2010

Seasonal movement of the American horseshoe crab *Limulus polyphemus* in a semi-enclosed bay on Cape Cod, Massachusetts (USA) as determined by acoustic telemetry

Mary-Jane James-Pirri
University of Rhode Island, mjjamespirri@uri.edu

Citation/Publisher Attribution

James-Pirri, M.-J. (2010). Seasonal movement of the American horseshoe crab *Limulus polyphemus* in a semi-enclosed bay on Cape Cod, Massachusetts (USA) as determined by acoustic telemetry. *Current Zoology, 56*(5), 575-586. Retrieved from http://www.currentzoology.org/paperdetail.asp?id=11667
Available at: http://www.currentzoology.org/paperdetail.asp?id=11667

Current Zoology 56 (5): 575–586, 2010

Seasonal movement of the American horseshoe crab *Limulus polyphemus* in a semi-enclosed bay on Cape Cod, Massachusetts (USA) as determined by acoustic telemetry

Mary-Jane JAMES-PIRRI*

Box 6, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882,USA

Abstract American horseshoe crabs *Limulus polyphemus* were tracked using acoustic telemetry and traditional tagging in a semi-enclosed bay on Cape Cod (Pleasant Bay), Massachusetts, USA, to determine seasonal movement patterns. Fifty-five actively spawning females were fitted with transmitters in 2008 and 2009 and were tracked using acoustic telemetry from May 2008 through July 2010. Fifteen crabs with transmitters also had archive depth-temperature tags attached. In addition, over 2000 spawning crabs (males and females) were tagged with US Fish and Wildlife (USFWS) button tags over the same period. Ninety-one percent of the crabs with transmitters were detected during this study. In the spring, crabs were primarily located in the northern section of the bay near spawning beaches, whereas in the fall crabs moved towards the deeper portions of the bay, and some may have overwintered in the bay. There was evidence that a majority (58%–71%) of the females with transmitters spawned in two sequential seasons. One archive tag was recovered resulting in a year-long continuous record of depth and temperature data that, when integrated with telemetry data, indicated that the crab overwintered in the bay. The live recapture rate of crabs with USFWS button tags was 11%, with all re-sighted crabs except one observed inside Pleasant Bay. Eighty-three percent of recaptures were found within 2.5km of the tagging location, and 51% were observed at the same beach where they were tagged. This study provides further evidence that horseshoe crabs in Pleasant Bay may be philopatric to this embayment [*Current Zoology* 56 (5): 575–586, 2010].

Key words Horseshoe crab, New England, Telemetry, Seasonal movement

The American horseshoe crab *Limulus polyphemus* is an economically important fisheries species and an integral component of the marine ecosystem. In Delaware Bay, horseshoe crab spawning is directly linked to the spring migration of shorebirds, and is vitally important to the reproductive success and survival of shorebirds, especially the red knot *Calidris canutus rufa* (Clark, 1996; Walls et al., 2002; Karpanty et al., 2006). Horseshoe crabs are harvested commercially as bait, for American eel *Anguilla rostrata* and whelk (*Busycon* spp.), and by the biomedical industry. The biomedical industry produces Limulus Amebocyte Lystate (LAL) from their blood. LAL is the standard test used to detect endotoxins in all injectable and intravenous drugs and implantable devices (Novitsky, 1984, 2009).

Horseshoe crabs move into shallow waters to spawn on Atlantic coast beaches during the mid- to late spring. It is generally thought that in the fall adult horseshoe crabs migrate from shallow coastal waters to the deeper waters of the continental shelf to overwinter (Schuster and Botton, 1985; Botton and Ropes, 1987; Walls et al., 2002); however, this behavior may not be universally true throughout the animal's range. Evidence from populations in New England (USA) suggests that horseshoe crabs may be philopatric to embayments where they spawn (Baptist et al., 1957[1]; James-Pirri et al., 2005; Moore and Perrin, 2007). If horseshoe crabs tend to remain in or return to specific embayments year after year, this could have important implications not only for fisheries management but also for conservation of critical habitat. One example of a potential philopatric population is the Pleasant Bay, MA, population.

Pleasant Bay is a semi-enclosed embayment on Cape Cod, MA (USA) (Fig. 1). Horseshoe crabs in Pleasant Bay have been subjected to both commercial bait and biomedical harvest for over three decades (Rutecki et al.,

[1] Baptist JP, Smith OR, Ropes JW, 1957. Migrations of the horseshoe crab *Limulus polyphemus* in Plum Island Sound, Massachusetts. U.S. Fish and Wildlife Service, Special Scientific Report – Fisheries No. 220.

Received June 26, 2010; accepted Aug. 25, 2010

∗ Corresponding author. E-mail: mjjp@gso.uri.edu

2004) with harvest regulations only instituted within the last decade (Pleasant Bay Resource Management Alliance, 1998). The bait fishery in Pleasant Bay rapidly increased in 2005 and 2006, due to a red tide ban on shellfish that resulted in many fishermen switching to harvesting horseshoe crabs as an alternative source of income (Leschen and Correia, 2010). The drastic increase in bait harvest (194 crabs in 2001 to nearly 40,000 crabs in 2006) prompted managers to close the bay to bait fishing in 2006, but still allowed the biomedical harvest, except within the boundaries of Cape Cod National Seashore along the eastern shoreline of the bay (Commonwealth of Massachusetts, 2006). There is only one LAL producing facility in New England (Associates of Cape Cod in Falmouth, MA) and the population of horseshoe crabs in Pleasant Bay are an important source for this facility, but unfortunately specific statistics on the proportion of the biomedical harvest attributed to the bay are not available due to confidentiality issues. The State of Massachusetts does not manage the biomedical fishery with quota and the biomedical harvest is not counted against the Massachusetts bait harvest quota since crabs are returned to the water after bleeding, although there is a daily limit of 1000 crabs (Leschen and Correia, 2010). Both the bait and biomedical harvests preferentially target female crabs as they are larger and yield a greater volume of blood (Rutecki et al., 2004). Estimates of mortality due to biomedical bleeding and handling may be higher, almost 30% mortality (Leschen and Correia, 2010), than the previously estimated mortality of 15% (Rudloe, 1983). Horseshoe crab spawning surveys in Pleasant Bay over the past ten years have consistently revealed an extremely male-biased sex ratio, with a 1:9 ratio (female to male) observed during the most recent surveys in 2009 (James-Pirri et al., 2005; Commonwealth of Massachusetts, 2008; James-Pirri, unpublished data). The preferential harvest of females, extreme male biased sex-ratios, and recent observations of females on spawning beaches without amplexed males (males attached during spawning) (Commonwealth of Massachusetts, 2009) has caused concern about the sustainability of the Pleasant Bay population.

James-Pirri et al. (2005) first suggested that horseshoe crab populations in Cape Cod embayments were localized based on traditional tag-recapture data. In that study, the majority of re-sighted tags were reported during the spawning season on beaches, and thus there was a lack of information on post-spawning sub-tidal movement between the time of tagging and the time of recapture. Telemetry is a valuable tool to track sub-tidal animal movement and has previously been used in both short-term (<2 mo) and long term (>12 mo) studies of horseshoe crab behavior (Kurz and James-Pirri, 2002; Brousseau et al., 2004; Moore and Perrin, 2007; Schaller et al., 2010; Smith et al., 2010; Watson and Chabot, 2010). The objective of this study was to use acoustic telemetry to elucidate the pattern of post-spawning sub-tidal movements of horseshoe crabs in Pleasant Bay.

1 Materials and Methods

Actively spawning adult female horseshoe crabs (mean and *SD* prosomal width: 238 ± 20 mm) were tracked using passive acoustic telemetry from May 2008 to July 2010 in Pleasant Bay, MA. Pleasant Bay is a 2703 ha semi-enclosed bay on the eastern side of Cape Cod, MA, with two shallow tidal inlets allowing water exchange with the Atlantic Ocean; the northern-most inlet (New Inlet) is recent, formed in 2006 during a Nor'easter storm (Fig. 1). The majority of the bay is shallow (<2 m) with expansive tidal flats particularly along the eastern edge, and has a central deep area (~6 m depth, Lower Pleasant Bay) (Fig. 1). Fifty-five spawning female horseshoe crabs were tagged, with 15 animals tagged in 2008 (CT-05 transmitter, 63 mm by 16 mm, 10 g weight in water, 36 month lifespan, Sonotronics, Tucson, Arizona) and 40 tagged in 2009 (CT-82 transmitter, 54 mm by 16 mm, 9 g weight in water, 14 month lifespan, Sonotronics, Tucson, Arizona). Each transmitter had a unique frequency (69–83 kHz) and was able to emit a signal up to 500 m, but due to the shallow nature of Pleasant Bay the signal was attenuated to 50–200 m (based on field tests) depending on water depth and hydrographic conditions. Fifteen (5 in 2008 and 10 in 2009) of the 55 crabs with transmitters were also tagged with a depth-temperature archive tag (DST milli-TD, 12.5 mm × 38.4 mm, 5 g weight in water, 3 year lifespan, Star-Oddi, Reykjavik, Iceland). Archive tags continuously logged depth and temperature at 20 min and 1 hr intervals, respectively. Archive tags must be physically retrieved to access stored data. Both transmitter and archive tags were attached to the top of the prosoma with cyanoacrylate glue and Velcro (after Brousseau et al., 2004). To allow easy removal of archive tags at recovery they were wired to a base plate that was glued to the Velcro attachment assembly. Both tags were attached during the spawning season in May of each year (except for one crab in 2008 that was tagged with a transmitter in June) and the signal from

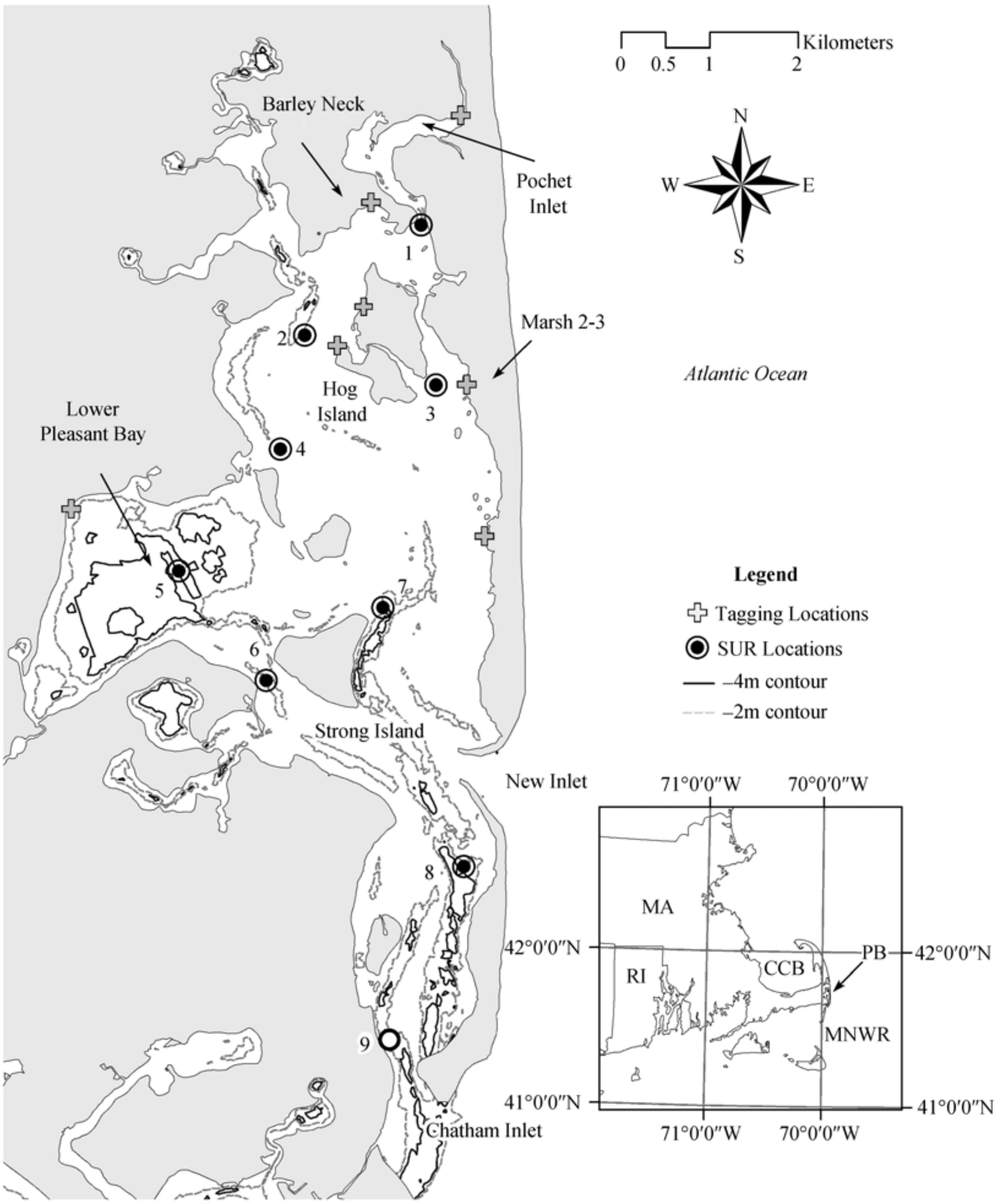

Fig. 1 Map of Pleasant Bay, MA with bathymetric contours (-2 m and -4 m contours), location of Submersible Ultrasonic Receivers® (SUR), and spawning beaches where crabs were tagged and released

Arrow on inset map points to Pleasant Bay (PB). Numbers on map refer to individual SUR locations (refer to Figure 2 for operational deployment times). Open circle indicates SUR that was never recovered. CCB: Cape Cod Bay; MNWR: Monomoy National Wildlife Refuge.

each transmitter was verified in the field as operational with a manual hydrophone prior to the crab's release. Crabs that were fitted with transmitter and archive tag(s) were also tagged with US Fish and Wildlife Service (USFWS) button tags (see methods below).

Female horseshoe crabs were primarily tracked using passive receivers (Sonotronics Submersible Ultrasonic Receivers® or SURs) placed throughout Pleasant Bay, although manual tracking with a directional hydrophone was done intermittently. Five to six SURs were placed in the bay each year near known spawning beaches, along potential corridors to spawning beaches, in the deeper portion of the bay, and near tidal inlets (Fig. 1). The SURs were moored on 25 lb mushroom anchors with the receiver rigged so it was suspended 1 to 2 m off the bottom, and marked with a buoy. SURs scanned for transmitters continuously, completing a scan for all 55 frequencies in approximately 3 min. Data recorded when a transmitter frequency was detected included the unique transmitter frequency (kHz and millisecond interval), identity of the SUR, and date and time (hr:min:sec). All detections were logged into the receiver's memory until data were downloaded.

In 2008, five SURs were deployed from early June to late August 2008; however, data were retrieved from only two SURs (Figs 1 and 2, SURs 4 and 6) as three were not recovered because the marker buoys were not relocated or the units were irreparably damaged by boat collision. In 2009, six SURs were deployed from early May to late summer or early winter depending on the unit (Figs 1 and 2, SURs 2, 3, 5, 6, 7, 8) (two units had less battery reserve and were not operational as long as other units). In 2010, five SURs were deployed in late April and early May to July 2010 (Figs 1 and 2, SURs 1, 2, 3, 5, 7). Configuration of the SUR array was changed slightly in 2010 to optimize detection of the females during their second and/or third spawning season since being tagged as the battery life on the majority of transmitters would end in July or August 2010 (14 mo operational life for 40 of the transmitters).

Data were downloaded from SURs at 10–14 d intervals from May through December. SURsoftDPC Version 6.6.beta (Sonotronics, 2010) was used to process the data using a 5 millisecond interval and were exported into a spreadsheet and spatially depicted in ArcMap version 9.1 (ESRI, 2005). Temporal and spatial movements of individual crabs were mapped by chronologically linking the daily detections from the different SURs. Occasionally, a crab with a transmitter was re-sighted by the public while spawning and this information was integrated with the SUR data. Time-specific detection data (hr:min:sec) were also summarized by each day to yield the number of days each individual crab was detected (hereafter referred to as daily detections). Data from archive depth-temperature tags were processed using SeaStar version 4.46 (Star-Oddi, 2010) and exported into a spreadsheet for graphical display.

Concurrent with the telemetry study, spawning adult (male and female) horseshoe crabs were tagged with USFWS button tags as part of the Horseshoe Crab Cooperative Tagging Program coordinated by the Maryland Fisheries Resources Office (MFRO) (US Fish and Wildlife Service, 2010). All button tags carried a unique identification number, a toll free number (1-888-LIMULUS), and the words "Report" and "Release". Signage, provided by MFRO, indicating the presence of tagged crabs was placed at major boat landings on Pleasant Bay to encourage the public to report tagged horseshoe crabs. Several interns also searched for tagged crabs in 2008 and 2009 while working on other components of this study (e.g., spawning surveys). Tags were attached to the lower point of the prosoma by drilling a 2.8 mm hole and securely inserting the tag stem into the hole. Information recorded for each crab included prosomal width, sex, tagging location, and tagging date. Crabs were tagged at spawning beaches in Pleasant Bay (Fig. 1) from May to July in 2008 and 2009. Tagging data were sent to MFRO and information on re-sighted individuals (location and date of re-sight, disposition of crab [dead or alive]) was received from MFRO in the fall of each year. Since horseshoe crabs reach a terminal molt upon maturity (Shuster, 1955; Smith et al., 2009), the tags are retained for a long time. Horseshoe crabs tagged with the USFWS button tags have been reported alive as long as nine years after tagging (S. Eyler, US Fish and Wildlife Service, personal communication).

2 Results

2.1 Telemetry data

Acoustic telemetry in Pleasant Bay logged just over 56,600 detections from the transmitters, representing 895 days (daily detections) when individual crabs were detected (Table 1). Data from the two SURs (Fig. 2, SURs 4 and 6) that were recovered in 2008 indicated that 60% (9 of 15 crabs) of the crabs tagged in that year were detected in June through August of the same year (SURs were removed from the bay at the end of August 2008). Five additional crabs tagged in 2008 were detected by the six SURs in the Bay in 2009 (Table 1) for a total detection of 14 of the 15 (93%) crabs that were tagged in 2008. In 2009, 36 of the 40 (90%) crabs tagged in 2009 were detected by the SURs. Twenty-seven crabs (24 tagged in 2009 and 3 tagged in 2008) were detected in 2010 (Table 1). In all, 91% (50 of 55) crabs with transmitters were detected by the SURs in Pleasant Bay. Fifty-eight percent of these crabs (29 crabs), were detected during the subsequent spawning season in the vicinity of known spawning beaches (SURs 1, 2, 3). The mean length of detection (date of tagging to date of last detection), was 289 d (2008 mean: 301 d, 2009 mean 285 d). Three crabs had detection periods longer than 700 d, with the longest period being 781 d (22 May 2008 to 12 July 2010). An additional 28 crabs (51%) had detection periods that spanned from one spawning season to the next (300–700 d).

Only six crabs (11%) had detection periods less than 3 wk, five of these crabs were never detected after release. Nine crabs were only sporadically detected (<10

Table 1 Summary of acoustic telemetry effort in 2008 to 2010

Acoustic Data Summary	Year			
	2008	2009	2010[1]	All years
Number tagged crabs	15	40	-	55
Total number of days individual crabs were detected (No. crabs)	45 (13)	631 (42, 6 from 2008)	219 (27, 3 from 2008)	895 (50)
May-June, spawning	31 (12)	159 (33)	204 (26)	394 (47)
July-Aug, post-spawning	14 (6)	221 (35)	15 (7)	250 (41)
Sept-Dec, fall	-	251 (23)	-	251 (23)
Acoustic detection summary				
Total detections	2017	36,037	18,606	56,660
May-June, spawning	1,812	4,517	17,680	24,009
July-Aug, post-spawning	205	12,064	926	13,195
Sept-Dec, fall	-	19,456	-	19,456

Acoustic telemetry was based primarily on passive detection by fixed position Submersible Ultrasonic Receivers® placed throughout Pleasant Bay.
[1] Includes data from last week of April 2010 through 22 July 2010.

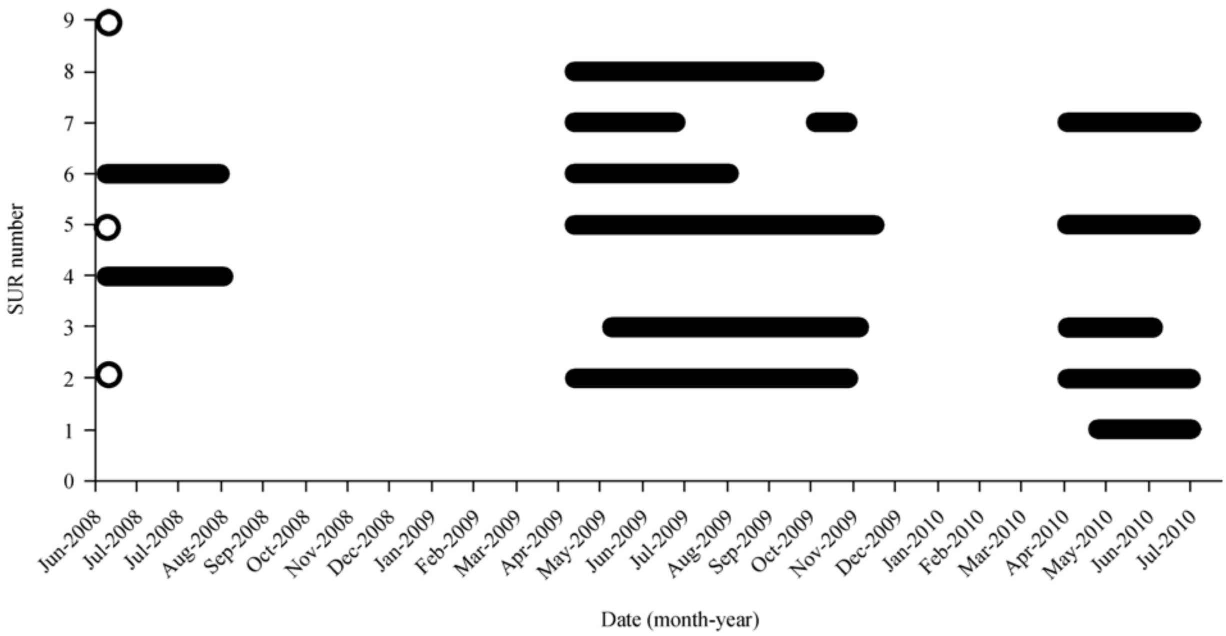

Fig. 2 Temporal record of data and operational deployment times (dark bars) for Submersible Ultrasonic Receivers® (SUR) in Pleasant Bay

Numbers refer to locations where SURs were placed in Pleasant Bay in each year (refer to Figure 1). Open circles indicate SURs that were never recovered in 2008. SURs 2 and 5 were replaced and re-deployed in 2009, SUR 9 was not replaced.

daily detections), although they were detected in the bay for two or more spawning seasons. For example, one individual (crab #106) tagged in May 2008 was detected during June 2008 on four dates, never detected in 2009, but was detected in the northern portion of the bay in May and June 2010 (SUR 4). Crab #110 tagged in 2008, was detected only once in 2008 and 2009, but was detected several times in May 2010. Another crab tagged in 2009 (crab #143) was only detected once in 2009 (in November), but was detected in May of 2010 near a spawning beach (SUR 1).

Detection data from 2009 and 2010 showed a seasonal pattern of movement of crabs within the bay when grouped by biologically meaningful periods: April to June spawning period, July and August post-spawning, and the fall, September to early December (since telemetry data from 2008 were limited, these data were omitted). The distribution of detected crabs varied seasonally (Fig. 3 A–D). During the May to June 2009 spawning period, the proportion of days (number of days detected standardized by the total number of days in the period) when crabs were detected (31 of 55 crabs detected) was higher in the northern, upper section of the bay where the majority of spawning beaches were located (Fig. 3A). After spawning (July and August 2009, 35 crabs detected) the distribution was fairly uniform throughout the bay (Fig. 3B). In the fall of 2009 (23 crabs detected) the distribution shifted to the lower and western deep portion of the bay (Lower Pleasant Bay, Fig. 3C). The following spawning period (late April and through June 2010, 26 crabs detected) the crabs again moved to the upper portion of the bay to spawn (Fig. 3D). Thirty-one crabs were detected in the deeper portion of Lower Pleasant Bay over the course of the study, 22 (71%) of these crabs were detected the following spring near spawning beaches in the upper portion of the bay (SURs 1, 2, 3). Eighty percent of the crabs (44 of 55) were detected in the bay during the post-spawning period or the fall (data from all years included).

To determine if the number of daily detections differed among the seasonal periods, the SUR locations were grouped by upper bay (SURs 1, 2, 3, and 4) and lower bay (SURs 5, 6, 7, and 8), and daily detections were compared for the 2009 data (the only year when all seasons were monitored). The number of daily detections was significantly different (χ^2=35.1, *df*=2, *P*<0.0001) between the upper and lower bay during the spawning period and fall. Freeman-Tukey deviates indicated that there were more daily detections than expected in the upper bay during the spawning period and fewer than expected in the lower bay. The opposite was true during the fall when daily detections were lower than expected in the upper bay and higher than expected in the lower bay. Distribution during the post-spawning period (July to August 2009) was similar between the upper and lower bay.

The mean number of detections, an indicator of the length of time any one individual remained in the in the vicinity of the SURs, was used to assess vagility of the crabs in terms of large scale (>500 m) movements within the bay. The higher the number of detections at a particular SUR, the longer the crab remained in proximity to the SUR. When the crabs were actively moving around the bay, the mean number of detections per SUR would be lower as they would transit past the units. An Analysis of Variance, followed by Least Squares Means post-hoc test was used to evaluate if average number of hits per SUR per crab (standardized as the mean proportion across all three seasons) differed by seasonal period.

In 2009, the mean proportion of detections (arcsin transformed proportions) was higher during the fall (mean and *SD*: 0.022±0.037) when compared to the spawning period (ANOVA, *P*=0.0133, *df*=2, Least Squares Means, *P*=0.0031, mean and *SD*: 0.011±0.02) and to the post-spawning period (Least Squares Means, *P*=0.0398, mean and *SD*: 0.004±0.011). This indicated that the crabs tended to be most active during the spawning period (fewer detections) and progressively became less vagile as the fall approached (more detections) as they remained for a longer time in the vicinity of the SURs. The percent of total detections more clearly shows the partitioning of movement among the seasons, with the spawning period accounting for only 13% of the total detections, while the post-spawning period accounted for 33% and the fall period accounted for 54% of the total detections in 2009 (Table 1).

Twenty-seven crabs had detailed telemetry records where they were detected on several dates spanning the post-spawning and fall periods or even into the spring and summer of 2010. Two general patterns of movement were evident. The first pattern was comprised of individuals that after being tagged on the spawning beach, were detected in the proximity of spawning beaches and often remained in the same location during the post-spawning period, fall, or even the next spawning season (these individuals were alive as they were detected on either different SURs or on non-sequential dates). The second pattern (Fig. 4), exhibited by 74% of the individuals (20 crabs), included crabs that after being tagged on the spawning beach moved south either to Lower Pleasant Bay (SUR 5) and/or out to the southeastern portion of the bay near the New Inlet (SUR 8) in the post-spawning period (Fig. 4). In the fall, these individuals would then move into the deep waters of Lower Pleasant Bay. The following spring, many of these individuals (10 crabs) were detected in the northern portion of the bay near spawning beaches (refer to Fig. 4). The receiver (SUR 8) was placed just south of the New Inlet with the intent of detecting crabs that may be exiting the bay. Ten individuals were detected near the New Inlet (SUR 8) in 2009. Nine of these crabs were later detected either in Lower Pleasant Bay (SUR 5, five crabs) in the fall of 2009, or during the 2010 spawning period (four crabs).

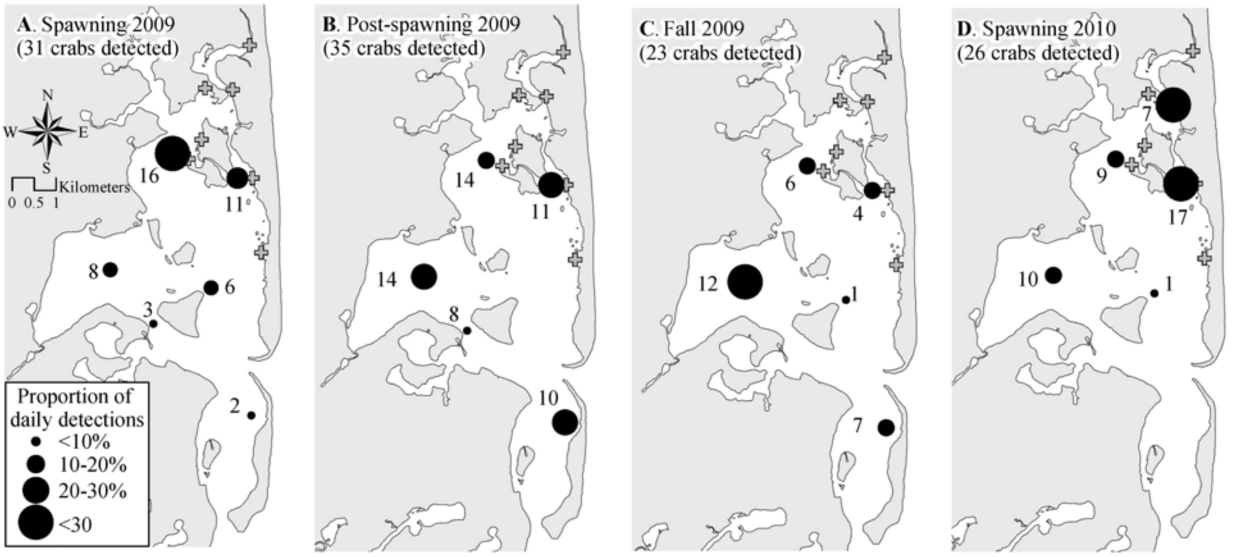

Fig. 3 Seasonal distribution of crabs in 2009 and 2010 spawning period (proportion of days when crabs were detected in each season) based on acoustic telemetry

A. 2009 spawning period (May to June). **B**. 2009 post-spawning period (July and August). **C**. 2009 fall (September to mid-December). **D**. 2010 spawning period (late-April to June). The number of individual crabs detected is indicated next to each SUR location. Crosses indicate spawning beaches

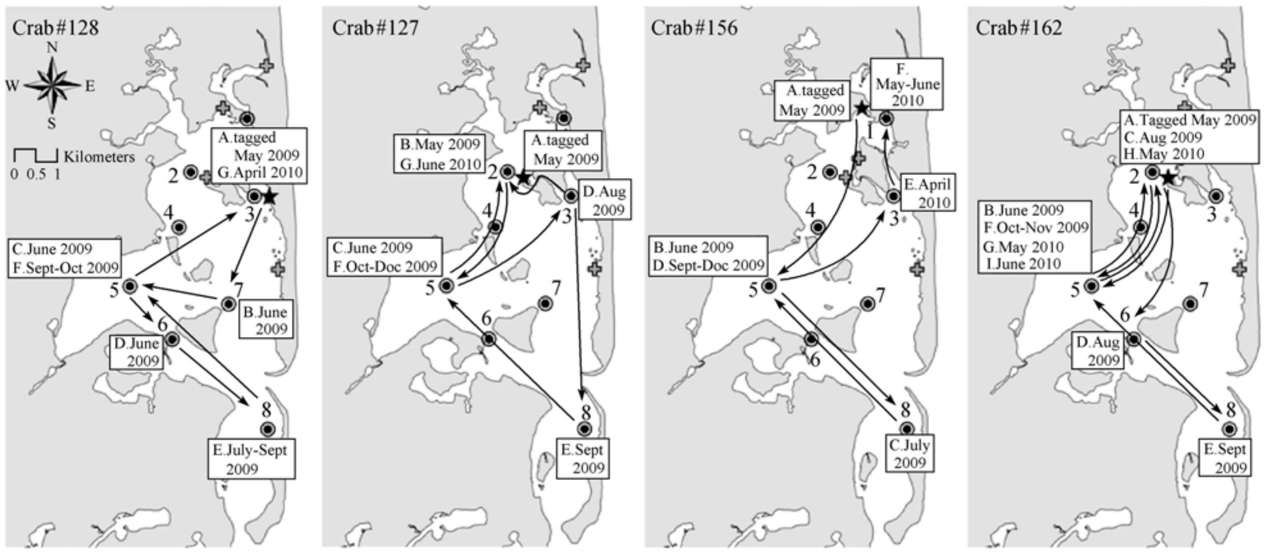

Fig. 4 Example of movement pattern of crabs detected over two or more spawning periods

SURs are identified by numbers (refer also to Fig. 1) and chronological order of detections are indicated by letters. Stars indicate tagging location.

Over the course of the study all fifteen crabs tagged with archive tags were detected on the SURs. One depth-temperature archive tag was recovered from a recently dead crab on 29 May 2010. The crab was originally tagged on 11 May 2009 at the Marsh 2-3 spawning beach, near SUR 3 (Fig. 1). It was detected on the SURs from July through December 2009, and again during the 2010 spawning period until it was found dead on a spawning beach near the entrance to Pochet Inlet (near SUR 1, Fig. 1) in the northern portion of the bay. The data from the archive tag and SURs for this individual were integrated to produce a depiction of the animal's movement and the associated depth and temperature profile from 11 May 2009 to 29 May 2010 (Fig. 5). After release, the crab was detected on the eastern side of Hog Island in early July, and it remained in shallow warm water (mean daily depth 1.1 m, mean daily temperature 17.5 °C) until 21 Sept 2009. It then moved

moved to the deeper and colder waters of Lower Pleasant Bay. During the late fall to late winter (23 September to 26 March 2010) it remained in the deep cold waters (mean daily depth 5.6 m, mean daily temperature 6.7 °C) of Lower Pleasant Bay and was detected almost daily from 23 September 2009 to 7 October 2009. The last detection in 2009 was on 21 November in Lower Pleasant Bay (Figure 5) (the SUR was removed from the bay for the winter in early-December). When the Lower Pleasant Bay SUR (SUR 5) was re-deployed in 2010, the crab was again detected daily from 24 April to 2 May 2010, in the same location as it was in November. It then moved into shallow warmer water (mean daily depth 0.9 m, mean daily temperature 15.5 °C, 5 May to 28 May 2010), moving north and passing to the western side of Hog Island (SUR 2) on 19 May 2010 and then into Pochet Inlet where it was detected on 21, 23, and 29 May 2010 (Fig. 5). The last detection (29 May, 4:01am on SUR 1) for this female was just prior to and just after the full moon of 27 May 2010. She presumably entered Pochet Inlet to spawn on the beaches along this back barrier beach or at the head of the inlet in a wash-over area that is a known spawning area (James-Pirri, unpublished data). The crab was found recently dead by a beachcomber in the afternoon of 29 May 2010 on a spawning beach on Pochet Island near SUR 1.

Although there was a gap in telemetry data from 21 November 2009 to 24 April 2010 for this crab, the depth profile confirms that she did not leave Lower Pleasant Bay over that period. The crab remained at 5–6 m depth through the end of March, only moving into shallow water at the onset of upcoming spring spawning period. The deep waters of this portion of the bay are surrounded by shallow water (<2 m, refer to Fig. 1) and if the female exited the bay and then returned between late November and late April 2009, the change in depth would have been recorded.

2.2 Tagging data

More than 2000 crabs were tagged with USFWS button tags in Pleasant Bay during 2008 (761 crabs) and 2009 (1266 crabs). The overall live recapture rate was 11% (233 live recaptures, overall recapture rate of 15%) as of August 2010. Fifty crabs (21% of the live recaptures) tagged during the previous spawning season(s) were re-sighted in subsequent years (48 crabs after one year at large, 2 crabs after two years at large). Specific recapture locations were known for 220 of the recaptures. Over the three years that recaptured crabs were reported (2008 to 2010), 83% of the live recaptures were found within 2.5 km of the spawning beach where they were tagged (Fig. 6). The majority of these, 67%,

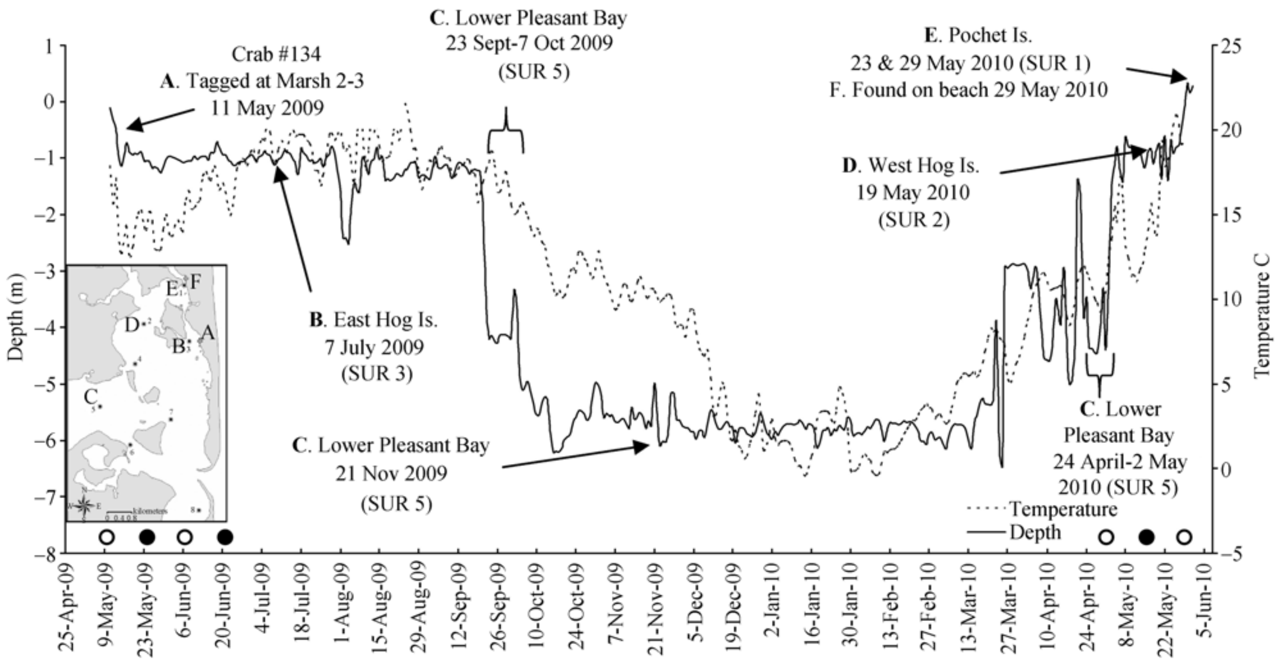

Fig. 5 One year depth-temperature profile (daily means) and SUR detections for a female horseshoe crab (crab #134) tagged with both an acoustic transmitter and archive data tag

Inset map shows locations of SURs with letters indicating chronological movement of the crab from SUR detections. Circles indicate spawning period for spring full moons (open circles) and new moons (closed circles).

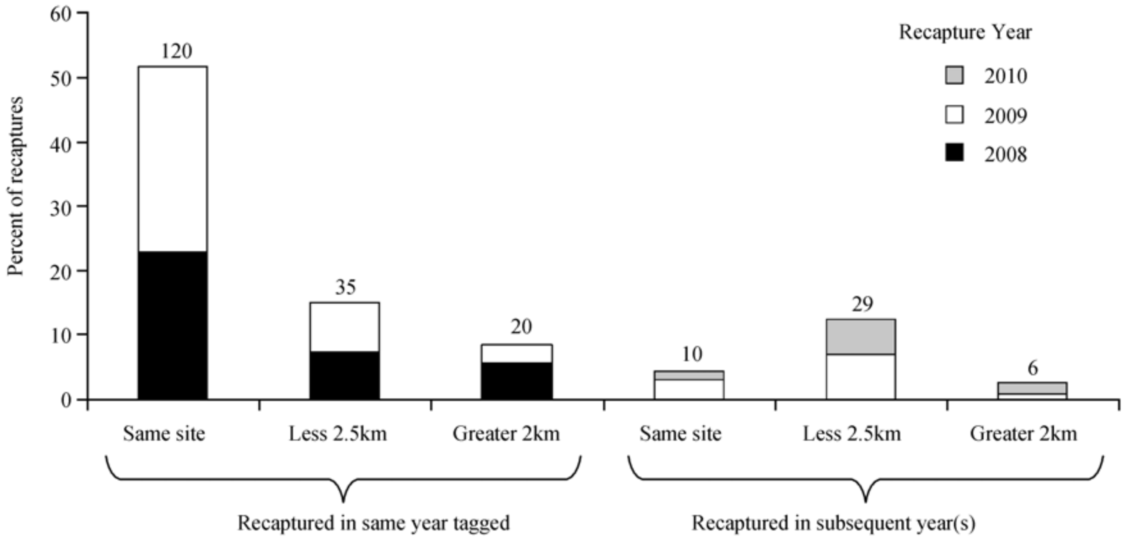

Fig. 6 Percent of live recaptured horseshoe crabs, by recapture year, in relation to original tagging location
Total number of recaptured crabs is indicated above bars.

were recaptured within 2.5 km of the tagging location in the same year they were tagged. All live recaptures were re-sighted in Pleasant Bay with the exception of one female that was tagged on 17 June 2008 on Hog Island and was recaptured by a trawler in Nantucket Sound on 21 July 2008.

3 Discussion

The acoustic telemetry data showed that after spawning, female crabs tended to remain within Pleasant Bay during the post-spawning period and some may have overwintered in the deeper waters of the bay (e.g., Lower Pleasant Bay). During the May and June spawning period, crabs were primarily located in the northern, upper section of the bay where the primary spawning beaches are located. Fifty-eight percent of the crabs were detected the following spring near spawning beaches. When grouped by individuals moved between the upper and lower portions of the bay, this increased to 71%. This indicated that the majority of females that moved into deeper sections of the bay likely spawned in two sequential years, once when tagged while spawning and again when detected the following spring in the northern section of the bay. During the post-spawning period (July-August) crabs were distributed throughout the bay. One hypothesis for the shift in distribution was that crabs were foraging on the shallow waters of the bay (Lee, 2010; Watson and Chabot, 2010). The majority of Pleasant Bay is very shallow (< 2 m), with extensive tidal flats, especially along the eastern edge of the barrier beach system, where beds of razor clam *Ensis directus* and soft shell clam *Mya arenaria* are present (Pleasant Bay Resource Management Alliance, 2008). During the fall, there was another shift in the distribution with the majority of the daily detections for this period occurring in Lower Pleasant Bay. During this time, 42% of the transmitters (23 of 55 crabs) were detected in the bay with an additional seven transmitters (54% of crabs with transmitters) detected during the 2010 spawning season. This indicates that the majority of the detected transmitters (30 of 55 transmitters) were either present in the bay several months after spawning or were present the following the spring. The vagility of the crabs also changed seasonally, with crabs becoming increasingly less mobile in the post-spawning and fall periods. Similar behavior was observed in a non-migratory population in Taunton Bay, ME, with a decrease in activity marking the onset of the wintering period (Moore and Perrin, 2007).

Even though crabs may have exited Pleasant Bay, there was evidence that they either remained in the bay, or if they left they returned, as many were detected during the winter or the following spring. Similar movement patterns have been observed in other New England estuaries (Taunton Bay, ME, and Great Bay, NH, USA) (Moore and Perrin, 2007; Schaller et al., 2010). In Taunton Bay, horseshoe crabs overwintered in subembayments and showed no mixing between subembayments even though they were <4 km apart (Moore and Perrin, 2007). Brousseau et al. (2004) observed in Delaware Bay (DE, USA), a population that migrates to either the deep waters of Delaware Bay or to the continental shelf, that nearly all the females tagged with telemetry tags left the immediate study area (which extended 1 km from the spawning beaches) by 3 d after the last spring tide spawning event. If the crabs in Pleasant Bay migrated out of the bay, it is likely that they would have left by the end of June, ~5 to 10 d after the last spring tide spawning event (last spawning spring tides were 18 June 2008, 22 June 2009, and 26 June 2010). However, it was evident that the crabs did not immediately leave the bay after the last spawning event, as 58% of the total detections (representing 80% of the telemetry tagged crabs) were observed in the bay from July through December.

Five crabs with transmitters (9%) were never detected after release (the 50 other transmitters were detected on least two dates, several days to months apart, after release indicating that these crabs were alive). Possible explanations for the non-detection of transmitters were that the transmitter could have detached from the crab and remained out of the SURs range, the crab could have died out of the SURs range, or the crab was present in the bay but never passed within the detection range of the SURs.

Pleasant Bay is the largest embayment on Cape Cod, and the maximum detection area (250 m range) of the SURs, when all six were operational, was approximately 30 ha or only ~1% of the bay's area. Even though the SUR array was arranged to achieve optimal detection (by locating them close to spawning beaches and along corridors to beaches), it was possible that a crab with a transmitter may not have been detected over the course of the study. Interestingly, the fact that this study observed such a large volume of transmitter detections (just over 56,600 detections and 895 daily detections) is additional evidence as to the philopatry of this population of horseshoe crabs to this embayment.

Although only one of fifteen archive depth-temperature tags was recovered, the one tag yielded a wealth of information when the data were integrated with the telemetry data for this particular crab. The yearlong depth-temperature profile showed that after spawning in the northern section of the bay, the crab moved into the deeper waters of Lower Pleasant Bay where it overwintered until the following spring, when it travelled back to the same general area in the northern portion of the bay to spawn. Telemetry data from several other crabs exhibited this same type of movement pattern. After spawning, they moved to shallow tidal flats along the eastern portion of the bay or into deeper water during the fall, moving again into the shallow northern section of the bay the following spring to spawn (refer to Fig. 4).

The recapture results of the USFWS button tagged crabs from this study mirror the results previously reported for Pleasant Bay. Previous work in Pleasant Bay reported a 10% live recapture rate of tagged crabs and similarly observed that the majority of recaptures occurred within a short distance (2 km) of the original tagging location (James-Pirri et al., 2005). During the same time-period as this study, tagging was also conducted in other areas of Cape Cod (e.g., Monomoy National Wildlife Refuge and Cape Cod Bay, Fig. 1). Monomoy National Wildlife Refuge, for example, has consistently tagged approximately 500 crabs per year since 2000. No individuals tagged in these other areas have ever been reported as being recaptured inside Pleasant Bay (James-Pirri et al., 2005; M. Williams and S. Eyler, US Fish and Wildlife Service, personal communication).

Recruitment to a population can occur from the population itself via reproduction or from other populations through larval dispersal or immigration of new individuals. The horseshoe crab has a very limited larval dispersal, as trilobites tend to remain nearshore and do not to travel far offshore of the spawning beach, making larval recruitment from adjacent estuaries highly unlikely (Botton and Loveland, 2003; Botton et al., 2010). The contribution of juveniles or sub-adult immigration to populations is not well understood. Tagging data (data from previous studies and this study) for Pleasant Bay indicate that 99% of the recaptured individuals were located within the bay, with only 4 of 336 recaptured individuals found outside the bay and that crabs tagged outside of Pleasant Bay have not been recaptured inside the bay (James-Pirri et al., 2005; this study). This suggests that there is limited movement of adults between Pleasant Bay and adjacent embayments. This philopatric behavior may be specific to populations within semi-enclosed embayments like Pleasant Bay. Populations found in more open areas, such as those at Monomoy National Wildlife Refuge (refer to Fig. 1), may be more mobile as there is an active dragger fishery for horseshoe crabs in Nantucket Sound which of offshore of the Monomoy Islands.

There is concern among state managers about the sustainability of the Pleasant Bay fishery and that the long history of harvest is disproportionately affecting females, as spawning sex ratios, unlike those in other Massachusetts embayments, are highly skewed towards males (e.g., 1:9, female to male) (James-Pirri et al., 2005; Leschen and Correia, 2010; James-Pirri, unpublished data). An important tool for the sustainable fishery management of horseshoe crab stocks is knowing whether or not population(s) are localized within specific embayments. Populations that are philopatric to specific embayments may not benefit from the influx of new members from other populations and could be more likely to experience localized extirpation in the face of increasing fishery pressure, thus requiring specialized management. This is especially important to the New England horseshoe crab stock(s), as trawl data suggest a limited or non-existent migration to the continental shelf (Botton and Ropes, 1987) and tagging data show that horseshoe crabs in New England either remain or return to the embayment where they spawn (James-Pirri et al., 2005; Moore and Perrin, 2007; this study). The telemetry data from this study provide further evidence that horseshoe crabs in Pleasant Bay may be a localized population, and that spawning individuals remain in the bay after spawning and a portion may overwinter in the bay.

Acknowledgements I would like to thank National Park Service Bio-technicians Chris Keon, Matt Holt, and Nate Gavin, and Student Conservation Association interns Kelly Bowman, Michelle Fabie, Christopher Guy, Nikki Kirkton, Tessa Mosher, Stacey Ng, Kelly Racette, Meg Swecker, and Molly Williams for their enthusiastic help in the field. Carrie Phillips, Kelly Medeiros, Krista Lee, Alison Leschen, Brad Chase, Stuart Smith, and Dawson Farber provided logistical support on Cape Cod. Jennifer Mattei and Mark Beekey of Sacred Heart University kindly loaned additional SURs and other acoustical equipment for this study and Sonotronics provided exceptional technical support. Sheila Eyler of the US Fish and Wildlife Cooperative Tagging Program graciously provided tags, signage, and recapture data. Special thanks to Erica Parra and her family for allowing access to her Barley Neck property and for reporting tagged crabs. Four anonymous reviewers provided helpful suggestions. This study was supported by the National Park Service under Cooperative Agreement Number CA452099007 with the University of Rhode Island.

References

Botton ML, Loveland RE, 2003. Abundance and dispersal potential of larval horseshoe crab *Limulus polyphemus* in the Delaware estuary. Estuaries 26: 1472–1479.

Botton ML, Ropes JW, 1987. Populations of horseshoe crabs *Limulus polyphemus* on the northwest Atlantic continental shelf. Fish. Bull. (Washington D.C.) 85: 805–812.

Botton ML, Tankersley RA, Ehlinger GS, Loveland RE, 2010. Developmental ecology of the American horseshoe crab *Limulus polyphemus*. Curr. Zool. 56: 550–562.

Brousseau LJ, Sclafani M, Smith DR, Carter DB, 2004. Acoustic-tracking and radio-tracking of horseshoe crabs to assess spawning behavior and subtidal habitat use in Delaware Bay. N. Amer. J. Fish. Manage. 24: 1376–1384.

Clark KE, 1996. Horseshoe crabs and the shorebird connection. In: Farrell J, Martin C ed. Proceedings of the Horseshoe Crab Forum: Status of the Resource. Publication No. DEL-SG-05-97. Lewes, Delaware: University of Delaware Sea Grant College Program, 23–25.

Commonwealth of Massachusetts, 2006. Massachusetts Compliance Report for the Horseshoe Crab *Limulus polyphemus*, 2006 Compliance Report. New Bedford, MA: Massachusetts Division of Marine Fisheries.

Commonwealth of Massachusetts, 2008. Massachusetts 2008 Compliance Report to the Atlantic States Marine Fisheries Commission: Horseshoe Crab. New Bedford, MA: Massachusetts Division of Marine Fisheries.

Commonwealth of Massachusetts, 2009. Massachusetts 2009 Compliance Report to the Atlantic States Marine Fisheries Commission: Horseshoe Crab. New Bedford, MA: Massachusetts Division of Marine Fisheries.

ESRI, 2005. ArcGIS 9, ArcMap version 9.1

James-Pirri MJ, Tuxbury K, Marino S, Koch S, 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.

Karpanty SM, Fraser JD, Berkson J, Niles LJ, Dey A et al., 2006. Horseshoe crab eggs determine red knot distribution in Delaware Bay. J. Wildlife Manage. 70: 1704–1710.

Kurz W, James-Pirri MJ, 2002. The impact of biomedical bleeding on horseshoe crab *Limulus polyphemus* movement patterns on Cape Cod, Massachusetts. Marine Freshwater Behav. Phys. 35: 261–268.

Lee W-J, 2010. Intensive use of intertidal mudflats by foraging Atlantic horseshoe crabs *Limulus polyphemus.* Curr. Zool. 56: 611–617.

Leschen AS, Correia SJ, 2010. Mortality in female horseshoe crabs *Limulus polyphemus* from biomedical bleeding and handling: Implications for fisheries management. Marine Freshwater Behav. Phys. 43: 135–147.

Moore S, Perrin S, 2007. Seasonal movement and resource-use patterns of resident horseshoe crab *Limulus polyphemus* populations in a Maine, USA estuary. Estuaries and Coasts 30: 1016–1026.

Novitsky TJ, 2009. Biomedical applications of *Limulus* amebocyte lysate. In: Tanacredi JT, Botton ML, Smith DR ed. Biology and Conservation of Horseshoe Crabs. Springer: New York, 315–329.

Novitsky TJ, 1984. Discovery to commercialization: The blood of the horseshoe crab. Oceanus 27: 19–26.

Pleasant Bay Resource Management Alliance, 1998. Pleasant Bay Resource Management Plan, April 1998. http://www.pleasantbay.org/plan.htm. Accessed 28 May, 2010.

Pleasant Bay Resource Management Alliance, 2008. Pleasant Bay Resource Management Plan 2008 Update. http://www.pleasantbay.org/plan.htm. Accessed 13 June, 2010.

Rudloe A, 1983. The effect of heavy bleeding on mortality of the horseshoe crab *Limulus polyphemus* in the natural environment. J. Invert. Pathology 42: 167–176.

Rutecki D, Carmichael RH, Valiela I, 2004. Magnitude of harvest of Atlantic horseshoe crabs *Limulus polyphemus* in Pleasant Bay, Massachusetts. Estuaries 27: 179–187.

Schaller SY, Watson WH, Chabot CC, 2010. Seasonal movements of horseshoe crabs *Limulus polyphemus* in the Great Bay Estuary, New Hampshire (USA). Curr. Zool. 56: 587–598.

Shuster CN Jr, 1955. On the morphometric and serological relationships within Limulidae, with particular reference to *Limulus polyphemus* (L.). PhD dissertation New York University, New York, New York.

Shuster CN Jr, Botton ML, 1985. A contribution to the population biology of horseshoe crabs *Limulus polyphemus* (L.) in Delaware Bay. Estuaries 8: 363–372

Smith DR, Brousseau LJ, Mandt MT, Millard MJ, 2010. Age and sex specific timing, frequency, and spatial distribution of horseshoe crab spawning in Delaware Bay: Insights from a large-scale radio telemetry array Curr. Zool. 56: 563–574.

Smith DR, Mandt MT, MacDonald PDM, 2009. Proximate causes of sexual size dimorphism in horseshoe crabs *Limulus polyphemus* of the Delaware Bay. J. Shellfish Res. 28: 405–417.

Star-Oddi, 2010. SeaStar version 4.46. http://www.star–oddi.com/ Accessed 4 June 2010.

Sonotronics, 2010. SURSoftDPC version 6.6.beta. http://www.sonotronics.com/Accessed 28 May 2010.

U.S. Fish and Wildlife Service, 2010. Maryland Fisheries Resource Office, Horseshoe crab tagging program. http://www.fws.gov/northeast/marylandfisheries/projects/Horseshoe%20crab.html. Accessed 28 May 2010.

Walls EA, Berkson JM, Smith SA, 2002. The horseshoe crab *Limulus polyphemus*: 200 million years of existence, 100 years of study. Reviews Fish. Sci. 10: 39–73.

Watson WH, Chabot CC, 2010. High resolution tracking of adult horseshoe crabs *Limulus polyphemus* in a New Hampshire estuary using a fixed array ultrasonic telemetry. Curr. Zool. 56: 599–610.