); 1993 (61.7M, 38.3F); 1994 (61.6M, 38.4F).

New Jersey Department of Environmental Protection and Energy, Bureau of Marine Fisheries:

1989–present, unpublished fishery resource data (otter trawl data from New Jersey offshore waters).

A preliminary analysis of the data (1989 through 1994) by Drs. Robert E. Loveland and Mark L. Botton on 16 June 1995 indicated a steady decline in the offshore horseshoe crab population. Among the analyses used was a running average on the data for catch per unit effort, by numbers of horseshoe crabs, for all tows. They concluded that the New Jersey trawl data appeared to show the same trend as the Delaware Bay shoreline spawning survey and the Delaware DNREC Division of Fish and Wildlife trawl data within the bay and was consistent with the impression that the spawning population within the bay has been declining in the past few years.

Other Delaware Bay Fisheries Information:

Fowler, H. W. 1908. The king crab fisheries in Delaware Bay, 113–119 + pls. 59–65. 1907 Annual report of the New Jersey State Museum, Trenton.

Cites Professor George H. Cook (Geol. Cape May Co., 1857—King crabs, or Horse-feet: pp. 105–112) as the first important account of the horseshoe crab in the waters of the bay shore of Cape May County: "The whole strand for many miles would be covered with them, sometimes 2 or 3 deep. A resident of Town Bank reported that on his shore of 100 rods he could get 100,000 in a week. Of about half a mile of the strand 750,000 were taken in 1855, and 1,200,000 . . . on about a mile in 1856."

Shuster, C. N., Jr. 1960. Horseshoe "crabs"—In former years, during the month of May, these animals dominated Delaware Bay shores. *Estuarine Bull.* (University of Delaware) 5(2):1–9.

By 1953, the 78-year-old Samuel Compton of Dias Creek, one of the last of the old-timers in the horseshoe crab fishery, tended a pound net in a horse-drawn cart (from *The Sunday Bulletin*, Philadelphia, 21 June 1953).

Annual Volunteer Survey of Horseshoe Crabs Spawning on the Delaware Bay Shores:

Finn, J., C. N. Shuster, Jr., and B. L. Swan. 1991. *Limulus* spawning activity on Delaware Bay Shores, 1990. Private printing (Finn-Tech Industries), brochure. (Reprinted in The Society of Natural History of Delaware, 1991:6.)

Swan, B. L., W. R. Hall, Jr., and C. N. Shuster, Jr. 1992. *Limulus* spawning activity on Delaware Bay shores 25 May 1991. Fact Sheet of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

Swan, B. L., W. R. Hall, Jr., and C. N. Shuster, Jr. 1993. *Limulus* spawning activity on Delaware Bay shores, 16 May 1992. Fact Sheet of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

Swan, B. L., W. R. Hall, Jr., and C. N. Shuster, Jr. 1994. *Limulus* spawning activity on Delaware Bay shores on June 5, 1993. *Estuary News* 4(4):7. Newsletter of Delaware Estuary Program. Available from Pennsylvania Environmental Council, Philadelphia.

Unpublished 1994 data.

Annual horseshoe crab spawning survey data indicate a general decline in abundance of spawners over the years (based on an annual one-day survey of the numbers of horseshoe crabs spawning on the shores of Delaware Bay checked, in 1993 and 1994, against weekly data at a few major spawning areas). These data are considered to be only very rough indicators of the peak spawning activity during these years:

- 8 June 1990 (1,241,000; 2.19 males/female)
- 25 May 1991 (1,225,000; 2.64 males/female)
- 16 May 1992 (399,000; 3.13 males/female)
- 5 June 1993 (394,039; 2.49 males/female)
- 21 May 1994 (104,000; 2.46 males/female)
- 11 June 1994 (535,000; 3.74 males/female)

Maryland Department of Natural Resources, Tidal Fisheries Division:

A new fisheries program in Chesapeake Bay and the coastal bays. The Maryland program has two major components:

1. **Studies on the Horseshoe Crab Population and Its Habitats:**
   - Survey of horseshoe crab spawning population, including delineation of spawning habitat.
   - Shorebird activity associated with horseshoe crab spawning.
   - Installation of a horseshoe crab "hotline" to alert staff of the location of spawning horseshoe crabs, etc.
   - Initiation of a tagging program in 1995 (about 1,600 tagged so far).
   - Collection of morphometric and "age" data, by sex.
   - Initiation of a study, in 1996, on the environmental factors affecting the temporal variability in the utilization of spawning beaches by horseshoe crabs.
   - Initiation of a study, in 1996, to determine if Maryland's horseshoe crab spawning survey methodology could be used to develop a statistically valid index of abundance.

2. **Resource Management:**

In recognition of the importance of horseshoe crabs, Maryland and Virginia, in 1994, adopted a joint management plan on horseshoe crabs that included the following:

- Development of a mandatory reporting procedure for MD horseshoe crab harvesters.
- Beginning in 1996, prohibition by Maryland on the use of all benthic collection gear and hand-harvest within Chesapeake Bay, the coastal bays, and within 1 mile off the Atlantic coast shoreline, from 1 April through 30 June, except on Mondays and Thursdays.
- In 1996, a survey of eel harvesters to ascertain the scope of the use of horseshoe crabs for bait.
- In 1996, initiation of a study to characterize the offshore horseshoe crab fishery in Maryland.

Sources of Information on the Natural History/Ecology of Horseshoe Crabs

Abundance and Distribution:

Baptist, J. P., O. R. Smith, and J. W. Ropes. 1957. Migrations of the horseshoe crab, *Limulus polyphemus,* in Plum Island Sound, Massachusetts. U.S. Dept. of the Interior, Fish and Wildlife Service, Special Fisheries Report. *Fisheries* 220:1–11.

From 1952 through 1954, 1,780 horseshoe crabs were tagged and released in or near Plum Island Sound. Recovery of the tagged horseshoe crabs revealed that (1) individual horseshoe crabs probably spent a relatively short time in the sound each year during the spawning migration; (2) although recoveries of individual horseshoe crabs indicated a fairly rapid seaward migration throughout the summer, the offshore migration was most evident during September; (3) tagged horseshoe crabs were recaptured at distances up to 7 nautical miles from point of release; (4) tagged horseshoe crabs were recovered four years after tagging; (5) there was a fairly discrete population of horseshoe crabs in Ipswich Bay; and (6) population estimates, based on tag returns, ranged from 151,000 (4 June 1954) to about 1,000,000 (summer of 1955).

Botton, M. L., and J. W. Ropes. 1987. Populations of horseshoe crabs, *Limulus polyphemus,* on the northwestern Atlantic continental shelf. *Fish. Bull.* 85(4):805–12.

Ninety percent of the horseshoe crabs obtained during the Northeast Fisheries Center (NMFS/NOAA), by bottom trawl and ocean clam surveys from southern New England to North Carolina, was between New Jersey and Virginia (where the estimated minimum standing stock was 2.3–4.5 million individuals).

Milne, L. J., and M. J. Milne. 1947. Horseshoe crab—is its luck running out? *Fauna* 9:66–72 (Zoological Society, Philadelphia).

Reported that a Cape May beach yielding only 150,000 annually was the same area where 500,000 horseshoe crabs were harvested only a decade before.

Botton, M. L., and J. W. Ropes. 1987. The horseshoe crab, *Limulus polyphemus,* fishery and resource in the United States. *Mar. Fish. Rev.* 49(3):57–61.

Based on the National Marine Fisheries Service groundfish surveys, the horseshoe crab population on the mid-Atlantic continental shelf remained relatively constant between 1975 and 1983, at 2.3 to 4.1 million individuals.

Shuster, C. N., Jr., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries* 8:363–72.

The 1977 peak population of spawning horseshoe crabs was estimated to be about 222,000 males and 51,000 females. This estimation was based upon a shoreline survey of spawning intensity, corroborated by a quantification of egg nests in a beach.

Shuster, C. N., Jr. 1950. Observations on the natural history of the American horseshoe crab, ***Limulus polyphemus.*** Contribution No. 564:18–23. Woods Hole, MA: Woods Hole Oceanographic Institution.

The Barnstable Harbor (Cape Cod, Massachusetts) population of horseshoe crabs was estimated to be between 50,000 and 100,000 (based on the results of a tagging study).

See also the following list on tagging studies.

Tagging Studies:

Shuster, C. N., Jr. 1950. Observations on the natural history of the American horseshoe crab, ***Limulus polyphemus.*** Contribution No. 564: 18–23. Woods Hole, MA: Woods Hole Oceanographic Institution.

First tagging study — on the Cape Cod Bay population — demonstrated that plastic tags remained on the horseshoe crabs for at least two years; one individual, a female, was recaptured 21 miles from point of tagging/ release, 56 days later; the shortest-time, longest migration of a female was 12.0 miles in 32 days.

Baptist, J. P., O. R. Smith, and J. W. Ropes. 1957. Migrations of the horseshoe crab, ***Limulus polyphemus,*** in Plum Island Sound, Massachusetts. U. S. Dept. of the Interior, Fish and Wildlife Service, Special Fisheries Report. ***Fisheries*** 220:1–11.

Tagged horseshoe crabs moved for at least 15 miles from release points in Plum Island Sound.

Rudloe, A. 1981. The effect of heavy bleeding on mortality of the horseshoe crab, ***Limulus polyphemus,*** in the natural environment. ***J. Invert. Path.*** 42:167–76.

Tags were used to identify the study population and its survival.

Shuster, C. N., Jr. 1990. Tracking horseshoe crabs. ***Underwater Naturalist, Bull. Amer. Littoral Soc.*** 19:22–23.

Describes tagging program instituted by the late James Finn, president of Finn-Tech. The tagging program has been continued by Benjie Lynn Swan of Limuli Laboratories who provided the following unpublished file data:

- 6,200 adult horseshoe crabs were tagged on the shores of Delaware Bay (Delaware = 3,300; New Jersey = 2,900) from 1990 to 1995, mainly in May and June although some were tagged earlier and later in the year. Of these, 49 live ones (20 females, 29 males) have been recaptured (16 of those tagged on New Jersey shores [16 males, 10 females]; 33 on Delaware shores [22 males, 11 females]).
- 28 were recaptured in less than one month after tagging (range 0 to 22 days; average 7 days) from the same site or area near site of release (5 New Jersey = 2 males, 3 females; 23 Delaware = 17 males, 6 females). [Note: actually, an additional 2 more males, tagged on 5 June 1995 at East Point, New Jersey, and recovered, also in June, at Martha's Vineyard, Massachusetts, have not been included in this summary; it can be assumed that they were transported to New England, and for some reason were discarded there alive.
- 11 were recaptured in two to five months; 6 of these were retaken at or near site of release but 4 were taken outside of Delaware Bay (3 near Ocean City, Maryland = 1 female tagged on 9 June 1990 at Cape Henlopen, Delaware, and recovered on 10 August 1990; and 1 male and 1 female tagged on 10 June 1993 at Pickering Beach and recovered on 4 September 1993 south of Ocean City, Maryland; and 1 female tagged on 16 May 1992 at Highs Beach, New Jersey, was retaken on 27 October 1992 at Hereford Inlet, New Jersey).
- 4 were recaptured in 7 to 11 months, 2 near point of release (1 female tagged at Highs Beach, New Jersey, was retaken at Reeds Beach, New Jersey; 1 female was tagged and recovered at Pickering Beach, Delaware; 1 female had migrated from East Point, New Jersey, to off Ocean City, Maryland; and the other, a male tagged at Big Stone Beach, Delaware, was recovered across the bay at Villas, New Jersey).
- 4 were recaptured from one to three years (average of two years) after release. Three were taken near point of release (1 male and 1 female were tagged and recovered at Highs Beach, New Jersey; 1 male was tagged and recovered at Pickering Beach, Delaware), and 1 [a male] released at Pickering Beach was retaken at Reeds Beach, New Jersey.

Comments

Distances traveled and time of travel are not revealed by tagging in most cases; all that are usually certain are the dates and places of tagging and the dates and places of recovery. Nevertheless, 1 female released at East Point, New Jersey, was recovered off Ocean City, Maryland, within seven months (from 10 June 1994 tagging to 4 January 1995 recovery).

Tagged horseshoe crabs were recovered, alive, up to three years after tagging, proving that both crabs and tags can survive that long.

10 recaptures had "overwintered":

- 1 recaptured during the first winter — a female horseshoe crab released at East Point, New Jersey, on 10 June 1994 was caught off Ocean City, Maryland, on 4 January 1995.

6 had overwintered one full winter:

- 1 female tagged on 8 June 1990 at Port Mahon, Delaware, and recovered on 5 May 1991 at Bowers Beach, Delaware.
- 1 male tagged on 9 June 1991 at Highs Beach, New Jersey, and recovered on 26 July 1992 at Highs Beach, New Jersey.

- 1 female tagged on 23 October 1991 at Highs Beach, New Jersey, recovered on 5 May 1992 at Reeds Beach, New Jersey.
- 1 female tagged on 10 June 1994 at East Point, New Jersey, recovered on 4 January 1995 off Ocean City, Maryland.
- 1 male tagged on 25 June 1994 at Big Stone Beach, Delaware, recovered on 11 May 1995 at Villas, New Jersey.
- 1 female tagged on 25 June 1994 at Pickering Beach, Delaware, recovered on 21 May 1995 at Pickering Beach.

2 over two winters:

- 2 males; both tagged 10 June 1993 at Pickering Beach, Delaware, with one recovery on 11 May 1995 at Reeds Beach, New Jersey, the other on 10 June 1995 on Pickering Beach.

1 female for three winters:

- tagged 16 May 1992 at Highs Beach, New Jersey; recovered 8 April 1995 at Highs Beach.

Ecological Considerations, Especially the Food Web:

Botton, M. L. 1984. Diet and food preferences of the adult horseshoe crab *Limulus polyphemus* in Delaware Bay, New Jersey, USA. *Mar. Sci.* 81:199–207.

This study found that adult horseshoe crabs in the Delaware Bay area fed on a wide variety of benthic invertebrates (plant material and some 41 groups of small animals). A comparison of the gut content with estimates of available prey showed that the most abundant clam, *Gemma gemma,* was avoided in preference to the thinner-shelled but comparatively scarcer clam, *Mulinia lateralis.* When present, the soft-shelled clam, *Mya arenaria,* was taken equally as same-sized *Mulinia.*

Botton, M. L. 1984. The importance of predation by horseshoe crabs, *Limulus polyphemus,* to an intertidal sand flat community. *J. Mar. Res.* 42:139–61.

The impact of predation on intertidal flats near spawning beaches was investigated using cages. In 1978 and 1979, protected sediments contained significantly more biomass and species than the unprotected sediments.

Botton, M. L., and H. H. Haskin. 1984. Distribution and feeding of the horseshoe crab, *Limulus polyphemus,* on the continental shelf off New Jersey. *Fish. Bull.* 82(2):383–89.

Horseshoe crabs were obtained during hydraulic dredge surveys of surf clam resources within 3 nautical miles of the coast of New Jersey. Various benthic organisms were consumed, primarily bivalves, arthropods, and polychaetes. Surf clams, from less than 1 mm to about 35 mm in length, were important in the diet of horseshoe crabs.

Botton, M. L., and R. E. Loveland. 1993. Predation by herring gulls and great black-backed gulls on horseshoe crabs. *Wilson Bull.* 105:518–21.

Over 60% of herring-gull and great black-backed-gull attacks on overturned adult horseshoe crabs were on the unprotected book gills. The horseshoe crabs usually responded by flexing their bodies and thrusting their telsons upward. Once the horseshoe crabs were weakened, the gulls removed the legs to get at the "liver" and in females, the eggs.

Botton, M. L., and J. W. Ropes. 1989. Feeding ecology of horseshoe crabs on the continental shelf, New Jersey to North Carolina. *Bull. Mar. Sci.* 45(3):637–47.

Horseshoe crabs, collected at 11- to 39-m depths along the continental shelf from North Carolina to New Jersey, fed primarily on bivalve mollusks. Prey ranged from 1 – 20 mm in shell length. Immature and mature horseshoe crabs had essentially the same diet, qualitatively and quantitatively. Food consumption was higher in September than in March or July. Horseshoe crabs attain their greatest densities in the relatively shallow waters (less than 30 m) between southern New Jersey and may be among the more significant predators of bivalves in that region.

Botton, M. L., R. E. Loveland, and T. R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and the abundance of horseshoe crab *Limulus polyphemus* eggs. *Auk* 111:605–16.

The distribution of migratory shorebirds on seven beaches within Delaware Bay was examined for prey abundance and shoreline characteristics, mid-May to early June, in 1990 and 1991. Red knots, sanderlings, ruddy turnstones, and "peeps" comprised nearly 100% of the shorebirds. Horseshoe crab eggs were the most abundant food item on those beaches. The shorebirds aggregated at places along the shore where shoreline discontinuities (jetties and spits at mouths of salt-marsh creeks), "trapped" water-borne horseshoe crab eggs and concentrated them. In general, both horseshoe crab eggs and shorebirds increased along the bay shore from Higbees Beach (near Cape May Point) to Moores Beach (32 km up-bay).

Castro, G., J. P. Myers, and R. E. Ricklefs. 1992. Ecology and energetics of sanderlings migrating to four latitudes. *Ecology* 73(3):833–844.

A study of the ecophysiological responses of sanderlings to their nonbreeding environments in New Jersey, Texas, Panama, and Peru. Their daily energy expenditure was temperature-influenced (being higher at colder locations and equivalent to 4.2 times the basal metabolism rate in New Jersey, 2.8 in Texas, 2.1 in Panama, and 2.7 in Peru). In New Jersey, feeding occurred for 55% of the daylight hours and roosting about 35%.

Castro, G., and J. P. Myers. 1993. Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. *Auk* 110:927–930.

The energy requirements of six species of migratory shorebirds, during their spring stopover at Delaware Bay, were calculated. The resultant high levels of energy

consumption clearly showed the importance of Delaware Bay to the migrating shorebirds and implied that the shorebird spring stopover might be a crucial and very important segment of the annual cycle of the birds.

Castro, G., J. P. Myers, and A. R. Place. 1989. Assimilation efficiency of sanderlings *(Calidris alba)* feeding on horseshoe crab eggs *(Limulus polyphemus)* eggs. *Physiol. Zool.* 62:716–31.

Metabolic assessments were made on seven captive sanderlings fed a horseshoe crab egg diet for three weeks (each bird ingested an average of 30.9 g of eggs/day) during which time the birds only maintained body weight (51.3 ± 5.2 g). The average metabolic efficiency was low (38.6% ± 1.0%), and 72% of the ingested eggs were passed through the digestive tract, unbroken, with a rapid gastrointestinal passage of 63 ± 2.5 minutes). When placed on a diet of mealworms *(Tenebrio larvae)* they rapidly gained weight (1.8 ± 0.20 g/day).

Clark, K. E., L. J. Niles, and J. Burger. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95:694–705.

Delaware Bay is the most important stopover in the eastern U.S. for the semipalmated sandpiper, ruddy turnstone, red knot, and sanderling. More than 216,000 of these birds were counted during a single day peak in May 1992. The abundant food resource provided by horseshoe crab eggs is one reason for this shorebird concentration.

de Sylva, D. P., F. A. Kalber, Jr., and C. N. Shuster, Jr. 1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary, with notes on other species collected in deeper water. University of Delaware Marine Laboratories, Information Series, Publication No. 5.

Horseshoe crab eggs and larvae were found in the stomach contents of several small fish species and the juveniles of large fish (several, when grown, are fished recreationally and commercially): American eel, striped killifish, white perch, striped bass, silver perch, weakfish, northern kingfish, Atlantic silversides, summer flounder, and winter flounder.

Kraeuter, J. N., and S. R. Fegley. 1994. Vertical disturbance of sediments by horseshoe crabs, *Limulus polyphemus,* during their spawning season. *Estuaries* 17(1B):288–94.

Horseshoe crabs are benthic creatures that spend much time in burrowing. This study examined the extent to which the large population of horseshoe crabs on the Cape May shore reworked the sediments of the intertidal flats, i.e. "plowed them up." Horseshoe crabs mixed the sediments up to a depth of 17.7 cm.

Shuster, C. N., Jr. 1955. On morphometric and serological relationships within the Limulidae, with particular reference to *Limulus polyphemus* (L.). Ph.D. diss., New York Univ.

Lists the 11 species of shorebirds that Capt. Harold N. Gibbs (personal communication) observed feeding on the eggs of the horseshoe crab during May 1948 on the Cape May shore of Delaware Bay: semipalmated plover, black-bellied plover, knot, pectoral sandpiper, least sandpiper, red back sandpiper, semipalmated sandpiper, dowitcher, sanderling, turnstone, and laughing gull.

Survival and Adaptability, Including Habitat Considerations:

Botton, M. L., and R. E. Loveland. 1987. Orientation of the horseshoe crab, *Limulus polyphemus,* on a sandy beach. *Biol. Bull.* 173:289–98.

Beach slope is more important than vision in determining orientation on beaches and returning to the water. Both "blinded" (by opaque adhesive duct tape) and normal-sighted horseshoe crabs were released on flat sandbars and "normal" sloped (6°) beaches. Orientation was poor on a flat beach, although sighted horseshoe crabs slightly out-performed "blinded" ones. This correlated with the observation that large numbers of horseshoe crabs failed to return to the water after spawning on sandbars or similar habitats lacking a slope gradient.

Botton, M. L., R. E. Loveland, and T. R. Jacobsen. 1988. Beach erosion and geochemical factors: influence on spawning success of horseshoe crabs *Limulus polyphemus* in Delaware Bay. *Mar. Biol.* 99:325–32.

Horseshoe crab spawning is not evenly spaced along Delaware Bay shores. This study investigated the importance of geochemical and erosional factors to the selection of breeding beaches by horseshoe crabs. Erosion, exposing underlying peat, results in significantly fewer horseshoe crabs utilizing such a beach. The high levels of hydrogen sulfide associated with the peat indicated that the horseshoe crabs can detect the nature of the sediments and avoid unsatisfactory areas. In addition to the erosion of beaches, exposing vast strands of peat, the use of bulkheading, including cinder blocks, etc., to deter beach erosion has also reduced the spawning area available to horseshoe crabs.

Botton, M. L., and R. E. Loveland. 1989. Reproductive risk: high mortality associated with spawning in horseshoe crabs *Limulus polyphemus* in Delaware Bay, USA. *Mar. Biol.* 101:143–51.

Massive strandings of adult horseshoe crabs occur after spawning on the shores of Delaware Bay; about 10% of the total spawning population dies from strandings. A complex of factors, including abnormalities of the telson (the "tail," which a horseshoe crab uses to overturn itself when upside down), the size of the spawning population, tidal and weather conditions, and beach slope influence the number stranded during the breeding season. The large loss of gravid females may represent a major input of organic material to intertidal regions in certain regions of the bay.

Brockmann, H. J. 1990. Mating behavior of horseshoe crabs, *Limulus polyphemus*. *Behaviour* 114:206–20.

Nesting is synchronized to a few hours each day at the time of the spring new- and full-moon high tides in Florida waters. Unattached males cluster around the nesting pair. Experimental manipulation demonstrated that satellite males are capable of fertilizing the eggs, which suggested that "sperm competition" is the primary explanation for the presence of unattached males on the beach.

Brockmann, H. J., T. Colson, and W. Potts. 1994. Sperm competition in horseshoe crabs *(Limulus polyphemus)*. *Behav. Ecol. Sociobiol.* 35:153–60.

A paternity analysis was conducted to determine the proportion of eggs fertilized by attached and satellite males. Eggs were collected from nests on beaches made by isolated pairs with one satellite male, in Florida and Delaware. The eggs then were reared to the late trilobite or first instar stage. DNA was extracted from these offspring and from each adult (female, attached male, and satellite male) for use in the paternity analysis. Satellite males fertilized 40% of the eggs on average, attached males fertilized 51%, and 4% of the eggs that were laid by the female were sired by neither the attached nor the satellite male (and 5% could not be determined unambiguously). The high variability of success by the satellite males, ranging from 0 to 88%, was in part due to the relative positions of the satellite and the attached male to the incurrent water being pumped by the female.

Brockmann, H. J., and D. Penn. 1992. Male mating tactics in the horseshoe crab, *Limulus polyphemus*. *Anim. Behav.* 44:653–65.

Males return to the beach more frequently than females (and most females arrive attached) resulting in a strong bias in the sex ratio during one tide. Experimentally, differences in attached and unattached males in mating tactics are condition-dependent.

Penn, D., and H. J. Brockmann. 1995. Age-biased stranding and righting in male horseshoe crabs. *Anim. Behav.* 49:1531–39.

Large numbers of horseshoe crabs may be stranded on the shores of Delaware Bay. Stranding, for males, has two interacting components: mating tactic and righting ability. First, unattached males were more likely to strand than attached males. Second, unattached males were, on average, older than attached males. Experiments revealed that overturned older crabs were less likely to right themselves than younger ones.

Impact of Bleeding Horseshoe Crabs:

Rudloe, A. 1983. The effect of heavy bleeding on mortality of the horseshoe crab, *Limulus polyphemus*, in the natural environment. *J. Invert. Pathol.* 42:167–76.

Approximately 10,000 horseshoe crabs were collected and tagged in St. Joe Bay, Florida. Half were bled and half were handled as controls; all were released. Analysis of the tags returned for the two groups indicated that bleeding increased the mortality by 10% during the first year after bleeding. Bled crabs, recaptured four weeks later, had regained their blood volume. Animals collected two years after the original bleeding experiment showed a mortality of 11% of the bled over the controls.

Life Cycle and Longevity:

Botton, M. L., R. E. Loveland, and T. R. Jacobsen. 1992. Overwintering by trilobite larvae of the horseshoe crab *Limulus polyphemus* on a sandy beach of Delaware Bay (New Jersey, USA). *Mar. Ecol. Prog. Ser.* 88:289–92.

Describes the overwintering of horseshoe crab larvae within the nests in beaches of Delaware Bay. These larvae escape from the nests during the early spring when predation by birds is minimal. Overwintering also introduces an early start for individuals forming the year-class developing the year that they emerge from the nests.

Botton, M. L., and J. W. Ropes. 1988. An indirect method for estimating longevity of the horseshoe crab *Limulus polyphemus* based on epifaunal slipper shells *(Crepidula fornicata)*. *J. Shellfish Res.* 7:407–12.

Horseshoe crabs have been called "walking museums" due to the several species of organisms that encrust their shells. One of these attached species, the slipper shell snail *(Crepidula fornicata)*, was aged by shell length/shell weight analyses; some were estimated to be 8 years old. The data suggested that a maximum age of at least 17 to 19 years is attainable by horseshoe crabs of both sexes: 10 years to mature and 7 to 9 as adults.

Eldredge, N. 1991. *Fossils: The evolution and extinction of species*, 100–111. New York: Harry N. Abrams, Inc.

Page 105: "Horseshoe crabs are ecological generalists." In discussing the broad ecological regimes in which modern horseshoe crabs live, the author states (p. 108) "the more flexible a species is ecologically, the greater the chances that it will be able to find suitable habitats as the environment changes through time."

Ropes, J. W. 1961. Longevity of the horseshoe crab, *Limulus polyphemus* (L.). *Trans. Amer. Fish. Soc.* 90:79–80.

Reported recovery of live horseshoe crabs five years after their tagging and release in Plum Island Sound, Massachusetts.

Loveland, R. E., and M. L. Botton. 1992. Size dimorphism and the mating system in horseshoe crabs, *Limulus polyphemus* (L.). *Anim. Behav.* 44:907–16.

Reported up to 15 males in a spawning group with 1 female.

Shuster, C. N., Jr. 1950. Observations on the natural history of the American horseshoe crab, *Limulus polyphemus*. Contribution No. 564:18–23. Woods Hole, MA: Woods Hole Oceanographic Institution.

On the basis of observations during the summers of 1949 and 1950, in the Barnstable Harbor area of Cape

Cod, the following aspects of the natural history of horseshoe crabs were described: food and feeding habits, growth and growth stages, breeding habits, migratory habits, and an estimate of the Barnstable Harbor/Cape Cod Bay population.

huster, C. N., Jr. 1953. Odyssey of the horseshoe crab. *Audubon Magazine* 55(4): 162–63, 167.

Page 167: By the early 1950s, horseshoe crabs were being taken for eel bait, but the larger numbers were still being harvested for fertilizer. "However, the greatest loss of life is at the beginning, when salt-water fishes, eels, and shorebirds follow along after the mating pairs or dig in the sand to feed upon the newly-laid eggs or larvae" of the horseshoe crab.

Shuster, C. N., Jr. 1955. On morphometric and serological relationships within the Limulidae, with particular reference to *Limulus polyphemus*. Ph.D. diss., New York University.

Established on the basis of adult horseshoe crab morphometry that the major populations of horseshoe crabs were relatively discrete. Gave life cycle data: 18 growth stages, differential increments of growth in juvenile males and females, and 9 to 10 years to reach maturity.

Shuster, C. N., Jr. 1979. Distribution of the American horseshoe crab, *Limulus polyphemus* (L.). In *Biological applications of the horseshoe crab (Limulidae)*, eds. E. Cohen et al., 3–26. New York: Alan R. Liss, Inc.

Page 17: On 24 July 1951, nearly 2,000 juvenile horseshoe crabs were collected on 16 square ft. of an intertidal flat in front of the New Jersey Oyster Research Lab on Cape Bay: 9 larvae, 336 "first-tailed," 950 Stage III, and 678 Stage IV. By 11 September, large numbers of juvenile horseshoe crabs were spread out, bayward, over five intertidal bars (a distance of over 140 m). Also described distribution of adult horseshoe crabs (pp. 19–21).

Shuster, C. N., Jr. 1982. A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus*, with reference to other Limulidae. In *Physiology and biology of horseshoe crabs*, eds. J. Bonaventura, C. Bonaventura, and S. Tesh, 1–52. New York: Alan R. Liss, Inc.

A synthesis of previous major studies and those of the author; the first comprehensive account of the natural history of horseshoe crabs in the twentieth century. Included much of the author's unpublished observations and data. Life cycle, including growth stages, breeding, and migrations (pp. 22–31); behavior and orientation, including locomotor activities and tolerance of waters of different salinities (pp. 32–34); food and feeding (pp. 34–35); symbiotic and other relationships (pp. 35–45).

Shuster, C. N., Jr., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries* 8:363–72.

In 1977, there was an average of 24 nests per square meter within a 6-m band, based on a series of beach transects (from the low-water to the high-water level). This computed to 288,000 nests in the 2-km strand just south of the New Jersey Oyster Research Lab on Cape May (24 x 6 m x 2,000 m). There was an average of 3,650 ± 232.5 eggs in each nest. On average, large-sized females had 88,000 mature eggs, although this number varied greatly, probably depending upon the age and size of the individuals and on the extent to which each female had or had not spawned prior to the examination.

Wigley, R. L., and R. B. Theroux. 1981. Atlantic continental shelf and slope of the United States — macrobenthic invertebrate fauna of the Middle Atlantic Bight region — faunal composition and quantitative distribution. Geological Survey Professional Paper 529–N.

This survey was conducted in the early 1960s. In terms of biomass, bivalve mollusks and annelids were dominant groups of the macrobenthic organisms. Organisms from both groups are major items in the diet of horseshoe crabs.

Appendix B

Horseshoe Crab Regulations for the Mid-Atlantic States

	NJ[1]	DE[2]	MD[3]	VA	SC
Gear Type Allowed — State Waters					
Hand	Yes	Yes	Yes	Yes	Yes
Trawl	No	No	Yes, outside 1 mile of Atlantic coast	No	Yes
Dredge	No	Yes	Yes	Yes, crab dredge by-catch in some areas only	Yes
Other	Yes	No	Yes (gill net, fyke)	Yes	Yes
Reporting Requirements	Yes	Yes	Yes	Yes	Yes
Season Restrictions/Area Closure	Yes	Yes	Yes	Yes	Yes
Number Permit Holders (1997 season)	Approximately 300	5 dredge 122 hand	17	Approximately 24 hand crab dredge by-catch	—
Personal Use — Exemption from Licensing	—	• hand-pick (6/day) • commercial eelers for personal use for bait in Delaware	—	5 per day	—
Returned to Water Unharmed	No	No	No	No	Yes
Reference	NJAC 7.25-18.16	7 Del. Code, Sec. 2701, 1902 & Shellfish Regs. S51-54	23:2 MDR 08.02.10.01	VMRC Reg. 4 VAC 20-900-10 ET. SEQ	Code of Laws of SC Sec. 50-17-165
Contact	Peter Himchak	Charlie Lesser	Tom O'Connell	Lewis Gillingham	Marine Resource Division
Telephone	(609) 748-2020	(302) 739-3441	(410) 260-8271	(804) 247-2243	(803) 795-6350

[1] New Jersey adopted new regulations, effective 9/25/97, which eliminate the trawl fishery and dredge by-catch, establish eligibility criteria, and modify the season.

[2] In Delaware, the Department of Natural Resources and Environmental Control has proposed regulations for the 1998 season that establish eligibility criteria, control time of harvest, establish daily limits for the dredge fishery, and require monthly reports on harvest.

[3] As this report goes to press, Maryland is considering an emergency order for the 1998 season that would establish a permit system and reduce catch by 50% through quotas, season, area, and daily limits.

Appendix C

Horseshoe Crab Commercial Landings by State and Water Area, Maine to Virginia, All Gears

1989

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs*	Total Percent
MA	—	—	—	—	—	—
RI	282,889	100.0%	—	—	282,889	26.5%
CT	—	—	—	—	—	—
NY	—	—	—	—	—	—
NJ	10,059	27.9%	26,030	72.1%	36,089	3.4%
DE	—	—	—	—	—	—
MD	553,620	47.2%	192,600	25.8%	746,220	70.0%
VA	117	28.1%	300	71.9%	417	0.0%
	846,685	**79.5%**	**218,930**	**20.5%**	**1,065,615**	**100.0%**

**This excludes 22,297 lbs. for which the area of landings is unknown.*

1990

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs*	Total Percent
MA	—	—	—	—	—	—
RI	170,150	—	—	—	170,150	19.9%
CT	—	—	—	—	—	—
NY	—	—	—	—	—	—
NJ	146,794	50.8%	142,374	49.2%	289,168	33.8%
DE	168,800	—	—	—	168,800	19.7%
MD	144,640	63.5%	83,040	36.5%	227,680	26.6%
VA	—	—	—	—	—	—
	630,384	**73.7%**	**225,414**	**26.3%**	**855,798**	**100.0%**

**This excludes 52,332 lbs. for which the area of landings is unknown.*

1991

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs*	Total Percent
MA	1,860	91.2%	180	8.8%	2,040	0.2%
RI	350,000	100.0%	—	—	350,000	32.8%
CT	—	—	—	—	—	—
NY	—	—	—	—	—	—
NJ	—	—	350,855	100.0%	350,855	32.9%
DE	—	—	—	—	—	—
MD	184,860	51.2%	176,120	48.8%	360,980	33.9%
VA	1,778	100.0%	—	—	1,778	0.2%
	538,498	**50.5%**	**527,155**	**49.5%**	**1,065,653**	**100.0%**

**This excludes 23,392 lbs. for which the area of landings is unknown.*

Horseshoe Crab Commercial Landings
by State and Water Area, Maine to Virginia, All Gears *(continued)*

1992

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs*	Total Percent
MA	—	—	—	—	—	—
RI	15,000	100.0%	—	—	15,000	1.5%
CT	10,000	100.0%	—	—	10,000	1.0%
NY	500	100.0%	-	-	500	0.1%
NJ	169,662	55.6%	135,360	44.4%	305,022	30.7%
DE	—	—	—	—	—	—
MD	371,364	56.0	292,260	44.0%	663,624	66.8%
VA	—	—	—	—	—	—
	566,526	**57.0%**	**427,620**	**43.0%**	**994,146**	**100.0%**

**This excludes 6,473 lbs. for which the area of landings is unknown.*

1993

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs	Total Percent
MA	—	—	—	—	—	—
RI	1,062	100.0%	—	—	1,062	0.1%
CT	—	—	—	—	—	—
NY	—	—	—	—	—	—
NJ	371,754	53.2%	327,019	46.8%	698,773	36.7%
DE	118,300	100.0%	—	—	118,300	6.2%
MD	869,492	80.2%	214,300	19.8%	1,083,792	56.9%
VA	—	—	2,768	100.0%	2,768	0.1%
	1,360,608	**71.4%**	**544,087**	**28.6%**	**1,904,695**	**100.0%**

1989–1993

STATE	State < 3mi Lbs	State < 3mi % of Tot.	EEZ > 3mi Lbs	EEZ > 3mi % of Tot.	Total Lbs*	Total Percent
MA	1,860	91.2%	180	8.8%	2,040	0.0%
RI	819,101	100.0%	—	—	819,101	13.9%
CT	10,000	100.0%	—	—	10,000	0.2%
NY	500	100.0%	—	—	500	0.0%
NJ	698,269	41.6%	981,638	58.4%	1,679,907	28.5%
DE	287,100	100.0%	—	—	287,100	4.9
MD	2,123,976	68.9%	958,320	31.1%	3,082,296	52.4%
VA	1,895	38.2%	3,068	61.8	4,963	0.1%
	3,942,701	**67.0%**	**1,943,206**	**33.0%**	**5,885,907**	**100.0%**

**This excludes 104,494 lbs. for which the area of landings is unknown.*

Source: NMFS Unpublished Weighout Data.

Appendix D:
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