POPULATIONS OF HORSESHOE CRABS, *LIMULUS POLYPHEMUS*, ON THE NORTHWESTERN ATLANTIC CONTINENTAL SHELF

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ABSTRACT

This report analyzes the distribution and abundance of horseshoe crabs, *Limulus polyphemus* (L.), on the Middle Atlantic continental shelf, based on Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys of the past two decades at depths beginning at 9 m. Crabs were collected from North Carolina to southern New England, with the highest abundance and frequency of occurrence between Virginia and New Jersey. Approximately 90% of the minimum estimated standing stock size in that area, 2.3-4.5 million individuals, was located at depths <30 m. The geographic distribution may reflect proximity of this shelf region to the principal spawning areas in Delaware and Chesapeake Bays. Seasonally, horseshoe crab abundance on the shelf declined during those months when spawning in estuaries peaked. Crabs were caught at depths to 290 m, the limit of sampling; most of the animals caught at depths >100 m were off Cape Hatteras, North Carolina. Despite the presence of horseshoe crabs in estuaries as far north as Maine, New York is the northward limit on the shelf. This suggests that inshore populations in New England may be relatively isolated from each other and from the large Middle Atlantic shelf population.

Generalizations about the natural history, behavior, and ecological importance of horseshoe crabs, *Limulus polyphemus* (L.), are primarily based on studies of the shallow-water phase of its life cycle (Shuster 1979, 1982; Wells et al. 1983). The populations in the mid-Atlantic region are most accessible in late spring and early summer, when adults spawn en masse on sandy estuarine beaches. Knowledge of behavior (Shuster 1950; Rudloe 1980; Barlow et al. 1982; Cohen and Brockmann 1983), orientation (Rudloe and Herrnkind 1976; Botton and Loveland in press), morphometrics (Shuster 1955; Riska 1981), sediment disturbance (Woodin 1978, 1981), and predation (Smith and Chin 1951; Smith et al. 1955; Botton 1984a, b) is all based on studies of shallow-water or intertidal individuals. Population estimates have been restricted to shallow-water adults (Baptist et al. 1957; Sokoloff 1978; Rudloe 1980; Shuster and Botton 1985), with the exception of Botton and Haskin (1984), who surveyed the population on the inshore New Jersey continental shelf.

Perhaps because of the spectacular intertidal mass spawning phenomenon and accessibility, estuarine populations have received a disproportionate amount of attention by ecologists. In contrast, most of the animal's life is spent sublittorally. An adult female may spawn completely over several successive high tides; in general, repeated breeding is more characteristic of males (Rudloe 1980). Juveniles, during their first and second summer, are abundant on intertidal flats (Shuster 1955, 1979), but the remainder of the species' 14-19 year life span (Ropes 1961) is spent subtidally except for the annual spawning migration.

This report summarizes latitudinal and bathymetric distributions of horseshoe crabs on the northwestern Atlantic continental shelf. Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys during the past two decades have provided extensive data on the abundance and distribution of horseshoe crabs, principally north of Cape Hatteras, NC (Ropes et al. 1982; NEFC unpubl. data). Seasonal and annual trends in abundance are also discussed in the present report. Concern for evaluating the general population characteristics of horseshoe crabs parallels expanding commercial exploitation of the species. Animals are presently harvested to extract blood for the *Limulus* amoebocyte lysate (LAL) test, and as bait in eel (*Anguilla rostrata*), conch (*Busycon* sp.), and other fisheries (Pearson and Weary 1980); the vast majority of the fishing ef-

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fort is concentrated between Virginia and New Jersey (Botton and Ropes in press).

MATERIALS AND METHODS

NEFC bottom trawl surveys ranged from Cape Fear, NC, north to the Scotian Shelf; clam surveys cover the Middle Atlantic region north to Georges Bank. Both are general purpose survey programs, collecting data for standing stock assessments for many finfish and shellfish species, as well as collecting specimens for age determination, dietary analysis, and many other purposes (Grosslein 1969; Clark 1979).

During the period covered by this study (1975-83), the #36 and #41 Yankee otter trawls were used as sampling gear during bottom trawl surveys. Both nets have a mesh size of 5 inches throughout the wings and body, and 4.5 inches in the cod end. A liner of 0.5-in nylon mesh is employed at the aft end of the top belly and the cod end. Trawls are equipped with roller gear to facilitate use over rough bottoms. All tows were 30 minutes in duration at a vessel speed of 3.5 knots; stations were located using loran. An average of 1,129 stations per year was sampled (range, 711 stations in 1975 to 1,547 stations in 1979). Cruises were conducted during fall (September through early December) and spring (March through May) in all years, with five additional surveys during the summers (July through August) of 1977-81 and two during the winters (January through February) of 1978 and 1983. Sampling was conducted both day and night. After sorting the catch, personnel recorded the number of horseshoe crabs taken in each tow and their total wet weight to the nearest 0.1 kg.

A stratified random sampling design was used in the surveys (Grosslein 1969). The region was divided into several strata based primarily on depth. Stations were allocated to strata roughly in proportion to the area of each stratum and assigned to specific locations within strata at random (Clark 1979). For the purpose of this paper, stations of 9-27 m (5-15 fm) depth were defined as "inshore" and those deeper than 27 m as "offshore". Preliminary inspection of the catch data compiled by Ropes et al. (1982) showed the bulk of the horseshoe crab population to be located between northern New Jersey and southern Virginia. Within this region, there were 27 inshore and 16 offshore strata, based on depth and location. Stratified mean number per tow and biomass per tow of horseshoe crabs were converted into estimates of standing stock by using the "area swept" by a standard survey trawl in relation to catch as an estimate of minimum absolute density. Tows within strata were used to calculate variances around the means. Total populations for the inshore and offshore regions were estimated by expanding the average stratified mean catch per tow by the ratio of total area surveyed to the area sampled by an average tow. Further details of statistical methods are found in Clark (1979).

Ocean clam surveys used commercial style hydraulic dredges, towed for 5 minutes at 1.5 knots. The design and performance of this sampling gear is discussed by Meyer et al. (1981). Cruises from 1965 to 1978 used either a 30-in (91 cm) or 48-in (122 cm) knife-width dredge; cruises from 1979 to 1983 used a 60-in (152 cm) dredge. There were no ocean clam surveys in 1968, 1971-73, and 1975. Station locations were selected using a stratified random sampling design; the average number of stations sampled per year was 370 (range, 139 in

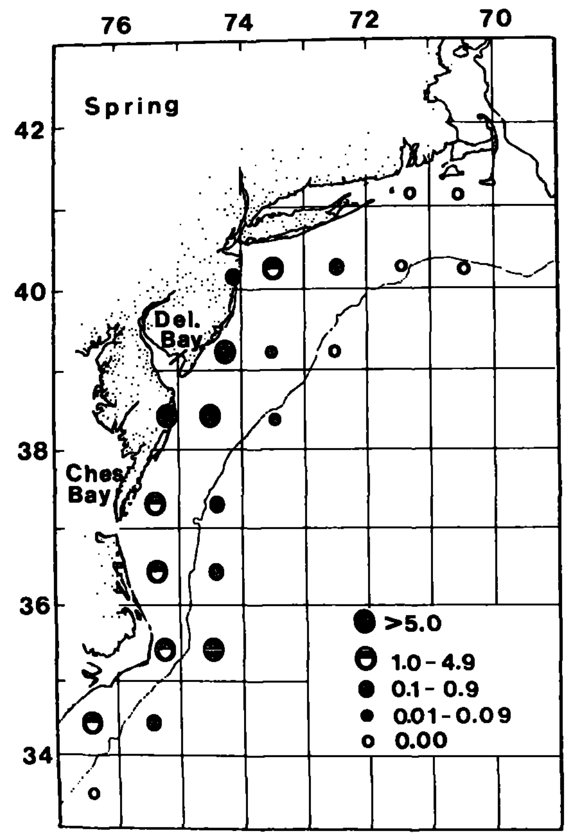

FIGURE 1.—Mean number of horseshoe crabs per tow,

1979 to 655 in 1966). Catches were not expanded into stock estimates, as for the bottom trawl survey data.

To analyze broad latitudinal variations in abundance and frequency of occurrence, catch and sampling effort were grouped by 1-degree latitude and longitude blocks. For example, stations at lat. 38°06′N, long. 74°02′W and 38°45′N, 74°50′W were both grouped together as 38°N, 74°W. Bottom trawl and ocean clam survey data were analyzed separately, because stratification schemes differed and the efficiencies of the two types of sampling gear cannot readily be compared.

RESULTS

Latitudinal Distribution

During groundfish surveys, 7,035 crabs were taken at 983 stations distributed from 33°N to 41°N; 75% of the crabs were caught between 37°N and 40°N (Fig. 1, App. Table 1). Highest abundance and frequency of occurrence was found on the shelf nearest the mouth of Delaware Bay. The maximum number of individuals per tow, 99, was obtained on 22 March 1976, from a station located off Assateague Island, VA, at 38°00′N, 75°14′W, in 13 m of water. Mean number per tow generally decreased with increasing distance from shore (Fig. 1).

Horseshoe crab abundance decreased both north of 40°N and south of 37°N (Fig. 1). Crabs were absent northeast of Montauk Point, Long Island (41°N, 72°W), and no crabs were found on or north of Georges Bank despite intensive sampling effort. Fewer than 2% of all horseshoe crabs collected were found south of 35°N (Cape Hatteras), and only one animal was caught south of 34°N.

The observed latitudinal distribution of horseshoe crabs in ocean clam surveys paralleled the above trends. A total of 1,640 animals was taken at 535 stations clustered primarily between Vir-

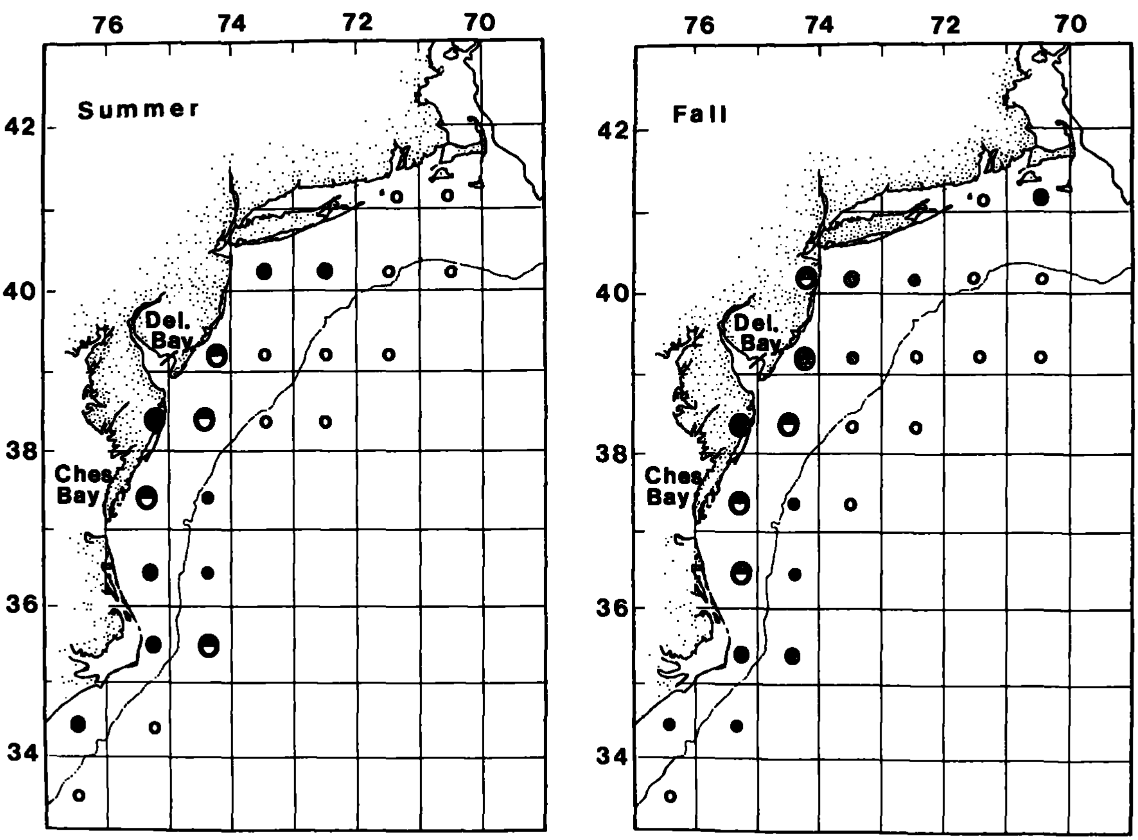

FIGURE 1.—*Continued*—by 1° latitude and longitude blocks, based on NEFC groundfish trawl data from 1975 to 1983.

TABLE 1.—Distribution of horseshoe crabs in clam surveys, 1965-83; 1,640 animals enumerated at 535 stations. Number of crabs over (number of stations with one or more individuals) in each row.

Latitude (N)	Longitude (W) 75°	74°	73°	72°
40°		4 (3)	23 (14)	4 (4)
39°		115 (46)	3 (3)	
38°	237 (77)	351 (103)		
37°	671 (176)	30 (16)		
36°	153 (76)	1 (1)		
35°	48 (16)			

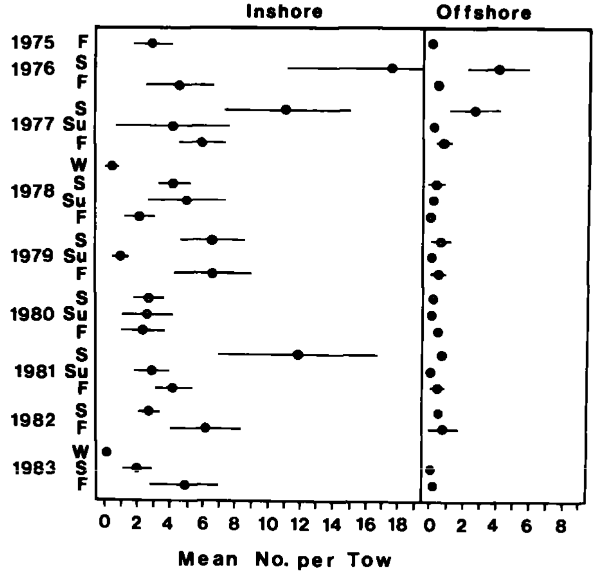

FIGURE 2.—Mean number of horseshoe crabs per tow (with 95% confidence limits) on the continental shelf from New Jersey to Virginia, based on NEFC groundfish trawl data from 1975 to 1983. W = winter; S = spring; Su = summer; F = fall; Inshore = all tows within sampling strata shallower than 27 m; Offshore = all tows within sampling strata deeper than 27 m. Where no confidence limit is shown, calculated limit was smaller than the width of the datum point.

ginia and New Jersey (Table 1). Thus, horseshoe crabs were most abundant along the continental shelf from Virginia to southern New Jersey in both groundfish and ocean clam surveys.

Seasonal and Annual Variations in Standing Stock

On the New Jersey-Virginia continental shelf, average abundance and biomass were highest during spring and fall cruises, lower in summer, and lower still (based on limited sampling) in winter (Fig. 1, Table 2). Horseshoe crabs were present in more than half the inshore tows throughout the year. Frequency of occurrence did not fluctuate as widely as abundance or biomass, and was consistently higher inshore than offshore.

Population estimates show considerable annual variation, with highest recorded catches in spring of 1976 and 1981 (Fig. 2). However, no clear trends in standing stock between 1975 and 1983 were evident. We estimate, based on the more complete fall and spring surveys, a minimum inshore population ranging from 1.8 to 3.1 million individuals (2,969 to 3,626 t), and a minimum offshore population ranging from 0.5 to 1.4 million individuals (972 to 1,975 t) (Table 2), for a total of some 2.3-4.5 million individuals. Coefficients of variation, based on individual stratum catches, ranged from 11.6 to 41.6 for individual inshore survey estimates, and from 23.6 to 87.5 for offshore estimates.

TABLE 2.—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. Strata shallower than 27 m were defined as inshore, and strata deeper than 27 m were defined as offshore.

	Winter	Spring	Summer	Fall
Inshore				
Mean no. per trawl	0.41	7.44	3.26	4.54
% occurrence	56	76	61	78
Population ($\times 10^6$)	0.410	3.103	1.258	1.881
Biomass (metric tons)	93	3,626	2,075	2,969
Offshore				
Mean no. per trawl	—	1.03	0.10	0.42
% occurrence	—	29	30	22
Population ($\times 10^6$)	—	1.445	0.129	0.530
Biomass (metric tons)	—	1,975	231	972

Bathymetric Distribution

Horseshoe crabs were taken at stations between the inshore sampling limit, 9 m, and 290 m depth (Fig. 3). Seventy-four percent of the total number caught in bottom trawl surveys were taken from stations shallower than 20 m; and 92% were caught at depths <30 m. This trend was not an artifact of sampling effort. Offshore stations (>27 m) comprised approximately 73% of the sampling effort but produced <10% of the catch. Mean abundance and biomass were nearly an order of magnitude higher at the inshore strata than the offshore strata, and horseshoe crabs were at least twice as likely to be caught inshore than offshore during all seasons (Table 2). The operation of the hydraulic clam dredge was limited to waters <80 m, and within this range, crabs were again most abundant at shallower depths. Sixty-two percent of the total catch was found shallower than 20 m, and 90% was found shallower than 30 m (Fig. 3).

Ninety-six animals were caught in 19 tows from 100 to 199 m depth, while 53 animals were taken in 7 tows below 200 m (Table 3). These deep-water individuals were caught between 34°21′N and 37°42′N (North Carolina to southern Virginia), with the majority from Cape Hatteras, south.

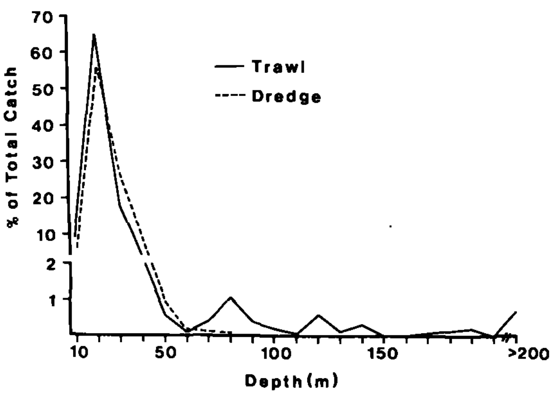

FIGURE 3.—Bathymetric distribution of horseshoe crabs, as percent of total catch, based on bottom trawl data (solid line) and ocean clam dredge data (dashed line).

DISCUSSION

Horseshoe crabs on the northwestern Atlantic continental shelf were most abundant between Virginia and New Jersey. On this section of the shelf, the population was estimated to be some 2.3-4.5 million individuals and was relatively constant between 1975 and 1983. The estimate of inshore abundance was necessarily conservative, because large survey vessels could not operate in shallow water. Horseshoe crabs may be abundant in areas inshore of the NEFC surveys; for example, in New Jersey State surveys, stations <1.8 km from shore frequently have over 10 horseshoe crabs/5-min hydraulic dredge tow in the Cape May area (Botton and Haskin 1984), and in areas of Narragansett Bay, 20-min otter trawls conducted by the State of Rhode Island have caught up to 40 horseshoe crabs (R. Sisson[3]). Both inshore and offshore stock estimates may also be conservative because the trawls, which are equipped with roller gear, may be <100% efficient in sampling horseshoe crabs, particularly if the animals are burrowed.

Seasonal surveys of the middle Atlantic continental shelf indicate a decline in horseshoe crab abundance during summer (July-August), which is consistent with the hypothesis that the shelf animals have seasonal inshore spawning migrations (Shuster and Botton 1985). More animals were caught during spring (April-early May) and fall (September-early December) periods, representing the prespawning and postspawning seasons, respectively. Therefore, the Virginia to New Jersey shelf population probably consist largely of individuals which spawn during the spring and early summer in the Chesapeake and Delaware Bays, and disperse offshore.

The range of horseshoe crabs on the continental

[3]R. Sisson, Division of Fish and Wildlife, Rhode Island Department of Environmental Management, Wakefield, RI 02879, pers. commun. December 1983.

TABLE 3.—Occurrence of all horseshoe crabs below 100 m depth on the continental shelf in groundfish surveys from 1975 to 1983.

Depth (m)	Latitude (N)	Longitude (W)	Date	Number of crabs
102	34°25′	75°53′	3/79	1
113	35°29′	74°50′	3/82	25
117	35°48′	74°52′	9/81	4
118	35°46′	74°51′	3/77	3
118	36°27′	74°47′	9/77	2
120	36°20′	74°48′	3/77	7
120	36°20′	74°48′	3/78	1
120	37°42′	74°15′	9/79	1
120	36°10′	74°48′	9/80	2
125	36°20′	74°55′	3/79	4
133	34°56′	75°21′	3/79	2
135	35°00′	75°16′	9/79	4
137	35°33′	74°49′	3/76	21
170	36°10′	74°47′	3/76	1
173	35°51′	74°52′	3/82	4
183	35°41′	74°49′	9/77	8
186	34°21′	75°55′	3/82	1
188	34°52′	74°24′	3/79	1
189	35°40′	74°48′	3/79	7
189	35°39′	74°48′	9/81	7
205	35°53′	74°50′	3/76	18
205	35°37′	74°49′	10/76	12
220	35°50′	74°51′	9/79	2
228	34°27′	75°44′	9/79	1
246	36°25′	74°46′	3/76	10
290	35°20′	74°54′	3/80	3

shelf is more limited than its estuarine distribution. Although substantial shelf populations are restricted to the south and west of Long Island, NY, breeding populations are found in estuaries as far north as Hog Bay, ME (44°35′N) (Born 1977). Populations in Narragansett Bay, Barnstable Harbor, Buzzards Bay, Cape Cod Bay, and Nantucket Harbor are large enough to be commercially exploited for *Limulus* lysate and/or bait (Botton and Ropes in press). Why such populations remain close to shore is unclear. However, it is consistent with the data of Baptist et al. (1957). They showed that individuals in Plum Island Sound, MA, remained in the local area 3 years after tagging.

The more northerly horseshoe crabs may be more discrete and isolated estuarine populations than those from North Carolina to New York. The small number of crabs on the southern New England shelf suggests that migrations of crabs between estuaries may be limited, although such populations may be occurring at depths too shallow to be sampled by large vessels. However, in the September 1985 trawl survey of the territorial waters of Massachusetts, only 34 horseshoe crabs were caught at 16 of the 94 stations sampled (mean depth 28 m, range 6-76 m) with similar numbers recorded during other recent surveys (B. Kelly[4]). If, in fact, these New England populations are isolated from the large Virginia-New Jersey stock, overexploitation may have serious detrimental effects. Although horseshoe crab larvae are weak swimmers, they are not commonly found in the plankton. Dispersal between discontinuous New England estuaries therefore depends on migration of juveniles or adults. However, the issue of stock identity may require further study. Shuster (1979) argued, based on morphometric data, that horseshoe crabs formed discrete populations throughout the geographic range. On the other hand, Saunders et al. (1986) found no evidence for genetic divergence between New England and middle Atlantic populations, based on their analysis of mitochondrial DNA.

The most noteworthy feature of the bathymetric distribution was the presence of horseshoe crabs at the edge of the continental shelf, at depths to 290 m. These animals were concentrated off North Carolina, where the continental slope is much closer to shore than at any other location in the Middle Atlantic Bight. This suggests that distance from shore, rather than depth per se, limits the dispersal of crabs on the continental shelf. Horseshoe crabs are eurythermal, tolerating temperatures from −1.1° to over 40°C (Mayer 1914; Fraenkel 1960); neither of these extremes are likely on the northwestern Atlantic continental shelf. Laboratory animals in an electronic shuttlebox arrangement voluntarily occupied temperatures from 15° to 40°C (Reynolds and Casterlin 1979), but the avoidance of cooler water may not apply to all populations, as all experimental animals were indigenous to the Gulf of Mexico. Our depth record at 290 m exceeds the 200 m record of Wolff (1977) but is not the maximum depth attained by this species. A submersible camera operated by the Duke Univeristy Marine Laboratory photographed a horseshoe crab at 1,097 m depth at 32°38′N, 76°33′W (D. Bunting[5]).

The potential orientation cues directing such deep-water animals to and from estuarine spawning beaches are of interest. Rudloe and Herrnkind (1976) showed that wave surge was important in determining the orientation of crabs in shallow waters near breeding sites, while Barlow et al. (1982) found that visual cues are important in the selection of cement "female models" by spawning males. Horseshoe crab eyes are sensitive to polarized light (Waterman 1950) and to low levels of visible light, and there are a variety of endogenous morphological changes that may permit photoreceptors to have high light sensitivity (Barlow et al. 1980). Whether such physiological properties are ecologically significant in enabling crabs to orient from the edge of the continental shelf to the estuarine spawning beaches is not yet known.

Much remains to be learned about the ecological relationships between horseshoe crabs and other shelf fauna. Botton and Haskin (1984) found that adult horseshoe crabs were dietary generalists off the New Jersey coast, both in terms of taxa and sizes of food items selected. Predation by horseshoe crabs in Delaware Bay affects bivalve abundance, size-frequency patterns, and spatial distributions (Botton 1984b, c). Significant commercial fisheries for surf clams, *Spisula solidissima*, and ocean quahaugs, *Arctica islandica*, overlap the range of horseshoe crabs on the northwestern Atlantic continental shelf. A study of horseshoe crab stomach contents is in

[4]B. Kelly, Massachusetts Department of Marine Fisheries, East Sandwich, MA 02537, pers. commun. October 1985.

[5]D. Bunting, Duke University Marine Laboratory, Beaufort, NC 28516, pers. commun. April 1985.

progress which will evaluate the importance of horseshoe crab predation to these bivalves.

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APPENDIX TABLE 1.—Abundance and frequency of occurrence of horseshoe crabs on the middle Atlantic continental shelf. Based on National Marine Fisheries Service trawl surveys from all seasons, 1975 to 1983.

Latitude/ longitude	No. stations sampled	No. stations with crabs	No. crabs	% occurrence	$\bar{x}$/trawl
41°N, 72°W	2	0	0	0.0	0.00
41°N, 71°W	187	0	0	0.0	0.00
41°N, 70°W	181	3	10	1.6	0.06
40°N, 74°W	13	4	9	30.8	0.69
40°N, 73°W	396	122	355	30.8	0.90
40°N, 72°W	399	39	72	9.8	0.18
40°N, 71°W	318	0	0	0.0	0.00
40°N, 70°W	303	0	0	0.0	0.00
39°N, 74°W	269	134	999	49.8	3.71
39°N, 73°W	250	5	9	2.0	0.04
39°N, 72°W	255	0	0	0.0	0.00
39°N, 71°W	61	0	0	0.0	0.00
39°N, 70°W	23	0	0	0.0	0.00
38°N, 75°W	92	74	1,208	80.4	13.13
38°N, 74°W	390	167	1,986	42.8	5.09
38°N, 73°W	233	1	1	0.4	0.04
38°N, 72°W	34	0	0	0.0	0.00
37°N, 75°W	323	174	1,085	53.9	3.36
37°N, 74°W	264	16	21	6.1	0.08
37°N, 73°W	7	0	0	0.0	0.00
36°N, 75°W	297	80	456	26.9	1.54
36°N, 74°W	183	17	54	9.3	0.29
35°N, 76°W	2	1	1	50.0	0.50
35°N, 75°W	247	77	413	31.2	1.67
35°N, 74°W	78	31	234	39.7	3.00
34°N, 77°W	102	4	4	3.9	0.04
34°N, 76°W	218	30	114	13.8	0.52
34°N, 75°W	75	3	3	4.0	0.04
33°N, 77°W	144	1	1	0.7	0.01
33°N, 76°W	58	0	0	0.0	0.00