Estuaries and Coasts Vol. 30, No. 6, p. 1016–1026 December 2007

Seasonal Movement and Resource-Use Patterns of Resident Horseshoe Crab (*Limulus polyphemus*) Populations in a Maine, USA Estuary

SLADE MOORE[1,]* and STEVE PERRIN[2]

[1] *Maine Department of Marine Resources, P.O. Box 8, West Boothbay Harbor, Maine 04575*
[2] *Friends of Taunton Bay, P.O. Box 585, Bar Harbor, Maine 04609*

ABSTRACT: Knowledge of resource-use and movement patterns is a missing component in the development of horseshoe crab (*Limulus polyphemus*) management strategies. Available evidence indicates the potential for a variety of possible migratory behaviors, but the lack of high-resolution, spatial-temporal data has hindered development of a year-round profile of ranging behavior. This need was addressed in the present study by using acoustic telemetry to track the movements of adult horseshoe crabs in two subembayments (Egypt and Hog Bays) of the Taunton Bay Estuary, Maine, from June 2003 to June 2005. Estimated mean total home range sizes were 64.1 and 61.4 ha for breeding crabs tagged in Egypt and Hog Bays, respectively. We observed no horseshoe crab dispersal to areas outside of the subembayments where they were tagged, so no mixing was observed between Egypt and Hog Bay individuals despite a < 4-km separation. Observed shifts in movement patterns, resource use (subtidal versus intertidal), and vagility facilitated a profile of seasonally partitioned horseshoe crab activity, which included late April to early May post-wintering, June–July breeding, August–September pre-wintering, and October–April wintering, where space usage represented about 10% of the mean total home range size. The apparent isolation of these resident populations implies a heightened vulnerability to overexploitation and large-scale habitat alteration that might be more easily sustained by larger, more vagile populations. This work underscores the need to apply horseshoe crab conservation, research, and management efforts at scales that are appropriate to the ranging patterns of crabs, which first requires application of high-resolution methods to identify those patterns.

Introduction

The horseshoe crab's (*Limulus polyphemus*) importance to estuary function and human populations with which estuarine systems are coupled is well documented. As both a consumer and prey source, horseshoe crabs are thought to strongly influence energy flow and community structure in estuarine systems (Botton 1984a,b; Castro and Meyers 1993; Kraeuter and Fegley 1994). The species is also notable for providing raw material for the biomedical and fishing industries, which in turn, contribute to coastal and inland economies (Novitsky 1984; Botton and Ropes 1987a; Berkson and Shuster 1999). In recent years, unsustainable increases in mid Atlantic coast horseshoe crab landings to supply bait for eel (*Anguilla rostrata*) and whelk (*Busycon* sp.) fisheries resulted in substantial horseshoe crab harvest quota reductions and fishery closures (Castro and Myers 1993; Berkson and Shuster 1999). At the northern extent of their range, horseshoe crab densities and distributions are far smaller than in the mid Atlantic (Born 1977) and extractive uses likewise may be correspondingly smaller. Recent observations indicated that expansions of the horseshoe crab bait market might have been responsible for attendant crab population declines in Massachusetts and Maine (Widener and Barlow 1999; Thayer personal communication). Although a heightened awareness of the horseshoe crab's vulnerability to overexploitation has prompted increased efforts to better understand the species' ecological requirements, most work has been limited to populations south of the Gulf of Maine.

During the narrow seasonal window encompassing the spawning period, horseshoe crabs are often easily observed in the shallows and emersed intertidal areas, yet an understanding of their movements and habits during the remainder of the year is largely lacking. To date, several types of data have been used to characterize specific aspects of horseshoe crab movement patterns. Tag returns have primarily reported to what extent spawning season residency and year-to-year philopatry at specific spawning areas occurs, as well as sometimes considerable distances (> 200 km) traveled to other spawning beaches or recovery sites (Rudloe 1980; James-Pirri et al. 2005; Swan 2005). Other studies have concentrated on or mentioned horseshoe crab subtidal occurrence, the data for which have been

---

* Corresponding author; current address: Biological Conservation LLC, 979 River Road, Bowdoinham, Maine 04008; tele: 207/737-5700; fax: 207-737-5700; e-mail: smoore@bioconserve.net

used to indicate the extent of offshore crab movements (Rudloe 1980; Botton and Ropes 1987b; Widener and Barlow 1999) in various portions of the species' range. Results from isotopic (Carmichael et al. 2004) and genetic (Pierce et al. 2000; King et al. 2005) investigations have suggested evidence of restricted horseshoe crab movements in some portions of their range. At least two published studies used radio and acoustic telemetry to describe short-term (< 1 mo duration) spawning season movements of horseshoe crabs (Kurz and James-Pirri 2002; Brousseau et al. 2004). These studies suggest a range of possible migratory habits although their low resolution or short duration makes it impossible to define the home range of horseshoe crabs. Spatial-temporal data leading to knowledge of year-round resource use, home range sizes, and core activity areas are necessary for informing conservation efforts, especially where potentially incompatible human benthic resource uses overlap into horseshoe crab home ranges. Telemetry is the most frequently used tool for acquiring high-resolution animal movement data and has proven valuable to the management of a variety of highly mobile invertebrate and vertebrate taxa (O'Herron et al. 1993; Freire and Gonzalez-Gurriaran 1998; Kramer and Chapman 1999; Holsman et al. 2006). The objective of the present study was to build on previous work by developing a telemetry-derived profile of horseshoe crab movement patterns and resource use throughout the entire annual cycle. This work focused on horseshoe crabs tracked in the Taunton Bay Estuary, Maine, between June 2003 and June 2005.

STUDY AREA

The Atlantic horseshoe crab ranges from the Yucatan Peninsula to the Gulf of Maine (Shuster 1979) and the Taunton Bay Estuary (68.26 W, 44.55 N) represents the northernmost documented extent of the species' range. The 1,400-ha polyhaline estuary is situated in a predominantly rural landscape in Hancock, County, Maine, that historically supported a variety of extractive industries (e.g., logging, agriculture, shipbuilding, quarrying, and mining) within and adjacent to its shores (Friends of Taunton Bay 1991). Currently, aquaculture and commercial harvesting of marine algae, shellfish, baitworms (*Nereis* spp. and *Glycera* spp.), lobster (*Homarus americanus*), cancrid crabs, and elvers (*Anguilla rostrata*) comprise dominant water-dependent uses. An extensive intertidal and shallow (4 m maximum depth), mud-dominated subtidal composes the majority of the estuary's area. The estuary's tides are in the 2 m range owing to a bedrock restriction near the mouth of the bay that accentuates a temporal lag in the tide cycle and truncates the full tidal amplitude (approximately 3 m) experienced in adjacent waters. Bottom temperatures during 2003–2005 ranged between −1.8°C and 24.4°C (Friends of Taunton Bay 2006).

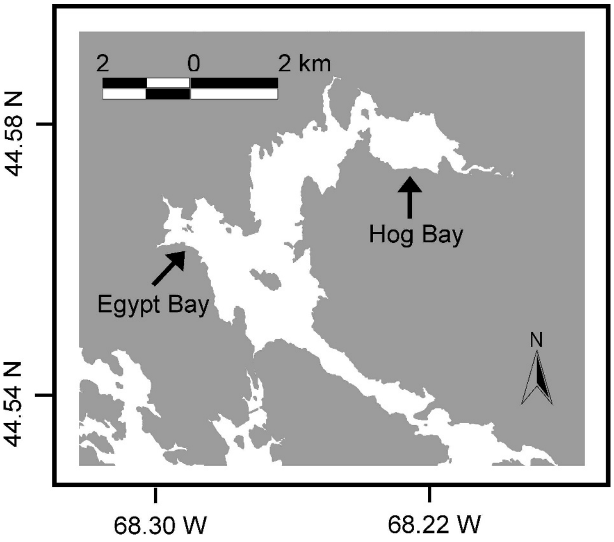

Fig. 1. The Taunton Bay Estuary, showing locations of subembayments Egypt and Hog Bays.

Within the Taunton Bay Estuary, we selected two subembayments (Egypt and Hog Bays; Fig. 1) as telemetry tagging sites because local knowledge and scouting by the authors indicated they were consistently the foci of core breeding activity. Egypt and Hog Bays are separated by 3.7 km of main channel that is flanked by several small coves and subtidal flats. Each of the subembayments exhibits a very different geomorphology. Egypt Bay merges with or includes broad flats to the southeast, making a size estimate (roughly 250 ha) somewhat subjective. Seabed classes in Egypt Bay are dominated by subtidal mud flat; depths over much of this area range from < 1 m (low tide) to 4 m (high tide). Intertidal flat and subtidal channel provide the balance of Egypt Bay's area. Hog Bay (244 ha) is almost completely encircled by uplands and mostly composed of intertidal mud flat, with the upper reaches of Taunton Bay's main channel providing most of the limited subtidal environment. Spawning beaches in Egypt and Hog Bays are south facing and about 90 and 340 m in length, respectively. The Egypt Bay beach was exposed to moderate fetch (2 km) only from southern winds and Hog Bay's beach was well protected from all directions. In addition to exposed bedrock, glacial till-derived sediments with grain sizes in the granule-pebble (2–64 mm) to cobble (64–256 mm) size range were common upper intertidal substrates at both spawning sites.

Methods

Tagging

Attachment of acoustic transmitters to crabs coincided with the peak of intertidal spawning in Taunton Bay reported by Schaller (2002), at which time the species is most accessible for handling. Six mated pairs of crabs and one female were selected from Egypt and Hog Bays each, resulting in an initial count of six males and seven females from each spawning area. The single female from Egypt Bay was subsequently replaced with a post-breeding season trawl caught male after her transmitter was found unattached. We attempted to minimize premature transmitter loss due to molting by selecting the largest adult specimens encountered, which are less likely to molt or molt infrequently (Shuster 1955; Botton and Ropes 1988). Male and female mean prosoma widths for crabs selected from both subembayments were 15.4 cm (standard deviation [SD] = 1.0 cm) and 18.0 cm (SD = 0.9 cm), respectively. Sex of horseshoe crabs was confirmed by examination of the pedipalps. Between June 12–July 1, 2003, each crab was fitted with a 4-g, cylindrical (66 × 16 mm) transmitter (model CT-82-2E; Sonotronics, Tucson, Arizona; www.sonotronics.com). We used the right longitudinal furrow on the prosoma as the acoustic transmitter attachment site. The site was scrubbed of epibionts, wiped clean, and swabbed with alcohol before a thick bead of quick-curing, two-part epoxy adhesive was applied. We then set the activated transmitter, which was tested just prior to attachment, into the epoxy and excess adhesive was smoothed around the lower front and sides of the transmitter to streamline its profile. Several minutes after transmitter attachment, the adhesive cured sufficiently to place tagged crabs in a partially submerged holding pen, where they were kept for about 10 min prior to release.

Tracking

We tracked horseshoe crabs during the following periods: June 16–November 24, 2003, April 21–November 23, 2004, and April 26–June 23, 2005. The late November to late April gap in tracking coincided with seasonal icing and/or marginal tracking conditions. All tracking occurred 3–4 h before or after high tide during daylight hours. We determined horseshoe crab locations using a handheld directional hydrophone (model DH-4; Sonotronics) and portable receiver (model USR-96; Sonotronics) that provided audible signal strength information to the operator's headset. Each transmitter was assigned a distinct operating frequency in the 70–82 kHz range to allow identification of individual horseshoe crabs. Prior to tagging, equipment field trials revealed that under optimal conditions (e.g., high tide, wind speed < 10 kph, both transmitter and hydrophone located over subtidal flats) we could expect acquisition ranges of 0.5 km. In the presence of even moderate wind and precipitation, acquisition ranges were reduced to ≤ 200 m; weather-associated range reductions at or below this point dramatically hindered tracking efficiency.

For the first 2.5 mo of sampling, we used triangulation (Samuel and Fuller 1994) to estimate crab locations, initially anticipating that efficiency could be maximized by obtaining simultaneous fix data on multiple crabs from several locations within each subembayment. The prevalence of submerged channels, boulders, bedrock, and a glacial-till shoreline represented a highly reflective environment that hindered acquisition of rapid fixes on crabs and also yielded inconsistent error polygon estimates that prompted a shift in tracking methodologies. We switched to homing (Samuel and Fuller 1994) to estimate horseshoe crab locations, which required us to follow each signal to its source and mark that location's coordinates with a global positioning system (GPS) receiver (model GPS 76s; Garmin International, Inc. Olathe, Kansas; www.garmin.com). Marking the exact location of crabs was hindered by water turbidity that often interfered with visual bottom observations at depths of $\geq$ 0.75 m. Field trials indicated that audible receiver feedback coincident with an on-top position could be used as a surrogate for visual acquisition of tagged crabs and consistently put location estimates within an acceptable ≤ 6 m radius of the transmitter.

Data Processing and Analysis

Estimated horseshoe crab locations based on triangulation data were obtained using the Locate II software program (Nams 2000). Points from triangulation and homing data were loaded into a geographic information system (GIS) with National Oceanic and Atmospheric Administration chart and aerial imagery thematic layers. We used ArcView Spatial Analyst (ESRI, Redlands, CA) and Animal Movement (Hooge and Eichenlaub 1997) extensions for various data manipulations and plotting.

Horseshoe crab home ranges were estimated using location data from seven crabs in Egypt Bay and 10 crabs in Hog Bay that were monitored during the July 2003–July 2004 portion of the tracking study. The mean number of locations used to develop home range estimates for Egypt and Hog Bay crabs were 31.4 (SD = 2.5; range = 26–33) and 29.6 (SD = 2.5; range = 26–34), respectively. Each home range estimator has its attendant weaknesses and must be considered in the context of the underlying research or management questions (Samuel and Fuller 1994). We used the minimum convex polygon (MCP) method (Mohr and Stumpf 1966) to develop estimates of total home range area (ha) used by crabs in each bay. MCPs are constructed by connecting a study subject's outermost observed location points and do not provide characterizations of animal distributions or core usage areas within the home range boundary. We felt that MCPs provided a satisfactory approach to characterizing the extent of horseshoe crab space usage because it captured all observed locations, including those associated with relatively long-distance excursions that were observed with regularity and might have biological significance (Samuel and Fuller 1994). We also acknowledged the MCP's potential for underestimating total home range size (Samuel and Fuller 1994) as an acceptably conservative attribute.

We used a probabilistic technique, the fixed-kernal home range estimator, to characterize how horseshoe crabs used space within the bounds of the overall home range (Worton 1989). The kernal analysis uses a smoothing factor calculated by least-squares cross-validation and we chose a 50% contour to identify areas of core activity. This method was suited to characterizing wintering ranges, the bounds of which tended to include dense aggregations of points associated with pre-winter loitering in the areas where crabs would eventually initiate full wintering behavior. We compared mean home range sizes of crabs segregated by bay and sex, but estimates of minimum effective sample sizes required to control Type I error (alpha = 0.05) discouraged testing for statistical differences (www.dssresearch.com). We also compared year-to-year distances between the foci of individual crab wintering sites to detect the possibility of wintering site fidelity and we calculated the distance between wintering ranges and spawning-tagging sites for males and females.

Partitioning seabed into subtidal and intertidal classes comprised a fairly coarse but useful delineation of habitat types through which seasonal resource-use patterns could be examined. We used all telemetry points from June 2003 to June 2005 tracking activities to calculate the monthly percentage of horseshoe crab locations in the intertidal for each subembayment. We then used monthly GIS plots of all crab locations in Egypt and Hog Bays to integrate a qualitative understanding of movement pattern characteristics (e.g., observed vagility and onshore versus offshore directional trends) with monthly resource-use data, which provided evidence of seasonal resource-use phases in the adult horseshoe crab annual cycle that were apparently biologically meaningful. After examining these seasonal (versus monthly) data for assumptions of normality and homogeneity of variances, we used a repeated measures analysis of variance (ANOVA) and Tukey (HSD) ad hoc procedure (alpha = 0.01) to determine whether apparent shifts in resource use were supported statistically. Because one seasonal group (October–November) violated assumptions of normality and equal variances, we also used the Friedman non-parametric alternative to the repeated measures ANOVA (alpha = 0.01) to identify the presence of differences in seasonal resource use.

Results

TRACKING

We performed 61 d of tracking from June 16 to November 24, 2003, 69 d from April 21 to November 23, 2004, and 13 d from April 26 to June 23, 2005 during which field crew determined the locations of tagged crabs on 1,159 occasions. Excluding two crabs that were located on ≤ 5 occasions, the mean number of locations per crab was 44.6 (SD = 19.2; range = 21–66). A mean of 3.5 locations mo^{-1} (range = 3.0–4.9 locations mo^{-1}; SD = 0.5 locations mo^{-1}) for all horseshoe crabs was calculated using the mean number of monthly locations for each individual.

Starting with 26 horseshoe crabs, we tracked 25 and 15 individuals throughout the 2003 and 2004 seasons, respectively. We reacquired contact with 14 crabs in the spring of 2005 and continued tracking these until most transmitters ceased functioning in June 2005. Transmitter detachment was responsible for loss of contact with at least one horseshoe crab. Throughout the study, repeated homing on nine crabs apparently in the same locations during periods when other crabs were highly mobile suggested several possible fates: transmitter detachment, molting of the carapace, or crab mortality. Because the condition and location of these crabs became questionable at some point during the sampling season, we only used location data obtained up to the last reliable tracking dates. Lost contact with the remaining crabs was likely due to discharge of transmitter batteries, most of which outlived the advertised life expectancy (14 mo).

HOME RANGE PARTITIONING AND AREA ESTIMATES

In 2003 and 2004, tracking activities ceased in late November and resumed in April and May of the following year. Before the first tracking season concluded, we observed a rapid decline in crab vagility that by November resulted in no perceived lateral movement in most individuals. When contact was reestablished with 21 of the original 26 crabs in April 2004, we found that the mean distance

TABLE 1. Mean distances between the latest fall and earliest spring location points for individual horseshoe crabs tracked in subembayments of the Taunton Bay Estuary, Maine, using acoustic telemetry, 2003–2005. n = number of crabs tracked during fall and spring periods.

Period	n	Egypt Bay	Hog Bay	Both bays
2003–2004	21	45.5 (17.1)	36.9 (30.3)	41 (24.7)
2004–2005	13	230 (238.2)	147.3 (136.7)	172.8 (168)

between coordinates of the last observed horseshoe crab locations in fall 2003 and the first reacquisitions of crabs documented in spring 2004 was 41 m (SD = 25 m; Table 1), suggesting that reduced crab vagility observed in the late summer to fall represented the onset of a wintering phase. During the 2004–2005 period, measurement of the same parameter yielded larger values (mean = 173 m; SD = 168 m), which we attributed to an earlier post-wintering dispersal of horseshoe crabs during the study's second year rather than a lack of restriction to established wintering ranges (Table 1).

During 2003–2005 tracking activities, we never observed evidence of horseshoe crabs exiting the Taunton Bay estuary nor did the two groups of study crabs appear to leave the subembayments where they were observed spawning. The mean area of total home ranges and wintering home ranges in Egypt Bay was 64.1 ha (SD = 20.6 ha) and 5.7 ha (SD = 1.7 ha), respectively (Table 2). On average, use of wintering areas in Egypt Bay was initiated by late September to early October and crabs dispersed from Egypt Bay wintering grounds late April to early May. Hog Bay total home ranges (mean = 61.4 ha; SD = 19.9 ha) and wintering ranges (mean = 5.9 ha; SD = 1.8 ha) were nearly identical to Egypt Bay values (Table 2). Horseshoe crabs initiated movement into Hog Bay wintering ranges late August to early September, nearly 1 mo before Egypt Bay crabs. Dispersal from Hog Bay wintering ranges occurred late April to early May.

Average male total home range sizes (range = 38.1–98.6 ha; mean = 67.7 ha; SD = 26.2 ha) were similar to female total home ranges (range = 46.5–87.3 ha; mean = 66.1 ha; SD = 14.7 ha), but were more variable. Wintering range sizes for males (range = 3.5–7.4 ha; mean = 5.2 ha; SD = 1.7 ha) and females (range = 4.7–8.0 ha; mean = 6.4 ha; SD = 1.4 ha) also did not appear substantially different.

The mean year-year distance between the foci of individual crab wintering sites in Egypt Bay was 387 m (range = 98–846 m; SD = 331 m; n = 5 crabs). Hog Bay's mean inter-wintering distance was 422 m (range = 50–692 m; SD = 222 m; n = 10 crabs). The mean distance for both bays was 394 m (n = 15 crabs; range = 50–846 m; SD = 233 m), providing little evidence of fidelity to specific wintering sites. Distances between 2003 horseshoe crab wintering home ranges and intertidal spawning-tagging sites were somewhat larger and more variable in Egypt Bay (mean = 802; SD = 424) than Hog Bay (mean = 504; SD = 167).

SEASONAL RESOURCE-USE PATTERNS

Horseshoe crab resource use among intertidal and subtidal areas was seasonally partitioned for both Egypt and Hog Bays (Fig. 2). The pattern based on all location points for each month from June 2003 to June 2005 demonstrated that post-wintering intertidal use did not occur until mid May. At month's end, the percentage of all location

TABLE 2. Home ranges for 17 horseshoe crabs tracked with acoustic telemetry in subembayments of the Taunton Bay Estuary, Maine, July 2003–July 2004. n = the number of horseshoe crab location points used for home range estimates. Total home range estimates were based on Minimum Convex Polygon calculations. Wintering ranges were characterized using fixed kernal (50% probability) estimates and include activity centers where late summer to fall movements are restricted to the impending wintering area.

Crab ID	n	Total Home Range (ha)	Wintering Home Range (ha)	Wintering Range % of Total Home Range (ha)	Wintering Area Use	
					Initiation Date	Conclusion Date
Egypt Bay						
Min	26	38.1	3.5	6.1	September 10	April 30
Max	33	98.6	8.0	11.4	October 28	May 6
Mean	31.4	64.1	5.7	9.2	October 2	May 4
Median	32	58.0	5.5	10.2	October 6	May 6
SD	2.5	20.6	1.7	2.2	±16 d	±3 d
Hog Bay						
Min	26	26.9	4.1	5.9	August 13	April 30
Max	34	87.3	9.2	20.9	September 29	May 19
Mean	29.6	61.4	5.9	10.6	September 7	May 6
Median	29	64.9	5.3	9.0	September 10	April 30
SD	2.5	19.9	1.8	4.7	±14 d	±8 d

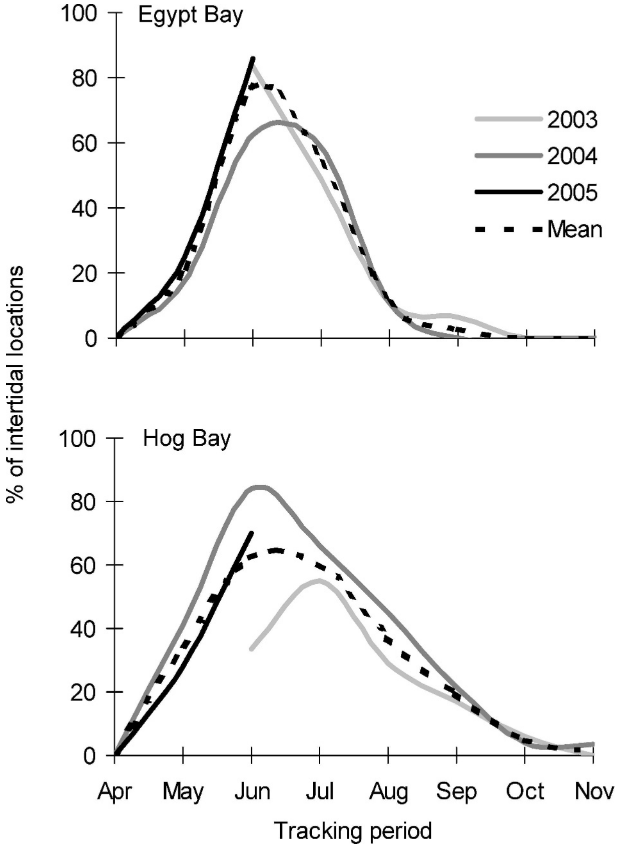

Fig. 2. Horseshoe crab resource partitioning as indicated by differential percent usage of intertidal versus subtidal seabed in Egypt and Hog Bays, Maine. The graphic plots are based on all horseshoe crab location points segregated by month, June 2003–June 2005.

points in the intertidal in Egypt Bay (mean = 21.3%; SD = 5.2%) and Hog Bay (mean = 34.6%; SD = 9.3%) had reached moderate levels. By June, mean intertidal use rapidly peaked as high as 77.2% (SD = 12.8%) and 62.5% (SD = 26.3%) in Egypt and Hog Bays, respectively. In Egypt Bay, the rapid decline in intertidal use after June or July consistently reached its nadir by fall; in October, no intertidal use was observed until the following spring. In Hog Bay, the percentage of intertidal points also declined rapidly after June or July and was consistently < 10% by October of each year.

Examination of horseshoe crab movement characteristics such as vagility and directional trends supported expansion of monthly resource-use (intertidal versus subtidal) data grouping periods to every 2 mo, which segregated the data in a way that provided a more biologically meaningful analysis and eventually helped distinguish a profile of adult horseshoe crab annual activity in the study area. The period encompassing late April–May was notable for initially low vagility as horseshoe crabs slowly exited wintering ranges (Fig. 3 and Table 3). Vagility increased concomitant with crabs entering the intertidal during this period. June and July marked the peak and post-peak of spawning activity, which were characterized by relatively widespread movements and frequent intertidal use. In August and September, vagility declined and a reverse in resource-use favored subtidal areas, including the establishment of some wintering ranges. October and November marked the onset of wintering. In October, the establishment of most wintering ranges was attended by markedly decreased vagility and resource use was primarily restricted to the subtidal. By November, vagility decreased to a point where the presence of lateral crab movements was largely undetectable given the potential for error inherent in our tracking-location method ($\leq$ 6 m) and variability in GPS accuracy. Whether movements of crabs were minor or non-existent during this period, the sharp decrease in vagility suggested the initiation of a physiologically distinct wintering state. Comparisons of bimonthly percent intertidal use data based on movements of 20 crabs tracked for $\geq$ 12 mo (Table 3) indicated the presence of distinct seasonal shifts in horseshoe crab resource use (ANOVA repeated measures: $p < 0.01$; Tukey HSD: $p < 0.01$, Friedman's test: $p < 0.01$).

Beyond resource-use that focused on intertidal versus subtidal areas, several notable habitat observations warrant mention. Within subtidal wintering ranges, horseshoe crabs were located in both shallow flats and channels. In Hog Bay, the channel comprised most of the available subtidal habitat; all crabs wintered within this geomorphic class. During the winter of 2003–2004, seven (53%) of 13 Egypt Bay horseshoe crabs wintered in subtidal tributaries of the main channel; the balance of crabs used subtidal flats. During the second winter (2004–2005) of the study, three (60%) of the five remaining crabs in Egypt Bay used a tributary of the main channel. Two of these three crabs had used the channel in the previous winter.

Discussion

This study provided the first profiles of seasonal horseshoe crab movement patterns and resource use, but a weather-mediated temporal gap in tracking data would have left the question of crab wintering movements and residency largely unanswered were it not for several findings. In 2003 a reduction in vagility in October and November appeared to signal the onset of a wintering period. The lack of distance (mean = 41 m; SD = 25 m) between the last fall 2003 and earliest spring 2004 location points suggested that crabs moved little since November. During the first tracking days of

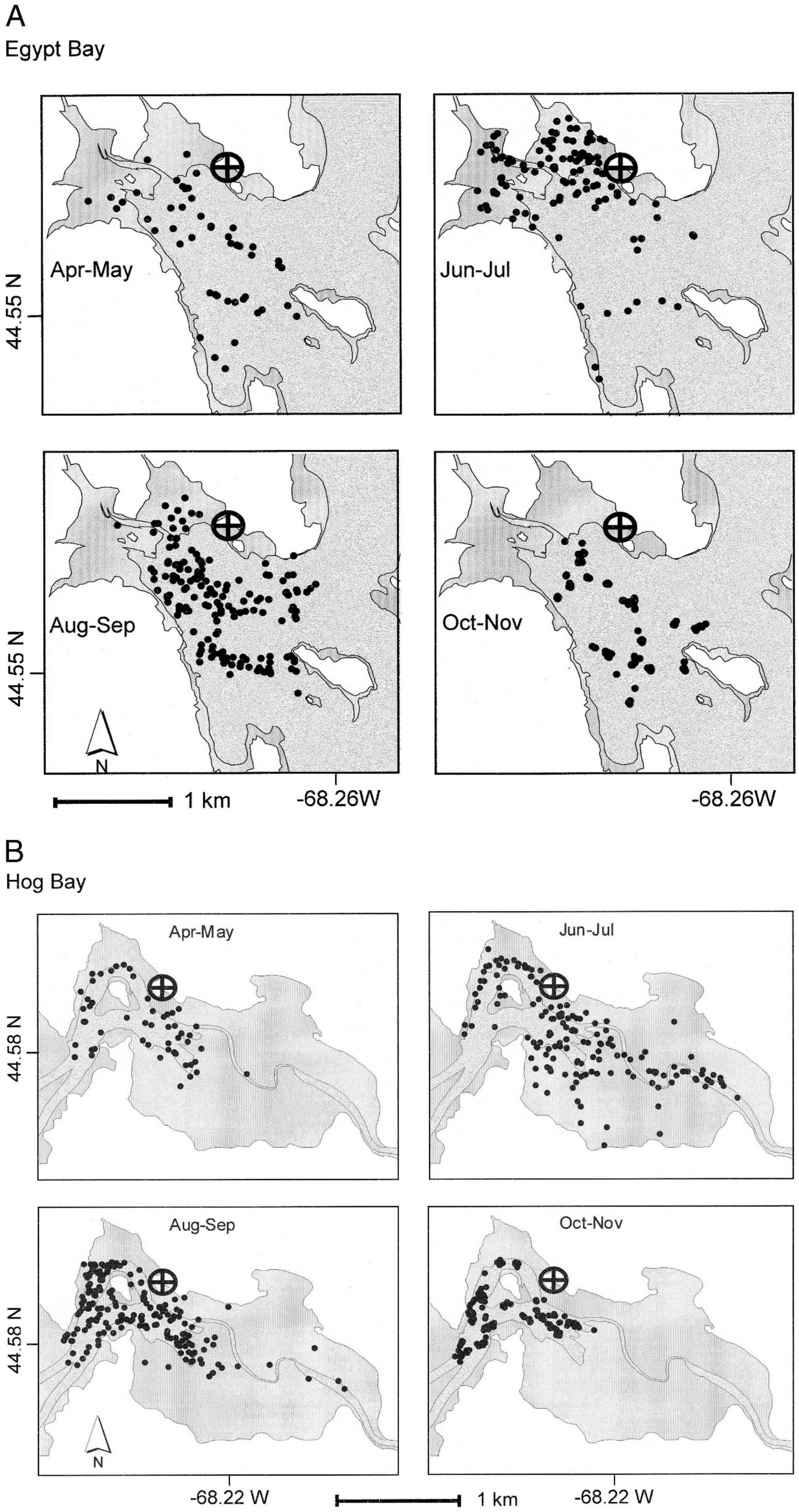

Fig. 3. Seasonal movements of horseshoe crabs in Egypt Bay and Hog Bay, Maine, based on acoustic telemetry locations obtained during June 2003–June 2005. All observations were obtained within 3–4 h before and after local high tide during daylight hours. White, stippled, and gray areas of the plots represent upland, intertidal, and subtidal portions of the estuary, respectively. Horseshoe crab locations

spring, vagility was similar to low fall levels and then increased during May, suggesting emergence from a physiologically distinct wintering state outwardly recognizable by relative inactivity.

During the first tracking days of spring 2005 crabs were located greater distances from supposed wintering sites than in spring 2004 (Table 1), prompting a reassessment of evidence for year-round residency. When they were reacquired in spring 2005, the movement pattern of crabs was very similar (e.g., initially low but increasing vagility, inshore direction of travel) to that observed some weeks after initiation of the post-wintering dispersal in 2004, suggesting the possibility of an earlier (1–3 wk) dispersal from wintering areas in 2005. If this was the case, dispersal in 2005 would have occurred as bottom temperatures in the subembayments increased to about 10°C, the point during which crabs dispersed from wintering grounds in 2004 (FTB 2006). Year-to-year concordance between observations of apparently temperature-mediated crab movements extended also to initiation of the wintering phase, which began as bottom temperatures dropped to 10°C in the fall of 2004 and 2005. The influence of temperature on movement patterns has yet to be confirmed, but when combined with other observations, these data strongly suggest that crabs remained in their respective subembayments for the duration of both winters, at or near their last known locations in late November.

Although geomorphic classes such as channels and flats were readily identified by aerial imagery and the authors' familiarity with the study area, our analyses did not support a more refined partitioning of horseshoe crab habitat beyond distinguishing between intertidal or subtidal categories of seabed. Intertidal use likely confers disadvantages to horseshoe crabs by way of increased predation risk or stranding that are only temporarily outweighed by spawning requirements (Botton and Loveland 1989). Subsequent habitat investigations may explain potentially important patterns that were supported by few data, such as subtidal channel use. Given the limited availability of channels (Fig. 3), use by wintering Egypt Bay crabs (53–60%) seemed disproportionately high, suggesting habitat selection by preference rather than chance. Likewise, subtidal channels apparently provided refugia to spawning horseshoe crabs by offsetting the risk of exposure associated with frequent intertidal use.

Tracking data allowed development of a predictable pattern of seasonal movement patterns for horseshoe crabs, but apart from the costs and benefits associated with intertidal versus subtidal use, factors influencing these movements are not well understood. Migration or residency in a variety of taxa may be prompted by any combination of endogenous (e.g., physiological, genetic) and exogenous factors (e.g., physical barriers to movement, resource abundance, predation risk, competition, and disturbance) comprising the context in which selection forces operate (Lack 1968; Dingle 1991; Bohning-Gaese et al. 1998; Alerstam et al. 2003). For horseshoe crabs, trawl and dredge survey data indicate that post-spawning movements include dispersals to $\leq$ 130 km from shore (Botton and Ropes 1987b), yet within the same latitudinal range where crabs winter on the continental shelf, Delaware Bay crabs also winter at inshore sites (Michels personal communication). The relative lack of migration reflected by our data and credible assertions that other populations are subject to similar residency patterns (Shuster 1982; Widener and Barlow 1999; Pierce et al. 2000; Carmichael et al. 2004; King et al. 2005) supports the prevailing view of migratory behavior variability within species and discrete populations (Dingle 1991; Jonsson and Jonsson 1993; Bohning-Gaese et al. 1998; Alerstam et al. 2003).

Physical factors can limit dispersal distances in mobile invertebrates (Hyland et al. 1984) and the residency pattern we observed in Egypt and Hog Bay crabs may also be related to such factors. Although the estuary's main channel separates Egypt and Hog Bays by $<$ 4 km, it may present risks that outweigh dispersal benefits. Crabs entrained in the main channel's swift currents may be transported far from natal subembayments into areas with substandard habitats and low crab densities where the likelihood of successful reproduction would be low. It is unlikely that the intense selection forces presumably operating at the periphery of a species' range would favor the prevalence of such outcomes.

The Taunton Bay Estuary represents the northern range extent of horseshoe crabs and responses to stressors such as low water temperatures may also influence dispersal behavior as physiological toler-

---

←

(black points) demonstrated a repeatable seasonal resource-use pattern typified by a gradual post-wintering emergence from subtidal wintering ranges (April–May), intense intertidal use and high vagility coincident with peak and post-peak spawning phases (June–July), and a reverse to primarily subtidal use and decreased vagility as crabs began establishing wintering ranges during the pre-wintering phase (August–September). The onset of wintering (October–November) was marked by dense aggregations of points representing increasingly restricted horseshoe crab movements that apparently ceased by November. Black circles with crosshairs represent spawning-tagging sites.

TABLE 3. Percent intertidal use by 20 horseshoe crabs tracked for > 12 mo in Egypt and Hog Bays, Maine, 2003–2005. Column headings are segregated into 2-mo periods based on observed shifts in resource use and vagility. Each successive period was distinct (Tukey HSD: $p < 0.01$) from the previous one.

	April–May	June–July	August–September	October–November
Range	0–60	29–100	0–50	0–16
Mean	22.5	67.9	17.9	1.3
SD	20	21.0	17.0	3.8

ances are approached. Larval crabs possess a limited ability to metabolically compensate for low water temperatures (Laughlin 1983), but adult responses to temperature are less well understood (Reynolds and Casterlin 1979). In both years of this study, the onset of low vagility wintering behavior in horseshoe crabs was concurrent with bottom temperatures dropping to 10°C in October (FTB 2006). When temperatures increased from a low of −1.8°C during January–March to 10°C in mid to late April (FTB 2006), crabs appeared to slowly emerge from wintering ranges. Although temperature-vagility correlations do not amount to causation, they suggest that a physically-induced wintering state may limit horseshoe crab dispersal and warrants further consideration.

If our data are representative of most years, one obvious implication of non-migratory behavior is that adult crabs in Egypt and Hog Bays are unlikely to experience appreciable exchange of individuals. Early developmental stages are unlikely to move beyond the vicinity of spawning areas (Shuster 1979; Rudloe 1981; Botton and Loveland 2003), although larger juveniles may have increased dispersal capabilities (Meury and Gibson 1990; Anderson and Shuster 2003). Only low densities of adult horseshoe crabs are observed along the Taunton Bay Estuary's intertidal outside of the Egypt and Hog Bay subembayments; some of these crabs may occasionally immigrate into the core populations at Egypt and Hog Bays, but whether they represent a meaningful source of recruitment is uncertain. The lack of documented horseshoe crab populations closer than 100 km from the study area makes recruitment from sources outside of the estuary very unlikely (Schaller and Thayer 2002).

The high fecundity and dispersal potential of some marine organisms may confer advantages that mediate extinction vulnerability, but this perceived resilience to population decline is not universal among the range of taxa or possible circumstances (Hutchings 2001; Dulvy et al. 2003). Where the likelihood of immigration is negligible or nonexistent, the resulting combination of small stock size and isolation could put crabs at a heightened risk of extirpation caused by chance events or deterministic processes more easily sustained by larger, more vagile populations (Botton and Ropes 1987b; Pierce et al. 2000; Dulvy et al. 2003; Hutchings and Reynolds 2004; King et al. 2005). In waters where crabs are present throughout the year, informed management efforts should consider not only use of spawning habitats, but also wintering ranges, which in this study comprised about 10% (6 ha) of each individual's total home range and represented core activity areas used exclusively by crabs for at least seven months (October–April) of the year. Without year-to-year fidelity to specific wintering locations, a sufficient percentage of subtidal wintering habitat should be closed to uses likely to induce significant benthic community change or interfere with pre-wintering and post-wintering movements of crabs. Other than overexploitation, demonstrated human-mediated population level effects on horseshoe crabs are not well understood or documented. In areas supporting resident populations, further research is necessary to determine if temporal and spatial overlap of human uses and crab habitat are compatible with horseshoe crab management goals, especially at the northern periphery of the horseshoe crab's range where resilience to multiple environmental stressors may be limited. By documenting year-round residency in horseshoe crabs, our findings also underscore the need to consider if managing at the regional scale sufficiently addresses local variability in horseshoe crab behavior. The relatively high-resolution, spatial-temporal data afforded by telemetry can aid managers in predicting encroachment into horseshoe crab ranges by habitat-altering activities common to multiple-use estuaries and gauge the potential of those activities to hinder attainment of horseshoe crab management objectives.

ACKNOWLEDGMENTS

John Sowles, Carmel Rubin, and two anonymous reviewers provided editorial advice that improved successive versions of this manuscript. Mary Beth Dorsey, Frank Dorsey, Pat Flagg, Al Younger, and Betsy Younger generously provided shoreside access to field crew. Mark Desmueles, Frank Dorsey, Sue Schaller, Matt Sclafani, and Stewart Michaels shared data or advice that benefited development of this project. Carole Beale, James Becker, Deborah Boswell Lane, Ken Perrin, and Elliott Spiker assisted with field activities. Pat Flagg freely extended her warmth, generosity, and support to us in countless ways and will be fondly remembered. Maine Sea Grant, the Maine Coastal Program, and the Sweet Water Trust provided funding.

LITERATURE CITED

ALERSTAM, T., A. HENDENSTROM, AND S. AKESSON. 2003. Long distance migration: Evolution and determinants. *Oikos* 103:247–260.

ANDERSON, L. I. AND C. N. SHUSTER. 2003. Throughout geologic time: Where have they lived? p. 189–223. *In* C. N. Shuster, R. B. Barlow, and H. J. Brockmann (eds.), The American Horseshoe Crab, VOLUME. Harvard University Press, Cambridge, Massachusetts.

BERKSON, J. AND C. N. SHUSTER, JR. 1999. The horseshoe crab: The battle for a true multiple-use resource. *Fisheries* 24:6–11.

BOHNING-GAESE, K., L. I. GONZALEZ-GUZMAN, AND J. H. BROWN. 1998. Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evolutionary Ecology* 12:767–783.

BORN, J. W. 1977. Significant breeding sites of the horseshoe crab (*Limulus polyphemus*) in Maine and their relevance to the Critical Areas Program of the State Planning Office. State Planning Office, Planning Report Number 28, Augusta, Maine.

BOTTON, M. L. 1984a. The importance of predation by horseshoe crabs, *Limulus polyphemus*, to an intertidal sand flat community. *Journal of Marine Research* 42:39–161.

BOTTON, M. L. 1984b. Diet and food preferences of the horseshoe crab *Limulus polyphemus* in Delaware Bay, New Jersey, USA. *Marine Biology* 81:199–207.

BOTTON, M. L. AND R. E. LOVELAND. 1989. Reproductive risk: High mortality associated with spawning horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA. *Marine Biology* 101:143–151.

BOTTON, M. L. AND R. E. LOVELAND. 2003. Abundance and dispersal potential of larval horseshoe crab (*Limulus polyphemus*) in the Delaware estuary. *Estuaries* 26:1472–1479.

BOTTON, M. L. AND J. W. ROPES. 1987a. The horseshoe crab, *Limulus polyphemus*, fishery and resource in the United States. *Marine Fisheries Review* 49:57–61.

BOTTON, M. L. AND J. W. ROPES. 1987b. Populations of horseshoe crabs, *Limulus polyphemus*, on the northwestern Atlantic continental shelf. *Fishery Bulletin* 85:805–812.

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*). *Journal of Shellfish Research* 3:407–412.

BROUSSEAU, L. J., M. SCLAFANI, D. R. SMITH, AND D. B. CARTER. 2004. Acoustic tracking and radio tracking of horseshoe crabs to assess spawning behavior and subtidal habitat-use in Delaware Bay. *North American Journal of Fisheries Management* 24:1376–1384.

CARMICHAEL, R. H., D. RUTECKI, B. ANNETT, E. GAINES, AND E. VALIELA. 2004. Position of horseshoe crabs in estuarine food webs: N and C stable isotopic study of foraging ranges and diet composition. *Journal of Experimental Marine Biology and Ecology* 299:231–253.

CASTRO, G. AND J. P. MYERS. 1993. Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. *The Auk* 110:927–930.

DINGLE, H. 1991. Evolutionary genetics of animal migration. *American Zoologist* 31:253–264.

DULVY, N. K., Y. SADOVY, AND J. D. REYNOLDS. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries* 4:25–64.

FREIRE, J. AND E. GONZALEZ-GURRIARAN. 1998. New approaches to the behavioural ecology of decapod crustaceans using telemetry and electronic tags. *Hydrobiologia* 371–372:123–132.

FRIENDS OF TAUNTON BAY (FTB). 1991. Inventory of the Taunton Bay Region. 2nd edition. Friends of Taunton Bay, Hancock, Maine.

FRIENDS OF TAUNTON BAY (FTB). 2006. The Taunton Bay Study: A pilot project in collaborative bay management. Indicators monitoring report 2005. Friends of Taunton Bay, Hancock, Maine.

HOLSMAN, K. K., P. S. MCDONALD, AND D. A. ARMSTRONG. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology Progress Series* 308:183–195.

HOOGE, P. N. AND B. EICHENLAUB. 1997. Animal movement extension to ArcView version 1.1. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, Alaska.

HUTCHINGS, J. A. 2001. Conservation biology of marine fishes: Perceptions and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Sciences* 58:108–121.

HUTCHINGS, J. A. AND J. D. REYNOLDS. 2004. Marine fish population collapses: Consequences for recovery and extinction risk. *Bioscience* 54:297–309.

HYLAND, S. J., B. J. HILL, AND C. P. LEE. 1984. Movement within and between different habitats by the portunid crab *Scylla serrata*. *Marine Biology* 80:57–61.

JAMES-PIRRI, M. J., K. TUXBURY, S. MARINO, AND S. KOCH. 2005. Spawning densities, egg densities, size structure, and movement patterns of spawning horseshoe crabs, *Limulus polyphemus*, within four coastal embayments on Cape Cod, Massachusetts. *Estuaries* 28:296–313.

JONSSON, B. AND N. JONSSON. 1993. Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3:348–365.

KING, T. L., M. S. EACKLES, A. P. SPIDLE, AND H. J. BROCKMANN. 2005. Regional differentiation and sex-biased dispersal among populations of the horseshoe crab *Limulus polyphemus*. *Transactions of the American Fisheries Society* 134:441–465.

KRAEUTER, J. N. AND S. R. FEGLEY. 1994. Vertical disturbance of sediments by horseshoe crabs (*Limulus polyphemus*) during their spawning season. *Estuaries* 17:288–294.

KRAMER, D. L. AND M. R. CHAPMAN. 1999. Implications of fish home range size and relocation of marine reserve function. *Environmental Biology of Fishes* 55:65–79.

KURZ, W. AND M. J. JAMES-PIRRI. 2002. The impact of biomedical bleeding on horseshoe crab, *Limulus polyphemus*, movement patterns on Cape Cod, Massachusetts. *Marine and Freshwater Behavior and Physiology* 35:261–268.

LACK, D. 1968. Bird migration and natural selection. *Oikos* 19:1–9.

LAUGHLIN, R. 1983. The effects of temperature and salinity on larval growth of the horseshoe crab *Limulus polyphemus*. *Biological Bulletin* 164:93–103.

MEURY, T. W. AND D. G. GIBSON. 1990. Force generation in juvenile *Limulus polyphemus*: Effects on mobility in the intertidal environment. *Bulletin of Marine Science* 47:536–545.

MOHR, C. O. AND W. A. STUMPF. 1966. Comparison of methods for calculating areas of animal activity. *Journal of Wildlife Management* 30:293–304.

NAMS, V. O. 2000. Locate II User's Guide. Truro, Nova Scotia.

NOVITSKY, T. J. 1984. Discovery to commercialization: The blood of the horseshoe crab. *Oceanus* 27:13–18.

O'HERRON, J. C., K. W. ABLE, AND R. W. HASTINGS. 1993. Movements of shortnose sturgeon (*Acipenser brevirostrum*) in the Delaware River. *Estuaries* 16:235–240.

PIERCE, J. C., G. TAN, AND P. M. GAFFNEY. 2000. Delaware Bay and Chesapeake Bay populations of the horseshoe crab are genetically distinct. *Estuaries* 23:690–698.

REYNOLDS, W. W. AND M. E. CASTERLIN. 1979. Thermoregulatory behavior of the primitive arthropod, *Limulus polyphemus*, in an electronic shuttlebox. *Journal of Thermal Biology* 4:165–166.

RUDLOE, A. 1980. The breeding behavior and patterns of movement of horseshoe crabs, *Limulus polyphemus*, in the vicinity of breeding beaches in Apalachee Bay, Florida. *Estuaries* 3:177–183.

RUDLOE, A. 1981. Aspects of the biology of juvenile horseshoe crabs, *Limulus polyphemus*. *Bulletin of Marine Science* 31:125–133.

SAMUEL, M. D. AND M. R. FULLER. 1994. Wildlife radiotelemetry, p. 370–418. *In* T. A. Bookout (ed.), Research and Management Techniques for Wildlife and Habitats, 5th edition. The Wildlife Society, Washington, D.C.

SCHALLER, S. Y. 2002. Final report: Survey of Maine horseshoe crab (*Limulus polyphemus*) spawning populations, 2001. Maine Department of Marine Resources, W. Boothbay Harbor, Maine.

SCHALLER, S. Y. AND P. THAYER. 2002. 2003 Maine horseshoe crab, *Limulus polyphemus*, scouting surveys. Maine Department of Marine Resources, W. Boothbay Harbor, Maine.

SHUSTER, C. N. 1955. On morphometric and serological relationships within the Limulidae, with particular reference to *Limulus polyphemus* (L.). Ph.D. dissertation. New York University, New York.

SHUSTER, C. N. 1979. Distribution of the American horseshoe ''crab'', *Limulus polyphemus* (L.), p. 3–26. *In* E. Cohen (ed.), Biomedical Applications of the Horseshoe Crab (Limulidae), VOLUME. Alan Liss, Inc., New York.

SHUSTER, C. N. 1982. A pictorial review of the natural history and ecology of horseshoe crabs, *Limulus polyphemus*, with reference to other Limulidae, p. 1–52. *In* J. Bonaventura, C. Bonaventura, and S. Tesh (eds.), Physiology and Biology of Horseshoe Crabs: Studies on Normal and Environmentally Stressed Animals, VOLUME. Liss, Inc., New York.

SWAN, B. L. 2005. Migrations of adult horseshoe crabs, *Limulus polyphemus*, in the Middle Atlantic Bight: A 17-year tagging study. *Estuaries* 28:28–40.

WIDENER, J. W. AND R. B. BARLOW. 1999. Decline of a horseshoe crab population on Cape Cod. *Biological Bulletin* 197:300–302.

WORTON, B. J. 1989. Kernal methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

SOURCES OF UNPUBLISHED MATERIALS

MICHELS, S. F. personal communication. Delaware Division of Fish and Wildlife, P.O. Box 330, Little Creek, Delaware 19961.

THAYER, P. personal communication. Maine Department of Marine Resources, P.O. Box 8, West Boothbay Harbor, Maine 04575.

Received, February 21, 2007
Revised, July 24, 2007
Accepted, August 15, 2007