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Assessing the movements of American horseshoe crabs (*Limulus polyphemus*) around a marine protected area in Cape Cod, MA, USA

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ABSTRACT

Marine protected areas (MPAs) can be useful for conservation efforts, yet the effectiveness of MPAs relies on their size and location, as well as the spatial ecology of the focal species. We investigated the effectiveness of a small MPA adjacent to Cape Cod, MA (USA) for protecting American horseshoe crabs (*Limulus polyphemus*). We used a fixed acoustic telemetry array to study the spatial ecology of 24 adult horseshoe crabs off the coast of Chatham, Massachusetts, from June 2010 to November 2011. Two groups of horseshoe crabs were tagged in spawning habitats (separated by ~2.0 km) with differing commercial harvesting pressure: one group inside Stage Harbor where harvesting is permitted, and the other within Monomoy National Wildlife Refuge and the Cape Cod National Seashore (the MPA) where harvesting is prohibited. In the first year of study, crabs tagged in the MPA did not go to Stage Harbor, but instead remained in the MPA and adjacent high-energy beach, whereas crabs tagged in Stage Harbor moved throughout the entire study area. In the second year of study, crabs from both tagging locations used all areas. All crabs generally moved greater distances in the MPA than in other areas, and the majority of movement we recorded was in late spring and summer. All crabs that we tagged used similar areas around Cape Cod. The MPA only provides protection when crabs are in that area, which may only be for a few months of the year. Given that all crabs used Stage Harbor, they were all exposed to potential harvest, but the MPA did provide some protection for all crabs.

1. Introduction

Marine protected areas (MPAs) are an important management tool used to shield marine life from anthropogenic disturbance. MPAs are commonly used to provide relief from marine fisheries, yet studies have documented that improperly designed MPAs can be ineffective at protecting marine species (e.g., Marra et al., 2016). MPAs must be well-designed in order to be effective (Kaiser, 2005), and must include large amounts of good quality habitat for focal species in order to maintain a large, healthy source population (Cabral et al., 2016; Grafton et al., 2005; Pelletier et al., 2008; Turgeon and Kramer, 2012), but must also account for the movement of highly mobile species (Kaiser, 2005). MPAs can even be designed to protect seasonally-important habitat, such as spawning grounds (Nemeth, 2005).

While MPAs are typically designated to protect vertebrates, entire communities, or ecosystems, very few examples exist for MPAs designated specifically for invertebrates. For example, an MPA (1722 km^2) was designated in Chesapeake Bay for spawning blue crabs (*Callinectes sapidus*) that effectively protected over half of all spawning females in this area during the spawning season (Lipcius et al., 2003). A large MPA (3885 km^2) was also designated near Delaware Bay for American horseshoe crabs (*Limulus polyphemus*), which does not allow any harvesting of horseshoe crabs (Smith et al., 2017). Since designation of the Delaware Bay MPA, the abundance of both juvenile and adult male horseshoe crabs has increased in Delaware Bay (Atlantic States Marine Fisheries Commission, 2011). While both of the aforementioned MPAs are quite large, we are interested in the ability of much smaller MPAs to protect invertebrate species. Smaller MPAs (< 100 km^2) typically have lower fish biomass than larger MPAs (> 100 km^2) (Edgar et al., 2014), and this trend likely also applies to invertebrates. Smaller MPAs will likely protect fewer individuals, and could be too small to protect a single individual throughout its entire

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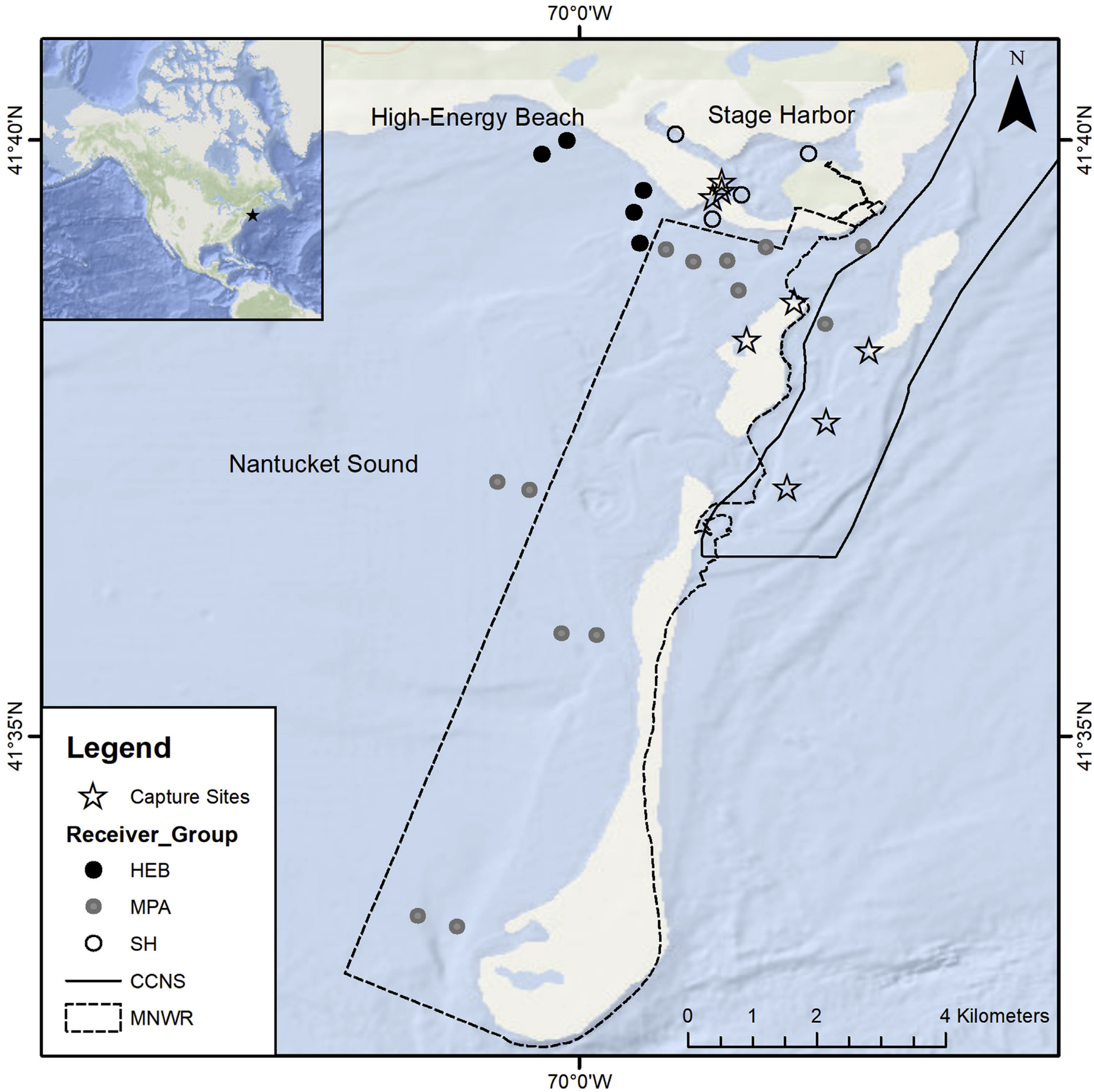

Fig. 1. Map of the study area for an acoustic telemetry study of American horseshoe crabs (*Limulus polyphemus*) near Cape Cod, MA, including capture locations in Stage Harbor and in the Marine Protected Area (MPA: MNWR = Monomoy National Wildlife Refuge; CCNS = Cape Cod National Seashore) and locations of acoustic receivers (HEB = high energy beach, MPA = marine protected area, SH = Stage Harbor). Harvesting of horseshoe crabs in the MPA is prohibited. The star in the inset shows Cape Cod.

home range or between seasons if the species' habitat preference changes between seasons.

We examined the spatial ecology of American horseshoe crabs in a small MPA (31 km^2) around the federally protected boundaries of Cape Cod National Seashore and Monomoy National Wildlife Refuge in Massachusetts, and compared the movements of horseshoe crabs from the MPA to those in adjacent Stage Harbor. Horseshoe crabs near Cape Cod are declining (Widener and Barlow, 1999), but are still harvested for use as bait in commercial fisheries and collected for use in biomedical applications (Smith et al., 2017). Horseshoe crabs are ecologically important (Botton and Loveland, 2003; Castro and Myers, 1993; Kraeuter and Fegley, 1994; Walls et al., 2002), have been used extensively in biomedical research and medicine (e.g., Melchior et al., 1995), and are economically important as a bait source for commercial fisheries and for their use in medicine (Walls et al., 2002). It is therefore critical to have a complete understanding of the effectiveness of the different tools used to manage this species. Horseshoe crabs within the MPA cannot be harvested, whereas those in Stage Harbor can be harvested. However, crabs moving between the MPA and unprotected areas can be harvested whenever they leave the MPA. Although this MPA was not designated specifically for horseshoe crabs, it does include major horseshoe crab spawning habitat and juvenile horseshoe crab

Table 1
Summary data for American horseshoe crabs (*Limulus polyphemus*) used in data analyses. Location Tagged is either Stage Harbor (SH) or the marine protected area (MPA). Date format is YY-MM-DD. Total detections is the total number of times that an acoustic receiver recorded a signal from that individual. Total Receivers is the total number of different receivers that detected that individual.

ID	Sex	Width (mm)	Location Tagged	Date Tagged	Date First Detected	Date Last Detected	Total Detections	Total Receivers
342	F	222	SH	10-06-14	10-06-15	11-07-21	2295	7
346	F	230	MPA	10-06-25	10-07-06	11-07-15	11	3
350	F	229	MPA	10-06-29	10-06-30	10-08-03	1860	4
352	F	253	SH	10-06-14	10-06-15	11-05-18	128	6
356	F	227	MPA	10-06-29	10-07-22	11-05-25	125	4
358	F	262	SH	10-06-14	10-06-15	11-09-01	911	2
360	M	180	MPA	10-06-29	10-06-30	10-09-01	138	4
363	F	184	MPA	10-06-13	10-07-05	11-06-06	2252	13
365	F	256	SH	10-06-14	10-06-16	11-06-05	1552	9
366	F	242	SH	10-06-04	10-06-04	11-05-21	72	2
437	F	246	MPA	10-06-13	10-06-15	11-07-09	50	6
440	M	175	MPA	10-06-29	10-06-29	10-08-09	18	4
441	F	231	SH	10-06-04	10-06-04	10-07-12	641	2
444	F	242	SH	10-06-04	10-06-04	11-05-26	275	5
447	F	226	SH	10-06-04	10-06-04	10-09-01	1413	2
451	F	255	SH	10-06-09	10-06-10	11-10-26	510	1
457	F	277	SH	10-06-14	10-06-15	11-06-06	53	8
458	F	248	MPA	10-06-29	10-07-01	11-06-03	80	9
460	M	195	MPA	10-06-30	10-10-21	10-11-22	300	1
472	F	270	MPA	10-06-13	11-05-16	11-11-25	114	1
498	F	248	SH	10-06-09	10-06-09	10-07-12	1185	2
500	M	170	MPA	10-06-29	10-06-30	10-10-27	440	5
502	F	230	SH	10-06-04	10-06-04	11-06-09	1582	17
503	F	226	MPA	10-06-29	10-06-30	11-05-24	561	7

nursery habitat (Massachusetts Division of Marine Fisheries, 2010). However, the population is understudied and the effectiveness of the MPA at replenishing nearby, possibly depleted horseshoe crab stocks is not known. We examined whether horseshoe crabs have strong site fidelity, or if crabs frequently moved between the MPA and adjacent Stage Harbor, and whether the MPA is acting as a source population for the harvested population at Stage Harbor. We used a fixed acoustic telemetry array to determine the degree and timing of adult horseshoe crab movement within and between the MPA and harvested areas. This information elucidates the degree of connectivity of the spawning habitats within and outside of the MPA, and tests the effectiveness of the MPA for fisheries managers.

2. Methods

2.1. Study site

We studied the spatial ecology of American horseshoe crabs in 2010–2011 in Nantucket Sound off the coast of Chatham, Cape Cod, MA, focusing on the unprotected population in Stage Harbor and the protected population in the MPA made up of Monomoy National Wildlife Refuge and Cape Cod National Seashore (Fig. 1). Stage Harbor is a semi-enclosed, small, shallow (~4 m deep) embayment that contains sandy beaches where high densities of adult horseshoe crabs spawn, and has subtidal sand flats where a substantial juvenile horseshoe crab population persists (Massachusetts Division of Marine Fisheries, 2010). The harvest of horseshoe crabs is permitted in this area and is usually accomplished by hand from a skiff adjacent to beaches (Massachusetts Division of Marine Fisheries, 2010). Approximately 2 km southeast of Stage Harbor are the federally protected boundaries of the US Fish and Wildlife Service's Monomoy National Wildlife Refuge and the National Park Service's Cape Cod National Seashore. Juvenile horseshoe crabs use the extensive and protected sand bars and tidal flats in the MPA for feeding (Massachusetts Division of Marine Fisheries, 2010; Ridings et al., 2002). The MPA is relatively exposed when compared to the semi-enclosed Stage Harbor and human use is minimal. Horseshoe crabs in the MPA are not vulnerable to harvest.

2.2. Horseshoe crab collection and tagging

We captured horseshoe crabs by hand from the shore on spawning beaches in Stage Harbor and in the MPA (Fig. 1), tagged individuals onsite with uniquely coded acoustic transmitter tags (V9-2L, VEMCO, Bedford, Nova Scotia, Canada) and a uniquely numbered button tag provided by the USFWS's Maryland Fisheries Resource Office, and then released individuals within 10 min of capture. We attached acoustic tags using a system of Velcro adhesive, cyanoacrylate glue, and a glue accelerant (after Brousseau et al., 2004) to the top of the prosoma in a longitudinal furrow (after Moore and Perrin, 2007). We sexed all individuals based on the presence or absence of pedipalps, and recorded prosoma width. We tagged 66 females and 9 males. We targeted female horseshoe crabs for this study since males can remain attached to females for extended periods of time during spawning, such that their movements merely duplicate those of their mates (Brockmann, 2003). However, towards the end of the tagging period, we had difficulty locating female horseshoe crabs; therefore, we also tagged 9 males.

2.3. Fixed acoustic telemetry array

We tracked tagged horseshoe crabs using an acoustic telemetry array consisting of 22 underwater remote autonomous receivers (VR2W, VEMCO) that we deployed on 27–28 May 2010 in Stage Harbor and the MPA (Fig. 1). Moorings for the receivers were created by installing PVC pipes vertically in the middle of large Rubbermaid® storage bins (50.8 × 76.2 cm) filled with cement. Each mooring sat on the ocean floor and was marked with a surface buoy. The receivers were inserted into the PVC pipe and secured with zip-ties, anchored into the mooring on the ocean floor. This apparatus kept the receivers vertical even in high currents to maximize reception radius and allowed for easy removal of the receivers for downloading of data.

We arranged the receivers in a pattern so that it was possible to detect when horseshoe crabs entered or exited Stage Harbor or Nantucket Sound and whether they moved to the west along the south coast of Cape Cod (Fig. 1). We grouped the receivers into three groups based on habitat type and/or management strategy. The first group, consisting of four receivers, was located inside Stage Harbor where low-

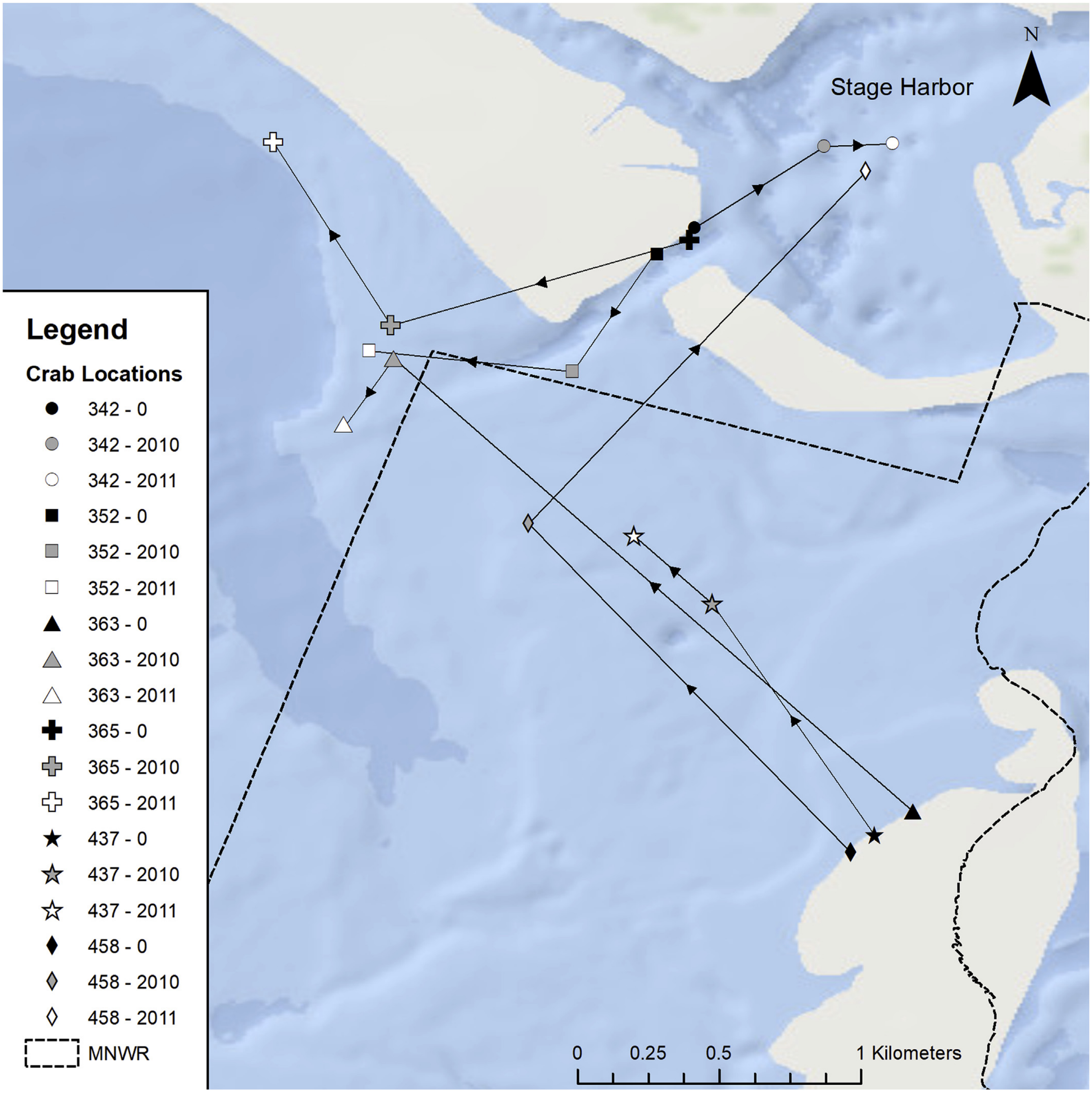

Fig. 2. Example movements by six American horseshoe crabs (*Limulus polyphemus*) near Cape Cod, MA. Three crabs were tagged inside Stage Harbor, and the other three were tagged inside Monomoy National Wildlife Refuge (NMWR – the MPA). Locations are averaged to one location in 2010 and one location in 2011, and movements are shown by the black lines connecting points for an individual crab. In the legend, the first three numbers under Crab Locations refer to each crab's unique ID, and the numbers following the ID denote what each location represents, where 0 is the original tagging location of the crab, 2010 is the average location for 2010, and 2011 is the average location for 2011. Movements shown in this figure do not accurately represent the total movements made by each crab, but rather show the main location used by each crab during each year.

energy, sandy beaches provide horseshoe crab spawning habitat. The second group, consisting of five receivers, was in a high-energy beach outside of Stage Harbor with direct access to Nantucket Sound. Horseshoe crabs in both of these groups were unprotected from harvest. Our third group, consisting of 13 receivers, was located in the sandy tidal flats and spawning beaches of the MPA and just adjacent to the MPA at the edge of the deeper waters of Nantucket Sound. Receivers in Stage Harbor and the MPA differed from the high-energy beach in water depth, water temperature, salinity and wave action. Stage Harbor and MPA receivers were in shallower water (< 1 m at low tide) compared to the high-energy beach (6 m at low tide). The water temperature inside the embayment in Stage Harbor was warmer, with a lower salinity and less wave action than for groups outside of the harbor.

We retrieved the receivers located in the high-energy beach and MPA on 1 December 2010 and redeployed them on 25 April 2011 to minimize loss over the winter. While this procedure had the disadvantage of creating a period during which no data outside of Stage Harbor were collected, horseshoe crabs are less vagile during the winter

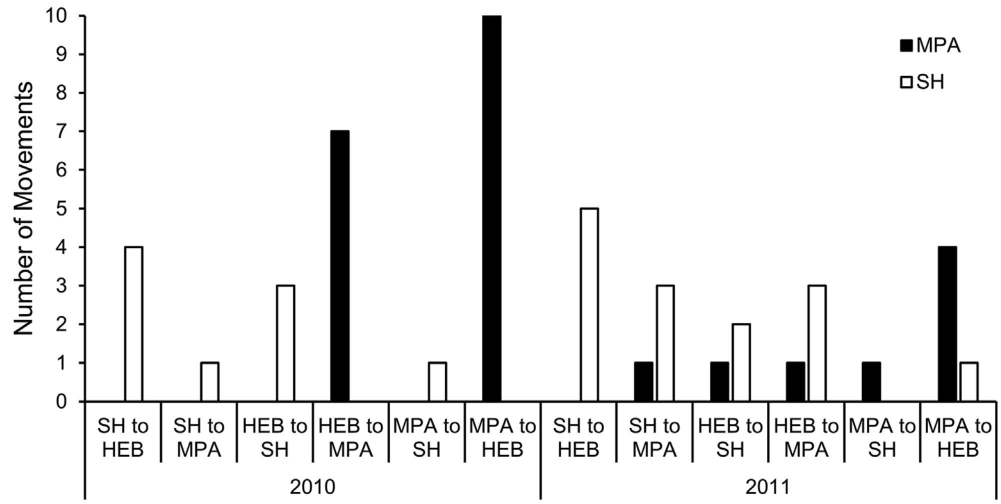

Fig. 3. Number of movements by American horseshoe crabs (*Limulus polyphemus*) between different groups of receivers in 2010 and 2011 for crabs tagged in Stage Harbor (SH – white bars) and the marine protected area (MPA – black bars). Crabs could move between Stage Harbor, the MPA, and the high-energy beach (HEB).

months (Ehlinger et al., 2003; Moore and Perrin, 2007; Schaller et al., 2010) and therefore we considered the loss of data less of a detriment to the study than the loss of a receiver.

2.4. Statistical analyses

We examined the detection data to create a pool of crabs for analysis (Table 1). We removed individuals that were never detected after release, had only a single detection, were active for less than 30 days, or for individuals with > 10,000 detections at a single receiver. For individuals with > 10,000 detections at a single receiver, we assumed that the individual died or the receiver fell off in range of one of our receivers. After filtering out crabs with no data or unusable data, the final sample size was 24 individuals, 12 of which were captured inside Stage Harbor, and 12 captured in the MPA. Twenty of these crabs were female, and the other four were male (Table 1). Detections for these crabs ranged from 11 to 2295 detections per individual, and they were detected at a minimum of 1 and maximum of 17 different receivers. Individuals had detections over a minimum range of 32 days and a maximum of 503 days.

For each crab, we calculated the minimum straight-line distance of all of their detected movements between individual receivers. If a crab was detected by two or more separate receivers within a few minutes, we considered that crab to be halfway between those receivers. We calculated the total straight-line movements for each crab during each month, season, and year for 2010 and 2011. Although we still had three receivers active in Stage Harbor between 1 December 2010 and 25 April 2011, we did not detect any crabs in December through March. We therefore calculated minimum winter movement for each crab as the distance between the location of their last detection in 2010 and their first detection in 2011.

We pooled female and male horseshoe crabs in all analyses due to the small sample size of males. We used three separate analyses to quantify the types, distances, and timing of movements made by horseshoe crabs. First, we examined monthly distance moved. However, these data were highly zero-biased, so we converted monthly distance moved into a binary variable describing whether a crab did or did not move in a month. We used a general linear model with a binomial error distribution in R (package: stats; function: glm; R Core Team, 2016) to quantify movement, with binary distance moved as the dependent variable, and year, month, group of receivers where movement occurred, and tagging location (inside Stage Harbor or the MPA) as independent variables. We could not effectively examine interaction terms in this analysis due to the low sample size.

In our second analysis, we examined distance moved by horseshoe crabs within season using analysis of variance in R (package: stats; function: aov). Our dependent variable was distance moved in a season, and independent variables were season, year, group of receivers where movement occurred, and tagging location. We used Tukey's Honest Significant Difference post hoc test (package: stats; function: TukeyHSD) to explore significant differences in the analysis of variance.

For our final analysis, we examined distance moved by horseshoe crab in one year (2010 or 2011) using analysis of variance. Our dependent variable was distance moved in a year, and independent variables were year, group of receivers where movement occurred, and tagging location. We used Tukey's Honest Significant Difference post hoc test (package: stats; function: TukeyHSD) to explore significant differences in the analysis of variance.

3. Results

American horseshoe crabs generally stayed in the area where they were tagged in June 2010, and then moved towards the edge of Nantucket Sound later in the summer, either along the edge of the MPA or at the high-energy beach (see example locations in Fig. 2). Crabs tagged in the MPA did not move into Stage Harbor in 2010, but crabs tagged in Stage Harbor did move out to the MPA. Almost no horseshoe crabs were detected in the autumn of 2010 (Figs. 4 and 5). The location where horseshoe crabs were first detected in the spring of 2011 was often different from the location where they were last detected in 2010, which led to large estimates of distance moved over the winter. Horseshoe crabs were typically first detected along the high-energy beach or entrance to Stage Harbor in the spring of 2011, then moved into Stage Harbor in May, presumably for spawning. After May, movements were dispersed throughout Stage Harbor, the high-energy beach, and the MPA, regardless of where crabs were originally tagged (Fig. 3). Movements between receivers mostly disappeared after July 2011.

American horseshoe crabs were more likely to move between receivers in May through July than in August through November (Fig. 4B). Monthly movement was also more likely in the MPA (z_{431} = 2.68, p < 0.01) and in the high-energy beach (z_{431} = 1.98, p = 0.047) compared to within Stage Harbor. The location where crabs were tagged did not influence monthly movements (z_{431} = 1.16, p = 0.25).

Horseshoe crab movement varied by season ($F_{3,219}$ = 8.26, p < 0.0001; Fig. 5), where crabs moved less in autumn than in all other seasons (p < 0.02), and also moved more over winter (i.e.,

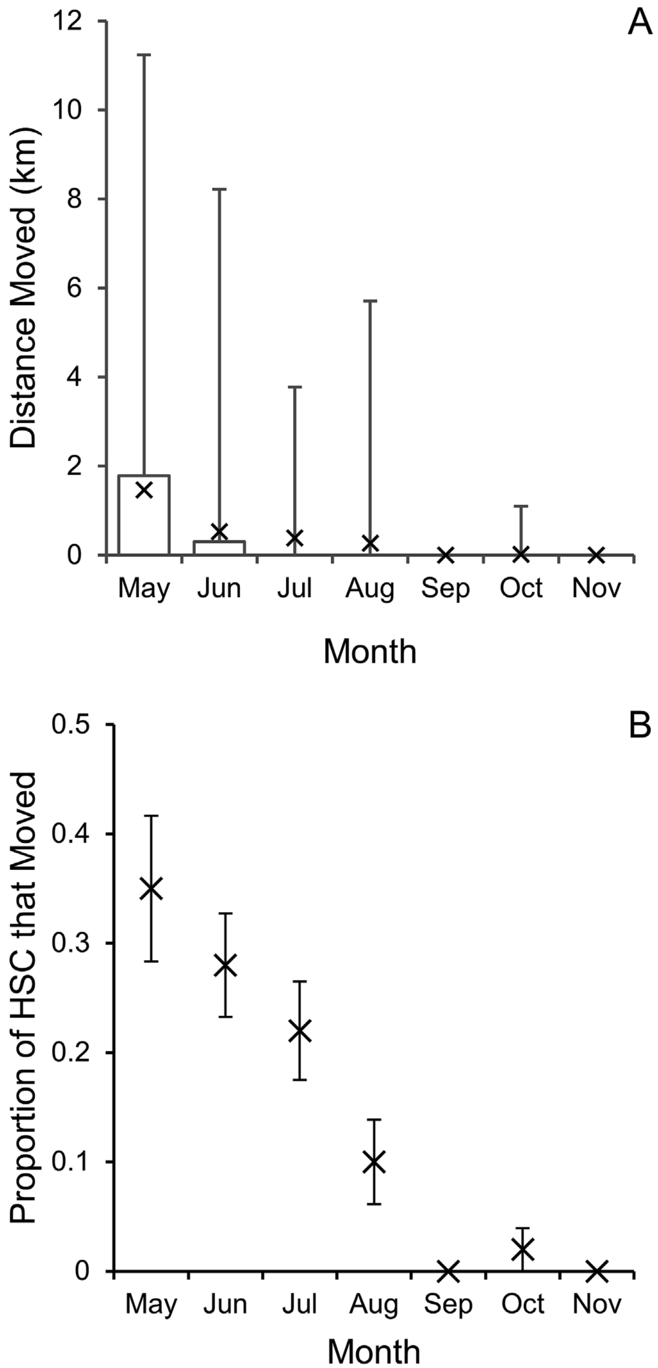

Fig. 4. Distance moved by American horseshoe crabs (HSC) (*Limulus polyphemus*) (A) and the proportion of crabs that moved (B) between May and November. Data are pooled between 2010 and 2011. In A, the line within the box is the median, X is the mean, the box is the interquartile range, and whiskers are the minimum and maximum values. In B, X represent the mean, and whiskers are the standard error around the mean.

between the last detection of 2010 and the first detection of 2011) than in summer ($p = 0.049$). The location where crabs were tagged had no influence on seasonal movement patterns ($F_{4,207} = 0.80$, $p = 0.53$), and seasonal movement did not differ between receiver locations ($F_{3,207} = 0.72$, $p = 0.54$).

Yearly movements for horseshoe crabs were greater in 2011 (mean = 6.0 ± 1.6 km) than in 2010 (3.1 ± 0.5 km) ($F_{1,99} = 4.29$, $p = 0.04$). Yearly movements were also different between receiver locations ($F_{2,99} = 4.37$, $p = 0.02$), where crabs moved more in the MPA per year than they did in either the high-energy beach or in Stage Harbor. The location where crabs were tagged did not affect yearly movements ($F_{1,99} = 0.07$, $p = 0.79$).

4. Discussion

American horseshoe crabs in our study did not show strong site fidelity to either the MPA or Stage Harbor, but rather crabs tended to use both areas. In 2010, crabs tagged in the MPA did not go into Stage Harbor, but in 2011, this pattern disappeared and crabs tagged in the MPA used all habitats. Crabs tagged in Stage Harbor moved through all habitats in both years. The difference between 2010 and 2011 for crabs tagged in the MPA is likely caused by the time of year when the study began. In 2011, most crabs moved into Stage Harbor in May, and began dispersing throughout the MPA after that. If the trend of entering Stage Harbor in May is consistent between years, then we missed this movement in 2010. Crabs did move more and spend more time in the MPA compared to Stage Harbor, but this was consistent for crabs tagged in both locations. This suggests that the MPA does provide some protection for horseshoe crabs; however, all crabs do spend time in areas where they are at risk of being harvested.

Our results show strong seasonal trends in movement by horseshoe crabs. Crabs moved frequently between our receivers in May through July, but we had very few detections from August to November. Although we removed most of the receivers over winter, horseshoe crabs often moved large distances between their last detection of 2010 and their first detection of 2011. Most of this movement likely occurred in the deeper waters of Nantucket Sound since most of the last detections in the autumn and first detections in the spring were on the edge of Nantucket Sound, either at the edge of the MPA or at the high-energy beach. Post-spawning migrations to deeper water have been observed in the mid-Atlantic states (Swan, 2005). These large movements between 2010 and 2011 are likely the result of a large movement in the autumn of 2010 into Nantucket Sound followed by a large movement to spawning beaches in the spring of 2011, rather than continuous small movements over the winter, since American horseshoe crabs are known to reduce movement over the winter (Ehlinger et al., 2003; Moore and Perrin, 2007; Schaller et al., 2010). Acoustic telemetry studies from New England and New Hampshire also found evidence of horseshoe crabs moving to deeper water (James-Pirri, 2010; Schaller et al., 2010; Watson et al., 2009, 2016), with deep water movements occurring following a drop in water temperature (Watson et al., 2016). The month with the greatest movement was May, where crabs moved from the edge of Nantucket Sound into Stage Harbor, and then often moved back out to the MPA. This timing of activity in the spring coincides with post-wintering intertidal habitat use documented in Maine (Moore and Perrin, 2007). Future work in this region should use methods that can assess deep-water movement for a more complete picture of the movement ecology of this species. For example, our estimates of winter movement are likely underestimates. Also, more specific details of the types of deeper water habitats used could be useful for managers.

The results of our straight-line distance analysis are consistent with other tagging studies which show that horseshoe crabs have the ability to move great distances, yet most tend to remain local (Rudloe, 1980; James-Pirri et al., 2005; Swan, 2005; Smith et al., 2006; Moore and Perrin, 2007; James-Pirri, 2010; Schaller et al., 2010). We found that the mean movement was 3.1 km in 2010 and 6.0 km in 2011, but 30% of crabs moved more than 10 km in 2011. This result is similar to movement patterns shown by telemetry in Delaware Bay, where individuals moved more than 5 km within a single spawning season (Smith et al., 2010). In the Taunton Bay Estuary, Maine, no movement was observed between two sub-embayments despite a < 4 km separation (Moore and Perrin, 2007). In Pleasant Bay, Massachusetts, most horseshoe crabs (85%) were detected < 2.5 km from where they were tagged (James-Pirri, 2010). In the Great Bay Estuary, New Hampshire, a majority of tagged horseshoe crabs remained within a 3 km stretch of

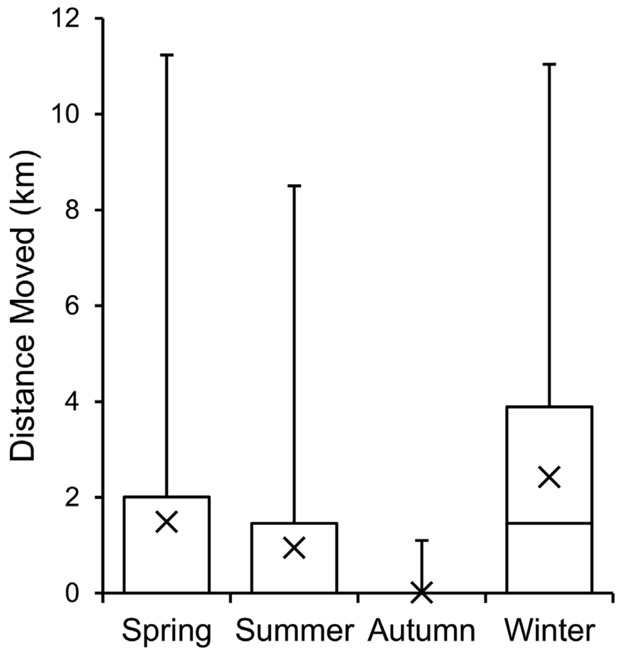

Fig. 5. Distance moved by American horseshoe crabs (*Limulus polyphemus*) in different seasons. The line within the box is the median, X is the mean, the box is the interquartile range, and whiskers are the minimum and maximum values.

estuary (Watson et al., 2009). Horseshoe crabs in our study generally moved farther than crabs in other studies, but still stayed relatively close to their tagging location. However, many of these other studies were in closed embayments where the movement of crabs was limited to a smaller area, whereas in our study, crabs had a much larger area in which to move. This may explain why crabs in our study generally moved farther.

5. Conclusions

This small MPA did protect American horseshoe crabs for part of the year, but given that all crabs spent significant time outside of the MPA, all crabs are also under threat of being harvested. Specifically, all crabs were in the unprotected high energy beach and in Stage Harbor in the spring during the beginning of the mating season, which is also a time when horseshoe crabs are harvested. Fisheries managers can therefore not rely fully on the MPA for protection of this species. Other management measures, such as catch limits or protecting some of the unprotected areas, could also be used to protect this species. Fisheries managers should consider trends in movement and habitat use by this species, such as those that we present in this study, in conjunction with population demographics to successfully manage this species.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2018.06.016.

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