Spatial Ecology of American Horseshoe Crab (Limulus polyphemus) in Chatham, Cape Cod, Ma: Implications for Conservation and Management

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Spatial Ecology of American Horseshoe Crab (*Limulus polyphemus*) in Chatham, Cape Cod, MA:
Implications for Conservation and Management

A Thesis Presented

by

Sarah Elizabeth Dorothea Martinez

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Wildlife and Fisheries Conservation
Spatial Ecology of American Horseshoe Crab (*Limulus polyphemus*) in Chatham, Cape Cod, MA:
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Information regarding spawning site fidelity and movement patterns of the American horseshoe crab (*Limulus polyphemus*) is crucial for developing effective conservation and management strategies on the correct spatial scale. To investigate the spatial ecology of American horseshoe crabs, 75 adult animals were tracked off the coast of Chatham, Cape Cod, MA from June 2010 to November 2011 using acoustic telemetry. 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 a Marine Protected Area (MPA) where harvesting is prohibited. Network analysis revealed that horseshoe crabs exhibited fidelity to spawning habitat, but not necessarily to the habitat where they were initially tagged. Fifty-nine percent of horseshoe crabs tagged inside Stage Harbor were detected in the MPA and 13% of horseshoe crabs tagged in the MPA were detected inside Stage Harbor. Although horseshoe crabs were utilizing both spawning habitats, predictive modeling revealed little temporal overlap, suggesting that horseshoe crabs from the two spawning habitats represent local populations. Isolated and local populations are more susceptible to overexploitation than are larger populations with many migrants. To protect against overharvest and extinction of isolated and local populations, the correct identification of management units (MUs) must be a priority of fisheries managers. Horseshoe crab populations around Cape Cod, Massachusetts and New England behave differently, requiring the collection of more information so that conservation tools such as MUs or MPAs can be used most effectively.
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<tr>
<td>ASMFC</td>
<td>Atlantic States Marine Fisheries Commission</td>
</tr>
<tr>
<td>CCNS</td>
<td>Cape Cod National Seashore</td>
</tr>
<tr>
<td>EEZ</td>
<td>Exclusive Economic Zone</td>
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<tr>
<td>GLMM</td>
<td>Generalized Linear Mixed Model</td>
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<tr>
<td>ISFMP</td>
<td>Interstate Fishery Management Plan</td>
</tr>
<tr>
<td>LAL</td>
<td><em>Limulus</em> Amebocyte Lysate</td>
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<tr>
<td>MADMF</td>
<td>Massachusetts Division of Marine Fisheries</td>
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<tr>
<td>MNWR</td>
<td>Monomoy National Wildlife Refuge</td>
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<tr>
<td>MPA</td>
<td>Marine Protected Area</td>
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<td>MU</td>
<td>Management Unit</td>
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CHAPTER 1

GENERAL INTRODUCTION

The American horseshoe crab (*Limulus polyphemus*) is the only extant arthropod in the family Limulidae and ranges from the Northern Gulf of Maine to the Gulf of Mexico (Widener and Barlow 1999; Pierce et al. 2000). Horseshoe crabs are typically found inshore, although animals have been located in > 200 m of water (Botton and Haskin 1984; Botton and Ropes 1987). Horseshoe crabs are most abundant in the middle of their geographic range, from Virginia to New Jersey, and 90% of horseshoe crabs in this area are captured in < 30 m of water (Botton and Ropes 1987). Delaware Bay contains the largest known population of horseshoe crabs (Widener and Barlow 1999; Pierce et al. 2000). Microsatellite DNA analysis indicated distinct horseshoe crab populations with the most variation occurring between a north (Georgia northward) and a south (Florida south into the Gulf of Mexico) population (Saunders et al. 1986). Genetic analysis on mitochondrial DNA has confirmed that Delaware Bay horseshoe crabs and upper Chesapeake Bay horseshoe crabs are genetically distinct, suggesting little gene flow and the possibility that animals remain resident in upper Chesapeake Bay (Pierce et al. 2000). King et al. (2005) performed analysis on 14 different microsatellite loci and identified four distinct “units”: a Gulf of Maine unit, a mid-Atlantic unit, an Atlantic Florida unit and a Gulf Florida unit.

In mid- to late spring, horseshoe crabs convene on sandy beaches to spawn (Rudloe 1980; Cohen and Brockmann 1983; Brockmann 1990; Penn and Brockmann 1994). Factors possibly contributing to the onset of horseshoe crab spawning include increases in duration of daily sunlight, water temperature and tidal height (Barlow et al. 1986) and wind direction and speed as it influences tide and wave height (Smith et al. 2002; Brockmann and Johnson 2011). As the tide floods, males arrive first and move parallel to the shoreline, intercepting and attaching themselves to females moving towards the shore, forming mating pairs (Rudloe 1980). The female then digs a nest and deposits eggs (Cavanaugh 1975). The attached male releases sperm, resulting in the external fertilization of the eggs (Cavanaugh 1975). Eggs are laid just above the mean high tide.
the area that is believed to minimize desiccation and predation, and maximize oxygen levels thereby optimizing egg development and survival (Rudloe 1980; Penn and Brockmann 1994). Horseshoe crabs tend to spawn around new and full moons on flood tides (Barlow et al. 1986; Smith et al. 2002), and spawning appears to be both nocturnal (Rudloe 1980) and diurnal (Cohen and Brockmann 1983) depending on regional location. Males are more prevalent than females during spawning events, assuring a mate and thus a successful egg-laying for each female per spawning event (Rudloe 1980; Cohen and Brockmann 1983; Barlow et al. 1986). Although some females do return to spawn multiple times during the spawning season, males’ return rates to spawning beaches are much higher (Rudloe 1980), suggesting that only a portion of females spawn during any spawning event (Cohen and Brockmann 1983). Since males are more abundant, some males will remain unattached throughout the spawning event (Brockmann 1990). However, these satellite males still release sperm near mating pairs in a nest (Barlow et al. 1986) or release sperm in nests that are already vacated (Cohen and Brockmann 1983, Brockmann 1990). As the tide ebbs, spawning pairs and satellite males leave the beach and their eggs.

The timing of emergence from the eggs has been attributed to many factors including water temperature, lunar cycle, time of day, tide height and salinity levels (Botton and Loveland 2003). After 2-4 weeks the eggs hatch and the animals enter the water column as weakly swimming larvae, where they remain for 7-10 days before settling to the benthos (Pierce et al. 2000; Burton et al. 2009; Botton et al. 2010). Post-settling larval behavior is poorly understood, although it is believed there may be up to 18 instars between the egg and adult life phase (Carmichael et al. 2003). Relative to larval behavior, more information exists on the behavior of juvenile or sub-adults (Rudloe 1981). It takes 8-10 years for a horseshoe crab to reach sexual maturity (Wall et al. 2002), yet little is known regarding where horseshoe crabs spend most of their time during this period. Post-settlement larvae stay close to the sandy beaches where they were spawned (Botton et al. 2003), but juvenile horseshoe crabs can be present in silty, anoxic estuarine salt marshes (S. Martinez, personal observation).
Horseshoe crabs and their eggs play an essential role in marine and estuarine ecosystems. Horseshoe crab eggs sustain many species of shorebirds at stopover locations along their northward migrations (Castro and Myers 1993), including sanderlings, *Calidris alba* (Castro et al. 1989), red knots, *Calidris canutus* (Karpanty et al. 2006), and ruddy turnstones, *Arenaria interprets* (Tsipoura and Burger 1999), in addition to many other shorebird species (for a complete list see Walls et al. 2002, pg. 46). Furthermore, many crustaceans and fish feed on horseshoe crab eggs, larvae and young juveniles (Walls et al. 2002). The endangered loggerhead sea turtle (*Caretta caretta*) has also been documented to eat adult horseshoe crabs (Walls et al. 2002) as do gulls, *Larus* spp. (Botton and Loveland 1993). Based on stomach contents analysis, horseshoe crabs act as predators in the near-shore food web, feeding upon other arthropods, polychaetes and bivalves (Botton 1984a; for a complete list, see Botton and Haskin 1984, pg. 387). Diet composition using stable isotope signatures showed selection for polychaete and molluscan prey types (Botton and Haskin 1984; Carmichael et al. 2004). While foraging for infaunal organisms, horseshoe crabs disturb the sediment, recycling nutrients for filter feeders, small fish and other invertebrates (Botton 1984b; Kraeuter and Fegley 1994). However, the ecological value of the horseshoe crab as a prey item, predator and sediment disturber in the littoral zone can be overshadowed by its role in several economies.

The American horseshoe crab resource supports the economy of many commercial industries. The unique body shape, prehistoric nature and spectacular mating aggregations of the horseshoe crab (Rudloe 1980) draw wildlife and birding enthusiasts to the coastline, enhancing tourism-based local economies (Walls et al. 2002). Horseshoe crabs are the preferential bait used in the conch, *Busycon* spp., and American eel, *Anguilla rostrata*, pot fisheries (Shuster and Botton 1985; Botton and Ropes 1987; Berkson and Shuster 1999) and are a supplemental resource for bait dealers and draggers, and the primary source of income for fishers in Massachusetts (MADMF 2010). Besides supporting several fisheries, horseshoe crabs sustain a multi-million dollar biomedical bleeding company located in Falmouth, Cape Cod, MA. This
company supplies hundreds of people with employment and also produces the life-saving extract *Limulus* Amebocyte Lysate (LAL), which is used worldwide to detect endotoxins in virtually all medical products injected or implanted into humans (Pearson and Weary 1980). LAL can also be used to detect endotoxins in seawater, sediments, drinking water, the air and food (Novitsky 2009). Unlike the bait industry where crab mortality is 100%, bled crabs are returned to the water after the bleeding process, and are believed to experience a mortality of 8-30% (Walls and Berkson 2000; Kurz and James-Pirri 2002; Rutecki et al. 2004; Leschen and Correia 2010).

Horseshoe crabs are the subject of many scientific studies associated with cell biology, immunology, biochemistry and the development of pharmaceuticals (Barlow et al. 1986; Rutecki et al. 2004). Most scientific studies focus on the horseshoe crab’s large optic nerve (Barlow et al. 1977; Barlow et al. 1986) or other aspects of neurophysiology (Watson et al. 2008; Chabot and Watson 2010; Wyse 2010). The American horseshoe crab is a heavily utilized resource and a possible keystone species whose populations must be properly conserved to ensure the sustainability of the resource and the persistence of the species.

American horseshoe crabs from the Delaware Bay have been utilized since the 1870s as a natural fertilizer and livestock feed (Berkson and Shuster 1999). Up to four million horseshoe crabs were harvested per year until the 1950s and 1960s when commercial horseshoe crab harvest was minimal as competition with commercial fertilizer producers increased (Berkson and Shuster 1999). The Delaware Bay population saw increases in horseshoe crab abundance and density for several decades. However in the 1990s, as the international demand for American eel and conch species increased, so did a need for horseshoe crabs as bait; horseshoe crab landings in the Delaware Bay doubled from 1995 to 1997 (HCTC 1998). Horseshoe crabs were aggressively harvested during this period and population declines became evident in the Delaware Bay (ASMFC 1998). Therefore in 1998, the Atlantic States Marine Fisheries Commission (ASMFC) instituted an Interstate Fishery Management Plan (ISFMP) to “conserve and protect the horseshoe crab resource to maintain sustainable levels of spawning stock biomass to ensure its continued
role in the ecology of coastal ecosystems, while providing for continued use over time” (ASMFC 1998).

The ISFMP focused mainly on the Delaware Bay region and resulted in stricter management of the horseshoe crab resource in that area. However, decreased harvest quotas in the Delaware Bay region may have redirected harvest efforts to New England and harvest quotas in this region may not be sustainable (ASMFC 2011). Each state on the Atlantic Coast is responsible for implementing sustainable regulations (ASMFC 1998; see MADMF 2010 for Massachusetts horseshoe crab regulations). Massachusetts horseshoe crabs are currently managed as one stock or management unit (MU) but horseshoe crab population studies from New England have found evidence of localized or isolated populations within specific embayments (Baptist et al. 1957; Widener and Barlow 1999; James Pirri et al. 2005; Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010). Therefore, the horseshoe crab resource in Massachusetts may not be one stock. Additionally, laboratory experiments determined that larval and juvenile dispersal between embayments is also limited (Botton and Loveland 2003; Botton et al. 2010).

If larval, juvenile and adult dispersal is low, and evidence continues to strengthen the claim that New England horseshoe crab populations are localized or isolated within an embayment or area, the annual quota set by MADMF may require revisions to more appropriate management units (Moore and Perrin 2007; Smith et al. 2009; James-Pirri 2010), especially if harvesting pressures are unevenly distributed. Unfortunately, information regarding movement patterns between spawning habitats, spawning site fidelity to an embayment or beach, and horseshoe crab seasonal habitat use in Massachusetts is limited (Baptist et al. 1957; Widener and Barlow 1999; James-Pirri et al. 2005; James-Pirri 2010). This knowledge is crucial to effective management and conservation (Schaller et al. 2010), especially if spatially-explicit tools, such as marine protected areas are used to reduce harvests (Jennings et al. 2001). A marine protected area (MPA) is an area where harvesting of one or more species is prohibited with several important conservation benefits including the protection of spawning stocks, the provisioning of
recruits, the protection of genetic diversity and the enhancement of catches in adjacent unprotected areas (Roberts and Polunin 1993). MPAs are becoming a popular tool for conserving marine species as they protect a proportion of individuals from overharvesting and maintain biodiversity, yet their effectiveness depends on the life history characteristics and population dynamics (e.g. the rate of movement) of the target species (Jennings et al. 2001). Depending on the movement and migration patterns of the American horseshoe crab, the implementation of an MPA could provide a source of adults and recruits, proving to be a useful management tool in conserving stocks in Massachusetts, especially if combined with other regulations such as quotas or effort and gear restrictions. Given the spatially-explicit nature of MPAs, understanding the localized movements of horseshoe crabs is critical for the MPAs design and management (Jennings et al. 2001).

The movement patterns of horseshoe crabs have been assessed via the use of uniquely numbered button tags provided by the US Fish and Wildlife Service’s Maryland Fisheries Resource Office (see James-Pirri 2010). While this tagging program creates the opportunity for the community to get involved with horseshoe crab conservation, there are some limitations when compared to acoustic telemetry techniques. The recapture rate for button tagged horseshoe crabs is much lower than that of acoustically tagged animals, even if a substantially larger amount of animals are button tagged (S. Martinez, personal observation). Recaptures are crucial for creating data for button tagged individuals and nothing can be assumed regarding the animal’s movement patterns in between recapture locations.

With acoustic telemetry, animals need not be recaptured and can be detected passively and continuously (Freire and Gonzalez-Gurriaran 1998) in habitats where movement data would be hard to obtain otherwise, like offshore (Brousseau et al. 2004). Acoustic telemetry techniques were employed in this study as they have successfully elucidated movement patterns in many benthic marine arthropods (Stone and O’Clair 2001; Golet et al. 2006; Holsman et al. 2006; Clark et al. 1999) including horseshoe crabs (Kurz and James-Pirri 2002; Brousseau et al. 2004; Moore
Acoustic telemetry is becoming an increasingly popular tool (Cooke 2008) that permits the tracking of individuals on a variety of spatial and temporal scales (Millspaugh and Marzluff 2001) as the location of receivers and rate of transmission can be set by the researcher.

The goal of my research was to use acoustic telemetry to quantify the movement patterns, spawning site fidelity, and seasonal habitat use of mature horseshoe crabs between two areas with differing commercial harvesting pressures off the coast of Chatham, Cape Cod, MA. The coast of Chatham consists of Stage Harbor, a small, shallow (~4 m deep), semi-enclosed embayment with an active spawning beach where the harvest of horseshoe crabs is permitted (Figure 1). Only 2.0 km from the mouth of Stage Harbor is an MPA consisting of the federally protected boundaries of Cape Cod National Seashore (CCNS) and Monomoy National Wildlife Refuge (MNWR). These protected areas were established to provide and protect core habitat for migratory birds and consist of major horseshoe crab spawning habitat and juvenile horseshoe crab nursery habitat (MADMF 2010). CCNS and MNWR consist of comparatively exposed spawning beaches where human use is minimal. One group of horseshoe crabs was tagged inside Stage Harbor, the other group was tagged within the MPA. Specifically, I wanted to determine if horseshoe crabs in this area belonged to one large panmictic population, two isolated populations or local populations with some degree of connectivity.

In Chapter 2 of this thesis, I present my research which employed the use of acoustic telemetry to 1) examine the degree of adult horseshoe crab movement into and out of Stage Harbor to determine if horseshoe crabs exhibit site fidelity to this embayment throughout the year, or whether offshore migrations were occurring; 2) explore the degree of movement between the unprotected Stage Harbor and MPA, as this information will elucidate the degree of connectivity of the two spawning habitats and thus the effectiveness of the MPAs; 3) quantify how many horseshoe crabs returned to spawning beaches the following spring to further explore spawning site fidelity in consecutive years, which will act as a gauge for what percentage of
females spawn every year and 4) predict (via the use of predictive models based on the acoustic telemetry data) when these migration events were most likely to occur, if at all. Acoustic telemetry proved to be a valuable tool for determining if horseshoe crabs are exhibiting strong embayment fidelity as has been shown by other studies in New England (Baptist et al. 1957; Widener and Barlow 1999; Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010). Acoustic telemetry was also useful in determining the movement patterns between Stage Harbor and the MPAs. The two areas are approximately 2.0 km apart, a reasonable distance for horseshoe crabs to travel (James-Pirri et al. 2005; Watson et al. 2009). Therefore, I expected horseshoe crabs from either area to be detected in the adjacent area. The animals’ acoustic transmitters (tags) lasted for longer than the duration of the study, making it possible to distinguish when horseshoe crabs were no longer detected on the array (presumably leaving the spawning area) and when they returned to the array, presumably to spawn the following spring.

The implications of these results are discussed in Chapter 3. I provide suggestions on how the management and conservation efforts of this animal may be improved, recommendations for future research of the species, and examples of the benefits of conservations tools such as MUs and MPAs.
CHAPTER 2

SPATIAL ECOLOGY OF AMERICAN HORSESHOE CRAB (*LIMULUS POLYPHEMUS*) IN CHATHAM, CAPE COD, MA: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Introduction

Evidence of localized horseshoe crab population declines throughout their range (ASMFC 1998; Widener and Barlow 1999; Smith et al. 2009; ASMFC 2011) prompted the Atlantic States Marine Fisheries Commission (ASMFC) to institute an Interstate Fishery Management Plan (ISFMP) in 1998. The ISFMP requires each state on the Atlantic Coast to implement regulations to sustain horseshoe crab populations, identify critical spawning and juvenile habitat, and execute monitoring of horseshoe crab populations (ASMFC 1998). Massachusetts horseshoe crab harvest is regulated (see MADMF 2010) by the Massachusetts Division of Marine Fisheries (MADMF) and horseshoe crabs are currently managed as one stock or management unit (MU) that is subject to an annual state-wide quota of 165,000 crabs (MADMF, 2010). However, studies indicate that horseshoe crabs in New England do not comprise one stock, but rather localized or isolated populations that are specific to coastal embayments (Baptist et al. 1957; Widener and Barlow 1999; James-Pirri et al. 2005; Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010).

Conventional tagging studies in New England observed little evidence that horseshoe crabs leave the embayment where they spawn (Baptist et al. 1957; James-Pirri et al. 2005). In Plum Island Sound, MA, horseshoe crabs were discovered inside the sound in every month but January and February when sampling did not occur (Baptist et al. 1957). Although crabs were found to make ocean-ward migrations in September, only 32 of 1,780 tagged crabs were ever located outside of the sound, implying that Plum Island Sound contains a localized horseshoe crab population (Baptist et al. 1957). James-Pirri et al. (2005) used external button tags to individually mark almost 8,000 horseshoe crabs in four embayments around Cape Cod, MA.
This was the first study to find evidence supporting localized populations in Cape Cod waters; 70% of recaptured horseshoe crabs traveled < 2 km from where they were originally tagged.

In addition to conventional tagging, acoustic telemetry techniques have been used to explore horseshoe crab spatial ecology and movement patterns in New England. In the Taunton Bay Estuary, ME, no movement was observed between two sub-embayments despite a < 4-km separation, nor was there any evidence of horseshoe crabs exiting the embayment (Moore and Perrin 2007). Moore and Perrin (2007) were the first to quantify seasonal variability in movement patterns via the use of acoustic telemetry and classified a distinct wintering phase in horseshoe crabs. In Pleasant Bay, Cape Cod, MA, 55 spawning females were tracked and half of the tagged horseshoe crabs were relocated at the same beach where they were initially tagged (James-Pirri 2010). Most individuals (85%) were detected < 2.5 km from where they were tagged, and there was no evidence that crabs exited Pleasant Bay (James-Pirri 2010). Twenty-seven horseshoe crabs were tagged and tracked in the Great Bay Estuary in New Hampshire to gain insight into both small- and large-scale movement patterns of horseshoe crabs and it was observed that a majority of the horseshoe crabs in this study remained within a 3 km stretch of estuary (Watson et al. 2009). Schaller et al. (2010) tracked 37 adult horseshoe crabs in the Great Bay Estuary and discovered interesting patterns in up-estuary, down-estuary migrations for spawning purposes, but no horseshoe crabs were detected outside the estuary. Regardless of the tagging method, studies have consistently indicated that New England horseshoe crab populations are isolated or localized (Baptist et al. 1957; Botton and Ropes 1987; Widener and Barlow 1999; Kurz and James-Pirri 2002; Moore and Perrin 2007; James-Pirri et al. 2005; James-Pirri 2010; Schaller et al. 2010).

Since larval and juvenile dispersal is low (Botton and Loveland 2003; Botton et al. 2010), and evidence continues to promote that New England horseshoe crab populations are localized or isolated within an embayment, the current consideration of Massachusetts horseshoe crabs as one MU subject to one annual quota could result in harvest rates that are too high and
may lead to overharvest or extinction of local populations (Allendorf and Luikart 2007). The correct delineation of MUs is necessary for the proper short-term management of a species (Moritz 1994) and should be a priority for fisheries managers, especially considering the horseshoe crabs’ ecosystem services (Castro and Myers 1993; Kraeuter and Fegley 1994; Walls et al., 2002;), the many stakeholders involved (Berkson and Shuster 1999; Novitsky 2009), and evidence of anecdotal and empirical declines throughout the state (Widener and Barlow 1999; Smith et al. 2009; ASMFC 2011). However, the identification of MUs depends on several factors, including genetics, geography, habitat type, morphology, behavior, socioeconomic factors and life history characteristics (Moritz et al. 1995). Information regarding movement patterns between spawning habitats, spawning site fidelity to an embayment or beach, and horseshoe crab seasonal habitat use in Massachusetts is limited (Baptist et al. 1957; Widener and Barlow 1999; James-Pirri et al. 2005; James-Pirri 2010); more data exploring these life history characteristics is crucial to effective management and conservation (Jennings et al. 2001; Schaller et al. 2010).

The goal of my research was to use acoustic telemetry to quantify the movement patterns, spawning site fidelity, and seasonal habitat use of mature horseshoe crabs within and between two areas with differing commercial harvesting pressures off the coast of Chatham, Cape Cod, MA. Specifically, I wanted to determine if horseshoe crabs from the two areas belonged to one large panmictic population, two isolated populations or local populations with some degree of connectivity.

**Methods**

Adult horseshoe crabs (n=75) were tracked passively using acoustic telemetry from June 2010 to November 2011 off the coast of Chatham, Cape Cod, MA. One group of horseshoe crabs (n=40) was tagged inside Stage Harbor, 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 (MADMF 2010). The
harvest of horseshoe crabs is permitted in this area and for the duration of this manuscript, these horseshoe crabs will be termed “unprotected” (Figure 1). Stage Harbor has a high level of human disturbance and exits to Nantucket Sound, which is largely unprotected from harvest as well. The other group of horseshoe crabs \((n=35)\) was tagged ~2.0 km to the south and east of the mouth of Stage Harbor within a Marine Protected Area (MPA) consisting of the federally protected boundaries of the US Fish and Wildlife Service’s Monomoy National Wildlife Refuge (MNWR; \(n=21\)) and the National Park Service’s Cape Cod National Seashore (CCNS; \(n=14\)). These wildlife refuges were established to provide and protect core habitat for migratory birds and consist of major horseshoe crab spawning habitat, along with a high density of juvenile horseshoe crabs on the tidal flats (Ridings et al., 2002; MADMF, 2010). Horseshoe crabs spawning in MNWR and CCNS are not vulnerable to harvest and for the duration of this manuscript will be collectively termed “protected”. These MPAs are relatively open when compared to Stage Harbor and human use is minimal (Figure 1).

Horseshoe crabs were captured by hand from the shore, tagged onsite and then released within ten minutes. Tagged horseshoe crabs were outfitted with uniquely coded acoustic transmitter tags (V9-2L; 29x 9mm diam; 4.7 grams dry; est. battery life of 738 d; VEMCO, Shad Bay, Nova Scotia, Canada). Acoustic tags were attached using a system of Velcro adhesive, cyanoacrylate glue and a glue accelerant (after Brousseau et al. 2004) to the top of the carapace in a longitudinal furrow (after Moore and Perrin 2007; Figure 2). In most cases, the attachment site needed to be cleared of epibionts using a handheld drill. All acoustic tags were confirmed as operational before attachment took place. Study animals were also tagged with a uniquely numbered button tag provided by the USFWS’s Maryland Fisheries Resource Office (Figure 2). Button tags are used throughout the eastern seaboard and, unlike the acoustic tags, provide a phone number that the public could call to report the location and condition of the animal. All horseshoe crabs were sexed based on the presence or absence of pedipalps and measured across the prosoma. Female horseshoe crabs were targeted 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, female horseshoe crabs could no longer be located. Therefore, the last nine animals tagged were males.

Horseshoe crabs were tracked using a telemetry array consisting of 22 underwater remote autonomous receivers (VR2W, VEMCO, Shad Bay, Nova Scotia, Canada) that were deployed on 27-28 May 2010 in Nantucket Sound, in and outside of Stage Harbor and to the south along South Monomoy. Moorings for the receivers were created by MADMF by installing PVC pipes in the middle of large Rubbermaid® storage bins (50.8 x 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.

The receivers were arranged in a pattern so that it was possible to detect when horseshoe crabs entered or exited Stage Harbor or Nantucket Sound, whether they traveled to the southern end of Monomoy, and whether they moved to the west along the south coast of Cape Cod (Figure 3). Receivers were grouped to create nodes, each representing a different habitat type and/or management strategy. Node 1 is comprised of three receivers located inside Stage Harbor where low energy, sandy beaches provide horseshoe crab spawning habitat (Figure 3). Node 2 consists of five receivers and represents a high energy beach outside of Stage Harbor (Figure 3). Horseshoe crabs in Nodes 1 and 2 are unprotected from harvest. Node 3 is made up of seven receivers and incorporates the sandy tidal flats of protected MNWR and CCNS (Figure 3). Node 4 is also protected from horseshoe crab harvest and consists of six receivers that run along the high energy barrier beach of South Monomoy (Figure 3). When horseshoe crabs were outside of the array, or before they were tagged and thus outside of the array, they were considered to be in Node 0. Nodes 1 and 3 differ from Nodes 2 and 4 not just in habitat type and management
regime, but also in water depth, water temperature, salinity and wave action. Nodes 1 and 3 were in shallower water (<1 m at low tide) compared to Nodes 2 and 4 (6 m at low tide). The water temperature inside the embayment in Node 1 is warmer, with a lower salinity and less wave action than nodes outside of the harbor.

The detection limit of each receiver was tested in September 2011 by crisscrossing each receiver in the cardinal directions with a test tag and recording the time and distance from the receiver. When the horseshoe crab’s transmitter emits an acoustic signal while the individual is within range of the receiver (300-700 m, depending on bathymetry), the receiver records the signal. Recorded transmitter data were retrieved and downloaded approximately once every 2 months using a portable handheld computer. Receivers located in highly dynamic areas were retrieved on 1 December 2010 and redeployed 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 months (Ehlinger et al. 2003; Moore and Perrin 2007; Schaller et al. 2010) and therefore the loss of data was considered less of a detriment to the study than the loss of a receiver.

Data Analysis

Acoustic telemetry arrays, especially those examining slower moving animals, can record hundreds of thousands of detections but some detections may not be representative of actual animal movements and must therefore be discarded. To remove transient effects of tagging, four horseshoe crabs were eliminated from any analyses as these animals were only detected within 36 h of tagging. Additionally, three horseshoe crabs were eliminated from analyses because they had >35,000 consecutive detections at one receiver (i.e., the horseshoe crabs had died or that the tag had become detached from the animal within the detection range of the receiver). Ten individuals were never detected after being tagged. In order to more clearly represent the amount of time spent in specific areas and to ensure the independence of all samples, detections for each horseshoe crab were consolidated to yield one location per day (referred to as a daily detection
throughout the rest of the manuscript; see James-Pirri 2010 and Schaller et al. 2010). Fifty-eight horseshoe crabs were available for analyses (horseshoe crabs initially tagged inside Stage Harbor (n=34); horseshoe crabs initially tagged in the MPA (n=24)). No analyses were run separately for male horseshoe crabs (n=9) in this study. Males can remain attached to females for extended periods of time during spawning and the small sample size made robust analyses complicated. Therefore, male horseshoe crabs were incorporated into all analyses with females.

The data obtained in acoustic telemetry arrays traditionally evaluate the presence or absence of the animal and, while presence-absence data have important management and conservation implications, the question of how tagged animals move within and between habitat patches or local populations is not addressed (Urban and Keitt 2001). The use of flow matrices to create movement networks allows researchers to explore spatial dynamics of large, often cumbersome data sets collected by acoustic telemetry arrays (Jacoby et al. 2012). To accurately perform this network analysis, all movements of horseshoe crabs had to be accounted for, including those that were only assumed. For instance, a particular horseshoe crab was only detected once in Node 2 two days after it had been tagged in Node 1. The tagging event was considered one movement into the system (Node 0 to Node 1 on Day 14 of the study). The crab was only detected in Node 2 on Day 16 of the study, however, the crab must have moved from Node 1 to Node 2. An “assumed movement” occurring on the day halfway between the tagging event and the day of the first actual detection was added to the data. This process created more accurate flow matrices; instead of this animal being eliminated from network analysis as it only contained a single daily detection and thus no movements, this crab was more accurately classified as moving into the system, then moving from Node 1 to Node 2, then moving from Node 2 out of the array to Node 0. Assumed movements are included as daily detections throughout the remainder of this manuscript.

In addition to grouping detections spatially via nodes, detections were also grouped temporally by season (after Schaller et al. 2010). The months of April, May and June were
considered spawning season and will be termed spring throughout the duration of the manuscript. July-August and September-November were considered summer and fall, respectively; these seasons will be collectively referred to as post-spawning periods. Winter ranged from December to March.

The straight-line distance a horseshoe crab traveled was calculated to determine how far horseshoe crabs moved from their initial tagging location. This movement information provides data relevant to understanding spawning site fidelity. Straight-line distances were calculated by measuring the distances between receivers where horseshoe crabs were detected since we could not identify exactly where the horseshoe crab was within the range of the receiver.

The probability of horseshoe crab movement was projected over the course of the study using the predictive power of generalized linear models (GLMs) with a binomial distribution (see Zuur et al. 2009), as movement events were considered 0-1 data (either a movement event did occur [1] or did not occur [0]). Generalized linear models assume that observations are not correlated and since the observational unit of daily detections should be highly correlated within the same individual, I decided to use generalized linear mixed models (GLMMs) to account for this nested structure. All GLMMs were performed in R using the lme4 library (R Development Core Team 2012). With movement event as the dependent variable, explanatory variables (fixed effects) included Day of the Study, Day of the Year, Day of the Year squared, Season, Day since last detection, Year (either 2010 or 2011) and the crab’s node location treated as a factor. All Day variables were centered on the mean. Each individual crab was treated as the random effect of the model. The best model was chosen using a comparison of Akaike’s Information Criterion. Separate GLMMs were run for both initial tagging locations.

**Results**

Horseshoe crabs were tracked passively on receivers from date of tagging (4-30 June 2010) until 28 November 2011 (end of study). Sixty-five out of 75 horseshoe crabs tagged in this study were detected again at least once (87% recapture rate). Before the removal of certain individuals
for reasons listed above (see Data Analysis section), the tracked horseshoe crabs \((n=65)\) logged 286,448 detections. After data screening, the study horseshoe crabs \((n=58)\) logged 35,330 detections, which were consolidated to 692 daily detections. The number of days that tagged horseshoe crabs (mean and \(SD\) prosomal width: females, 248 ± 20 mm; males, 187 ± 14 mm) spent at large (date of tagging to date of last detection) in the array was highly variable (mean and \(SD\): 147 ± 173.23 days, range 1-530 days). Horseshoe crabs that were tagged inside Stage Harbor in the unprotected area were detected more frequently than horseshoe crabs tagged in the adjacent MPA (27,501 and 7,829 detections, respectively) and were also detected on more days (478 and 214 daily detections respectively; Table 1).

**Spawning Site Fidelity**

Horseshoe crabs exhibited spawning site fidelity to spawning habitat (Nodes 1 and 3) but were not necessarily loyal to the spawning habitat where they were initially tagged. The study horseshoe crabs that were tagged inside Stage Harbor \((n=34)\) spent more time inside Stage Harbor (Node 1; 330 daily detections). However, 59% \((n=20)\) of these individuals exited Stage Harbor and most of those crabs \((n=13)\) entered the protected spawning habitat (Node 3) for a total of 68 daily detections (Table 2). The horseshoe crabs that were tagged in spawning habitat within the MPA \((n=24)\) spent more days within range of that spawning habitat (Node 3; 116 daily detections; Table 3). Even though 71% \((n=17)\) of horseshoe crabs tagged in the MPA moved into the unprotected area, few \((n=3)\) animals entered the spawning habitat inside Stage Harbor (Node 1), only spending 16 days within this habitat (Table 3).

Most (82%) of horseshoe crabs that were tagged inside Stage Harbor were detected within 3.0 km from where they were tagged yet some long distance movement patterns were observed. Crab ID 347 traveled the maximum distance for this group, moving 17.33 km in 2010 and 10.66 km in 2011. The average linear distance traveled for horseshoe crabs tagged inside Stage Harbor was 2.2 km and 7.3 km for 2010 and 2011, respectively. When compared to horseshoe crabs tagged inside Stage Harbor, horseshoe crabs tagged in the MPA were more vagile during 2010 but less
vagile during 2011, moving 4.3 and 4.0 km, respectively. Crab ID 363 traveled the maximum distance for horseshoe crabs tagged in the MPA, moving 21.31 km over the study period; 5.1 km in 2010 and 16.21 km in 2011. In 2010, more than half (54%) of horseshoe crabs tagged in the MPA traveled < 4.5 km from the spawning habitat where they were tagged. A linear regression revealed no correlation between prosomal width and distance traveled for either group ($R^2=0.016$ for horseshoe crabs tagged inside Stage Harbor and $R^2=0.052$ for horseshoe crabs tagged in the MPA).

Proportional flow matrices confirmed that horseshoe crabs were likely to remain within spawning habitat once they were located within this habitat. There was an 89% probability that a horseshoe crab would be detected inside Stage Harbor if the animal’s last daily detection was inside Stage Harbor and an 80% chance that horseshoe crabs tagged inside Stage Harbor would be detected in the protected spawning habitat if their last daily detection was in the protected habitat (Table 4a). Horseshoe crabs tagged inside Stage Harbor were unlikely to move from Node 1 directly to Node 3 (2.4% probability) and no crabs from this group moved from Node 3 directly to Node 1 (Table 4a). For horseshoe crabs tagged in the MPA, there was a 70% chance that these crabs would remain within the protected spawning habitat and an 81% probability that individuals would remain within Stage Harbor once they entered it (Table 4b). Horseshoe crabs from this group were unlikely (12.5% probability) to reenter Node 3 from Node 1 and were highly unlikely (0.9% chance) to move from the protected spawning habitat (Node 3) into the unprotected spawning habitat within Stage Harbor (Node 1; Table 4b).

**Overwintering**

There was no evidence that horseshoe crabs tagged inside the MPA overwintered inside Stage Harbor (Node 1)(Figure 4). Although 41% ($n=14$) of the horseshoe crabs tagged inside Stage Harbor were never detected outside of the harbor, only 12% ($n=4$) were detected during the winter (Figure 5). For instance, Crab ID 342 (Figure 6) was tagged inside Stage Harbor on 14 June 2010, was detected throughout July 2010 still within the harbor then was not detected again.
for 104 days, until October, still within the harbor. This individual remained within the range of one receiver for all of December 2010. Crab ID 342 was not detected in the month of January 2011 but was detected repeatedly inside the harbor throughout February, March and April. Although there was no evidence that horseshoe crabs tagged in the MPA overwintered inside Stage Harbor (Figure 6), there was evidence that these horseshoe crabs were moving towards the deeper waters of Nantucket Sound throughout the late summer and fall. Horseshoe crabs from the MPA moved from the spawning habitat where they were tagged into Node 2 (16% chance; Table 4b); half (n=12) of the tagged horseshoe crabs in this group were last detected in Node 2, usually only for a few days. For example, Crab ID 343 was last detected in Node 2 on two consecutive days (5-6 August 2010). Crab IDs 344 and 346 passed through Node 2 on 15 July 2010 and were never detected again. Crab ID 350 (Figure 7) was detected in Node 2 for three consecutive days (1-3 August) before exiting the array.

**Consecutive Year Returners**

Several horseshoe crabs exited the array, presumably to overwinter offshore in deeper waters, and then returned to spawning habitat the following spring. Horseshoe crabs were considered to have left the array when they were not detected for ≥120 days, the duration of the winter period designated at the beginning of the study (December 1, 2010-March 31, 2011). Twenty-one percent (n = 7) of horseshoe crabs tagged inside Stage Harbor were not detected in the array throughout winter yet were detected the following spring. Only one individual (Crab ID 502) entered Stage Harbor upon returning in spring 2011. Crab ID 502 (Figure 8) was tagged inside Stage Harbor on 4 June 2010 and within two days left the harbor and entered the MPA, before leaving the array on 14 June 2010. On 12 May 2011, 332 days later, she was detected in Node 2 for three days before entering Stage Harbor for six days. She then exited the harbor and entered the MPA (Node 3) for another five days before finally exiting the array via Node 2, 28 days after she had been detected again in the array. Nine of the 24 study horseshoe crabs tagged in the MPA returned the next spring to spawning habitat and interestingly, more crabs (n=3) that were
tagged in the MPA entered Stage Harbor upon returning in spring 2011 than horseshoe crabs initially tagged inside Stage Harbor (n=1). For example, upon her return, Crab ID 363 (Figure 9) moved through Node 2 to Node 3, then entered and remained in Node 1 for eleven consecutive days before returning to Node 3. Thirteen days after entering Node 3 she was detected passing through Node 2 again, exiting the array in the same pattern in which she entered it. Access to Nantucket Sound can be gained from Nodes 2-4, but Node 2 provides the most direct route to deeper offshore waters.

**Seasonality**

The generalized linear mixed models (GLMMs) predicted several patterns of seasonal movement throughout the 18-month study period and also revealed that horseshoe crabs from each group were not behaving similarly (see Figure 10 for inputs and outputs in R). When the GLMM predicted that a movement event was more likely to occur than not (> 50%), it was assumed that animals were migrating. Horseshoe crabs tagged in Stage Harbor were usually more likely to move out of Nodes 2 and 4 (Figure 11), which is consistent with findings from network analysis. Stage Harbor horseshoe crabs were never more likely to move out of spawning habitat in 2010 and only became more likely to move out of spawning habitats (Nodes 1 and 3; Figure 11) on approximately 15 July 2011 (Day 410 of the study). Like the GLMM run for horseshoe crabs tagged inside Stage Harbor, the GLMM run for horseshoe crabs tagged in the MPA also predicted that horseshoe crabs were always likely to move out of Nodes 2 and 4, regardless of time of year. However, the GLMM that best fit the data for horseshoe crabs tagged in the MPA revealed a time in 2010 when horseshoe crabs were likely to move out of spawning habitat (Nodes 1 and 3) between approximately 8 September 2010 to 27 December 2010 (Day 100 to Day 210; Figure 12). Following a sharp decline in movement probability for all nodes throughout winter, movement probabilities began to increase again in spring 2011 (Day 350 of the study; 16 May 2011). Horseshoe crabs that were tagged in the MPA were unlikely to move out of Nodes 1 and 3 until 3 September 2011(Day 460 of the study).
**Discussion**

The results of the study demonstrated that horseshoe crabs were exhibiting site fidelity to spawning habitat in Stage Harbor (Node 1) and MNWR (Node 3), yet a high level of connectivity between these unprotected and protected spawning habitats was observed. Little evidence suggested that horseshoe crabs overwintered within Stage Harbor or within the footprint of the array. The results show that some individuals from both groups returned to either spawning habitat in consecutive years. The data collected during this study will add to the knowledge of spawning embayment fidelity, movement patterns and seasonal habitat use, thus providing horseshoe crab conservation managers in Massachusetts with critical information for determining MUs in Massachusetts.

**Spawning Site Fidelity**

Both the flow matrices and generalized linear mixed models (GLMMs) revealed that adult horseshoe crabs in this area were spending consecutive daily detections within spawning habitat, insinuating a level of spawning site fidelity, yet horseshoe crabs were not necessarily loyal to the spawning habitat where they were initially tagged. The connectivity from one spawning habitat to the other was not equal: some \( n=12 \) of the horseshoe crabs tagged inside Stage Harbor exited it and entered the protected spawning habitat, while few \( n=3 \) horseshoe crabs tagged in the MPA entered Stage Harbor spawning habitat, all in the second spawning season. Results suggest that horseshoe crabs from the MPA are acting as a source population to the sink population of horseshoe crabs tagged inside Stage Harbor. However, long-term studies of habitat quality and population demographics must be explored to correctly classify source-sink dynamics (Dias 1996). This evidence supports that horseshoe crabs tagged in the MPA may be exhibiting more site fidelity within a spawning season, despite the relative non-isolated beaches of the protected spawning habitat and the animals’ capability to migrate long distances.

This study calculated average straight-line distance traveled for each crab. The values calculated 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). The acoustic telemetry data confirmed findings from a conventional tagging study also performed on Cape Cod (James-Pirri et al. 2005). In my study, 82% of horseshoe crabs tagged inside the embayment remained within 3.0 km of their initial tagging location. James-Pirri et al. (2005) discovered that 70% horseshoe crabs traveled < 2.0 km from their original tagging location. The results are also consistent with findings in NH. Horseshoe crabs there averaged a linear distance of 4.5 km (Schaller et al. 2010). Horseshoe crabs tagged in the MPA traveled an average linear distance of 4.3 and 4.0 km in 2010 and 2011, respectively. Horseshoe crabs in New England frequently travel 2.5 km within and between years, although within the same year, horseshoe crabs are most often captured at the same site (James-Pirri 2010). The distance between average tagging locations, and the proximity from each tagging location to Nantucket Sound for this study was ~ 2.0 km, well within the realm of possible distances a horseshoe crab can travel.

Overwintering

Only four of the 58 study horseshoe crabs were detected inside Stage Harbor during the winter (Crab IDs 342, 358, 366 and 451) and all of these individuals were initially tagged inside Stage Harbor. Of these four horseshoe crabs, only Crab IDs 342 and 358 displayed a reduction in vagility (increased detections) suggesting a distinct wintering state, which is consistent with the majority of horseshoe crabs observed in other New England embayments (Moore and Perrin 2007; Schaller et al. 2010; James-Pirri 2010). Crab ID 366 was detected only three times during the winter and Crab ID 451 was only detected once. Only a small proportion (7% of all tagged crabs) of horseshoe crabs remain resident inside Stage Harbor year-round.

Almost half of the tracked horseshoe crabs (n=23) were last detected in late spring, summer and fall in Node 2, the node with the most direct access to the deeper waters of Nantucket Sound. I propose that horseshoe crabs were overwintering in the deeper waters of Nantucket Sound, yet no receivers were located offshore and therefore I cannot infer how far
offshore horseshoe crabs actually traveled. Post-spawning migrations to deeper water have been observed in the Mid-Atlantic States (Botton and Haskin 1984; Botton and Ropes 1987; Swan 2005). Acoustic telemetry studies from New England also found evidence of horseshoe crabs moving to deeper water (Watson et al. 2009; James-Pirri 2010; Schaller et al. 2010), yet these horseshoe crab remained within the embayment, which is inconsistent with the findings in this study.

Several reasons could explain why horseshoe crabs exit Stage Harbor when spawning is presumably completed in late spring, summer and fall. Stage Harbor is smaller than the embayments where similar studies were performed and only ~ 4 m deep at its deepest point. Perhaps the deepest parts of Stage Harbor are not suitable wintering habitat, resulting in migrations from the harbor into the deeper waters of Nantucket Sound by most individuals. Increased wave action poses a mortality threat to horseshoe crabs (Botton and Loveland 1989). Stage Harbor exits into Nantucket Sound while the other embayments where horseshoe crabs were tracked exited to the Northwest Atlantic Ocean. Since the wave action of Nantucket Sound is relatively less than that of the Northwest Atlantic, horseshoe crabs may not experience high mortality risks if they leave Stage Harbor compared to the other study areas. This local population of horseshoe crabs is on the southern side of Cape Cod, and although it was not directly included in genetic analyses performed by King et al. (2005), it is inferred that this population is more genetically related to a mid-Atlantic regional group. As mentioned above, several studies provide evidence of a longer, post-spawning, off-shore migration by horseshoe crabs in the Mid-Atlantic States (Shuster and Botton 1985; Botton and Haskin 1984; Botton and Ropes 1987). Horseshoe crabs from Stage Harbor may be more genetically pre-disposed to post-spawning offshore movements.

Although most ($n=20$) of the horseshoe crabs tagged inside Stage Harbor exited the harbor post-spawning, the rest ($n=14$) were never detected outside of Stage Harbor. Some of these individuals could have overwintered inside Stage Harbor outside of the detectability of the
array (i.e. out of receiver range or buried in the mud thus reducing the transmitters’ ability to transmit the signal properly (Schaller et al. 2010)). Conversely, these animals may have passed by the semi-circle of receivers that surrounds the mouth of Stage Harbor without transmitting a signal or out of range of the receivers. This anomaly was confirmed for at least two individuals (Crab IDs 347 and 444) who were tagged and released inside Stage Harbor and later detected in Node 4 without being detected in either Node 2 or 3, which each form half of the semi-circle. Alternatively, these fourteen non-detected horseshoe crabs may have been removed from the system via natural mortality (i.e. washed above the high tide line and thus out of range of the receivers) or were harvested for bait and thus permanently removed from the array.

It is important to restate here that from 1 December 2010 to 25 April 2011 only three receivers remained in the water and all three were located inside Stage Harbor. It is likely that no animals spent the winter within the footprint of the array as the last non-overwintering horseshoe crab was detected in the array on 23 November 2010 and the first non-overwintering horseshoe crab to return to the array was on 1 May 2011.

Consecutive Year Returners

Twenty-eight percent ($n=16$) of the 58 horseshoe crabs tagged in spring 2010 were not detected on the array for $\geq 120$ days and were then redetected within the array in spring 2011. These animals presumably overwintered in the deeper waters of Nantucket Sound out of range of the receivers and returned to the array to spawn the next year. No individuals that were tagged in the MPA entered Stage Harbor in spring 2010, yet three individuals entered in spring 2011. Despite network analysis and the GLMM suggesting within-year site fidelity, the fact that only one of the individuals initially tagged inside Stage Harbor entered the harbor the following spring does not verify the hypothesis of between-year site fidelity to the embayment but admittedly the sample size ($n=7$) is small. Although between-year spawning beach fidelity was not observed, the fact that 28% of horseshoe crabs returned to the array in the following spring should affirm between-year site fidelity to the larger area of the array as a whole.
The GLMMs predicted that horseshoe crabs tagged inside Stage Harbor returned approximately 20 days before the predicted return date for crabs tagged in the MPA. Water temperature data were not collected during this study, but other studies also examining horseshoe crab spawning migrations reveal that water temperature is likely a factor inducing spawning (Moore and Perrin 2007; Watson et al. 2009; Schaller et al. 2010). Moore and Perrin (2007) documented horseshoe crab slowly emerging from their wintering states when the temperature on the estuary floor reached 10°C. Watson et al. (2009) discovered that when the water temperature exceeded 10°C in the spring, animals moved several km from deeper parts of the estuary to water < 4 m deep. Schaller et al. (2010) observed a dramatic increase in activity in spring as animals began to move towards shallower areas of the estuary when the water temperature exceeded 10-11°C.

**Seasonality**

Horseshoe crabs tagged inside unprotected Stage Harbor and those tagged within the protected-from-harvest boundaries of MNWR and CCNS appeared to complete spawning by mid-July, consistent with previous studies that explored spawning behavior in New England (Barlow et al. 1986; Moore and Perrin 2007; James-Pirri et al. 2005). At Mashnee Dike in Bourne, Cape Cod, MA, mating activity began to decrease after the second lunar phases in June in 1984 and 1985 and no spawning activity was observed in July (Barlow et al. 1986). Moore and Perrin (2007) noted a rapid decline in intertidal use after June and July in both sub-embayments they examined. James-Pirri et al. (2005) noted that spawning was usually completed by mid-July. Yet horseshoe crabs tagged in the MPA seemed to migrate to and from spawning beaches later than horseshoe crabs tagged inside the harbor. In 2010, horseshoe crabs tagged in the MPA were last detected in the array for one month after horseshoe crab that were tagged inside Stage Harbor and the GLMM proposed that horseshoe crabs from the MPA did not begin their 2010 post-spawning migration until 8 September 2010. In 2011, the post-spawning migration began on 3 September 2011, according to interpretation of the GLMM.
The fall migration observed in horseshoe crabs tagged in the MPA has been predicted (Shuster and Botton 1985; Botton and Ropes 1987) and is consistent with findings from other telemetry studies from New England examining horseshoe crab seasonal movement patterns (Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010). Moore and Perrin (2007) observed a decrease in vagility in late summer and early fall in Taunton Bay, ME and were the first to distinguish that this represented the onset of a distinct wintering state. Horseshoe crabs shifted to a deeper portion of Pleasant Bay, Cape Cod, MA in the fall of 2009 and were detected more frequently as movement decreased (James-Pirri 2010). Schaller et al. (2010) observed a summer and fall migration in 2006 and 2007 to deeper parts of the Great Bay Estuary, NH and proposed that horseshoe crabs may perform this migration to deeper water as it is warmer and more stable in the winter.

In spring 2011, horseshoe crabs that were tagged inside Stage Harbor were first re-detected in the array fifteen days before horseshoe crabs from the MPA and remained within the array for 20 days, therefore creating only a five day period when both groups of horseshoe crabs were in the vicinity of the same spawning beaches. Despite horseshoe crabs from inside Stage Harbor entering the MPA, interpretation of GLMMs and review of average dates of last detections in summer/fall and first date of re-detections in the spring determined that spawning for the two groups is likely occurring in the same place, but not necessarily at the same time, suggesting that these two groups behave as separate local populations.

**Implications for Management**

The results obtained from network analysis and generalized linear mixed models supports the notion that horseshoe crabs from each initial tagging location may be a separate local population in the same metapopulation since horseshoe crabs from either grouping had a moderate probability of interacting with each other in time and some dispersal did take place between the two areas (Hanski and Gilpin 1991). The dynamics of spatially and temporally separated populations must be understood so that proper management can be attempted to prevent
the possibility of local extinction (Hanski and Gilpin 1991). Prior to this study, fisheries managers were uncertain if horseshoe crabs spawning in Stage Harbor were exiting the harbor, or if they belonged to an isolated population. It was also unclear if individuals from the MPA were moving into and spending time in the unprotected area and more specifically, Stage Harbor, replenishing potentially overharvested stocks. This study is the first to quantify the movement within and between two adjacent areas with differing commercial harvesting pressures for two local populations of horseshoe crabs.

Local populations of horseshoe crabs may still be susceptible to local depletion (Rudloe 1980; James-Pirri 2005; Moore and Perrin 2007; Smith et al. 2009; James-Pirri 2010). Based on the findings of isolated populations of horseshoe crabs in other New England embayments, and the evidence of local populations in this study, management efforts in Massachusetts may need to be revised to focus on a more appropriate MU. MUs differ in genetics, geography, habitat type, morphology, behavior, life history or socioeconomic factors (Moritz 1995). The correct recognition of MUs is necessary for the proper short-term management of a species (Moritz 1994); splitting a population up into too many MUs could result in unnecessarily strict management practices, while too few MUs could result in harvest rates that are too high and could result in overharvest or extinction of local populations (Allendorf and Luikart 2007). For example, the horseshoe crab stock in Massachusetts might actually consist of five MUs including Cape Cod Bay, Nauset Estuary, Pleasant Bay, Nantucket Sound and Buzzards Bay, but these stocks are managed as one MU, with an estimated sustainable annual harvest quota of 165,000 crabs (see MADMF 2010 for more regulations). In an extreme case, if all harvest came from just one MU, this local population may experience harvest rates (and therefore mortality) that are higher than the population growth rate, resulting in overexploitation and perhaps driving the local population to extinction (Allendorf and Luikart 2007).

Identifying MUs can be difficult and is typically accomplished by confirming differences in allelic frequencies at many loci (Moritz 1994), however Taylor and Dizon (1999) argue that
MUs cannot be delineated solely on allelic frequency differentiation measures, and claim that policy objectives and anthropogenic activity must be considered. Harvesting is not the only anthropogenic pressure on horseshoe crabs in Stage Harbor. Besides being home to many artisanal shellfishers and anglers, several larger fishing and dragger fleets are based in Stage Harbor, requiring the dredging of the harbor every year. Dredging can cause horseshoe crab mortality and can also drastically alter spawning habitat. Pesticides and herbicides may also affect water quality as many well-manicured lawns overlook the harbor. The largest negative impact on horseshoe crab spawning may be habitat destruction from the armoring of beaches. Erosion control structures such as jetties, seawalls and revetments alter the direction and magnitude of sand movement. Sandy, intertidal beaches are critical to horseshoe crab egg development and without these habitats, recruitment will surely suffer. Reducing or eliminating the habitat destruction of this animal is just as important as managing the resource.

In order to properly define the MUs of Massachusetts horseshoe crab stocks, there is a need for more horseshoe crab population dynamic studies around Cape Cod, possibly with the use of acoustic telemetry. Unfortunately, the scale of Massachusetts horseshoe crab populations is largely unknown. An impressive tagging study performed by James-Pirri et al. (2005) determined that a majority of horseshoe crabs (62%) were recaptured at the same location where they were initially tagged. However, variability existed between embayments; 96% of the horseshoe crabs tagged within Nauset Estuary were recaptured on the same beach where they were tagged at least 9 months earlier whereas two horseshoe crabs tagged on MNWR traveled a linear distance of 10.5 and 29.0 km over the same period of time. James-Pirri et al. (2005) taught us that while there seems to be some degree of spawning beach loyalty, a high level of variation exists between embayments and the horseshoe crab population dynamics within each should be explored more thoroughly to properly define MUs.

The identification of MUs should be the priority for fisheries managers in Massachusetts for two reasons: MUs will ensure the proper management of the species and MUs are also the
logical unit for population studies (Moritz 1994). As MUs are identified throughout the state via the use of acoustic telemetry, some of these areas might be considered temporary MPAs where studies regarding horseshoe crab life history characteristics can be explored without anthropogenic effects. Temporary MPAs can be rotated throughout different MUs in Massachusetts, and are a potentially useful yet rarely utilized management tool (Jennings et al. 2001) that may benefit localized or isolated horseshoe crab populations in Massachusetts. Rotating, temporary MPAs work particularly well for shellfish and crustacean fisheries as it allows for temporarily protected stocks to rebuild to levels that are economically worthwhile (Jennings et al., 2001) yet does not entirely shut down the fishery. The duration of temporary MPAs will depend on the status of the stock in that MU, the geography of the MPA, the life history characteristics of the horseshoe crabs within the MPA, the management and conservation goals of the MU and perhaps the duration of studies being performed in the MPA.

One such horseshoe crab MPA was developed in 2001 off the coasts of New Jersey, Delaware and Maryland to “promote the long-term sustainability for fisheries that depend on horseshoe crabs for bait, research and medical purposes, and ensure an ample supply of horseshoe crab eggs for food for migratory shorebirds.” (NMFS 2001). The nearly 1,500 square mile Carl N. Shuster Jr. Horseshoe Crab Reserve is located in the exclusive economic zone (EEZ) near the mouth of Delaware Bay. Since the ISFMP was enacted and the Reserve was incorporated, patterns of increase in juvenile and adult male horseshoe crab abundance in the Delaware Bay are consistent with population recovery (ASMFC 2011). The use of MPAs as a management tool has successfully increased the abundance of many benthic marine invertebrates including lobsters and, as is true for determining MUs, the establishment of MPAs depends on the connectivity of populations, seasonal habitat use and movement patterns of the species being considered (Withy-Allen 2010). Invertebrate density and body size was significantly higher in MPAs when compared to non-reserve areas (Roberts and Polunin 1993; Halpern 2003).
The data obtained during this study via the use of acoustic telemetry has confirmed that horseshoe crabs are generally exhibiting spawning fidelity to an area, but not necessarily to a spawning beach or embayment. Some horseshoe crabs migrated seasonally at least 2.0 km but the extent of these movements could not be obtained. Although horseshoe crabs exited Stage Harbor, the movement patterns of the horseshoe crabs observed in this study is consistent with those found in other horseshoe crab population from New England (Moore and Perrin 2007; Watson et al. 2009; Schaller et al. 2010) and Massachusetts (James-Pirri 2010). Horseshoe crabs in Massachusetts do not appear to be one panmictic stock and should therefore not be managed as such. To protect against overharvest and extinction of isolated and local populations, the correct identification of management units must be a priority of fisheries managers. This study highlights the fact that horseshoe crab populations around Cape Cod, Massachusetts and New England behave differently, requiring the collection of more information so that conservation tools such as MUs or MPAs can be used most effectively.
CHAPTER 3

GENERAL DISCUSSION

Through the use of acoustic telemetry technology and novel analytical techniques, the goals of this thesis were successfully achieved. The examination of site fidelity to and movement patterns between spawning habitat revealed that horseshoe crabs tagged inside Stage Harbor and horseshoe crabs tagged in the adjacent MPA are most likely two separate local populations, as some connectivity was apparent. Although, past research has been conducted to explore horseshoe crab spatial ecology via the use of acoustic telemetry in both Delaware Bay (Brousseau et al. 2004; Smith et al. 2010) and in various New England embayments (Kurz and James-Pirri 2002; Moore and Perrin 2007; Watson et al. 2009; James-Pirri 2010; Schaller et al. 2010), the research presented in Chapter 2 of this thesis is the first horseshoe crab telemetry study to describe movement outside of a relatively small, semi-enclosed embayment and the first to describe the movement between two areas with differing commercial harvesting pressures. Previous horseshoe crab telemetry studies have called into question the most appropriate scale of management for New England horseshoe crab populations (Moore and Perrin 2007; James-Pirri 2010). This study is the first attempt to define the horseshoe crab stock’s MUs in Massachusetts, and while the MU could not be identified, it is now clear that larger, higher resolution horseshoe crab telemetry studies must be performed.

Findings and Implications

Over the 18-month course of this study, it was discovered through field observations and predictive models that horseshoe crabs were spending long periods of time within two major spawning areas: inside the unprotected embayment of Stage Harbor and on the sandy tidal flats of protected Monomoy National Wildlife Refuge (MNWR). However, horseshoe crabs were not necessarily exhibiting fidelity to the spawning habitat where they were initially tagged. My research is the first horseshoe crab telemetry study where many of the horseshoe crabs that were tagged inside the embayment were detected outside of it, yet the distance study horseshoe crabs
traveled is consistent with other findings since most traveled < 4.5 km within the array (Moore and Perrin 2007; Watson et al. 2009; James-Pirri 2010; Schaller et al. 2010). A large degree of connectivity was observed between the two spawning habitats with approximately two-thirds of the horseshoe crabs initially tagged in the MPA being detected in the unprotected area and approximately one-third of horseshoe crabs tagged in the embayment entering the adjacent protected spawning habitat. Despite the high connectivity observed between the unprotected and protected areas, no horseshoe crabs that were tagged in the MPA were detected inside Stage Harbor in 2010. Interestingly, few (n=3) horseshoe crabs from the MPA left the array for the winter and returned to Stage Harbor in spring 2011. In the second spring of the study, almost one-third of the tagged horseshoe crabs returned but few of these horseshoe crabs returned to the same spawning beach where they were initially tagged in the previous spawning season, a behavior that has been observed in the Delaware Bay (Smith et al. 2010). This thesis provided strong evidence that horseshoe crabs were exhibiting spawning site fidelity to a general area within and between years, but were not necessarily exhibiting spawning beach fidelity as many horseshoe crabs were detected during one or both spawning seasons in an area ~ 2.0 km from where they were initially tagged.

Horseshoe crabs are dispersing between the two areas but they are not necessarily at these spawning locales at the same time. In the first spring of the study, horseshoe crabs that were initially tagged inside the embayment appeared to complete spawning by mid-July. Horseshoe crabs from the MPA entered the unprotected part of the array during the late summer and fall, on an apparent post-spawning migration to the deeper waters of Nantucket Sound but by this time, most of the horseshoe crabs that were tagged inside the embayment had not been detected for at least one month. Acoustic telemetry data from spring 2011 showed that, on average, horseshoe crabs tagged inside the embayment in 2010 had exited the array within five days of the protected group returning to the array. Despite a spatial overlap in spawning locations, there was little evidence suggesting that horseshoe crabs from the two groups were spawning during the same
time. This variation in migration behavior has been seen before in studies of horseshoe crab population dynamics (Smith et al. 2009) and can occur between populations of the same species (Alerstam et al. 2003).

The evidence of spawning site fidelity coupled with variation in the timing of spawning implies that these two groups of horseshoe crabs are local populations within the same metapopulation (see Hanski and Gilpin 1991 for definitions). Region- and embayment-specific horseshoe crab populations were identified throughout the animal’s range via analysis of mitochondrial and microsatellite DNA (Pierce et al. 2000; King et al. 2005), conventional mark-recapture studies (Baptist et al. 1957; Widener and Barlow 1999; James-Pirri et al. 2005; Swan 2005), acoustic telemetry studies (Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010; Smith et al. 2010), and stable isotope analysis (Carmichael et al. 2004; O’Connell et al. 2003). Differences in a variety of life history strategies including movement patterns (as documented in this thesis), abundance, foraging habits, spawning density, sex ratios, and size and age structure can exist between local populations (Smith et al. 2009). Additionally, local populations can be under different human-induced stresses such as the level of harvest (allowed or prohibited), type of harvest (scientific, bait, biomedical) and method of harvest (hand, trawl, dredge); each with its own associated mortality, which further bolsters the notion that horseshoe crab populations should be conserved by the most appropriate management unit (MU).

The correct recognition of MUs is necessary for the proper short-term management of a species (Moritz 1994) as too few MUs could result in harvest rates that are too high and could result in overharvest or extinction of local populations (Allendorf and Luikart 2007). The identification of MUs can be difficult and is typically accomplished by confirming differences in genetics, geography, habitat type, morphology, behavior, life history or socioeconomic factors of populations (Moritz 1995; Taylor and Dizon 1999). Because only some life history characteristics were explored in this thesis, I cannot confirm that horseshoe crabs initially tagged inside Stage Harbor and those tagged in CCNS and MNWR are indeed separate MUs, despite
evidence supporting that two local populations exist. Horseshoe crab stocks within the study area more likely belong to a larger MU, one that potentially includes all horseshoe crab local populations in Nantucket Sound.

**Future Research Directions**

More research must be performed on horseshoe crab spawning site fidelity to harbors and embayments, and small- and large-scale patterns in movement around Massachusetts to identify MUs to ensure the sustainability of the horseshoe crab resource. Acoustic telemetry is a valuable tool in the exploration of these life history characteristics. A Vemco Radio Acoustic Positioning (VRAP) system could be used to continuously track individuals (Schaller et al. 2010). Brousseau et al. (2004) outfitted their tracked horseshoe crabs with combined acoustic and radio transmitters to locate animals when they emerged from the water onto the spawning beaches. The use of this technology would help researchers locate the exact location of individuals during spawning, which could be used to observe spawning site fidelity on an even finer scale than this study. Regardless of how finely horseshoe crabs are tracked, it is clear that more information regarding spawning site fidelity and seasonal movement patterns of adult horseshoe crabs needs to be obtained to properly manage the species.

The geography of Cape Cod, Massachusetts and the islands of Martha’s Vineyard and Nantucket creates several bodies of water of various sizes, each with a potentially localized population of horseshoe crabs. These include, but are not limited to Barnstable Harbor, Wellfleet Bay, Nauset Estuary, Pleasant Bay, Stage Harbor, Lewis Bay, Waquoit Bay, Buzzards Bay, Vineyard Sound and Nantucket Harbor and the larger embayments of Cape Cod Bay and Nantucket Sound. Horseshoe crabs were exhibiting strong, year-round site fidelity to Pleasant Bay, the largest semi-enclosed embayment on Cape Cod, and may be an isolated population (James-Pirri 2010). My study, however, found strong evidence of horseshoe crabs leaving the relatively small Stage Harbor and could only confirm that two individuals overwintered in Stage Harbor, insinuating that horseshoe crabs do not remain within Stage Harbor year-round. Within
or between years, Stage Harbor horseshoe crabs were not loyal to the embayment and were determined to be a localized population within a larger metapopulation. There are many unanswered questions regarding horseshoe crab metapopulation structure around Massachusetts. The information collected by more adult horseshoe crab telemetry studies will further elucidate the connectivity of embayments and spawning beaches within and between embayments, which will provide fisheries managers with the information needed to manage horseshoe crabs on the most appropriate management unit.

**Conclusions and Summary**

The American horseshoe crab is a species with valuable ecosystem services and a resource that is economically important to several industries. The proper management of this animal, throughout its range, is imperative and since conservation cannot be achieved without knowledge of the animal, more studies must be completed on the horseshoe crab. This thesis contributed data on spawning site fidelity, movement patterns, overwintering behavior and seasonality of horseshoe crabs in Chatham, Cape Cod, MA. Two local populations were identified but the MU could not be designated. My work has increased the knowledge of horseshoe crab life history characteristics but has also made it apparent that larger-scale, higher-resolution studies on horseshoe crab movement patterns must be completed. Future research will help fisheries managers to appropriately recognize MUs for the horseshoe crab stock in Massachusetts, which will lead to more effective conservation and management of this species.

My research has contributed to the scientific knowledge of the spatial ecology of American horseshoe crabs in the following ways:

**Confirmation of the spatial ecology of anecdotally and empirically observed American horseshoe crab populations.** Certain horseshoe crab movement patterns have been observed throughout the animal’s range and this thesis confirmed these behaviors. Horseshoe crabs in Cape Cod waters migrate to shallow, sandy beaches to spawn in spring (May and June), complete spawning by summer (mid-July), then perform an off-shore migration to deeper water in late
summer and fall (mid-July through November), where they remain during the winter months before returning to spawning beaches in early spring (late-April).

**Continued research is necessary to assess spawning site fidelity to and movement within and between other embayments on Cape Cod.** Horseshoe crab telemetry studies from around New England have found that horseshoe crabs exhibit year-round fidelity to large embayments. Contrarily, this study found that most horseshoe crabs exited a relatively small, shallow embayment post-spawning. Generalizations cannot be made about horseshoe crab site fidelity to embayments warranting further exploration of horseshoe crab site fidelity in other embayments on Cape Cod. This information may help fisheries managers delineate the entire Massachusetts stock into more appropriate MUs.

**Suggested that rotating, temporary MPAs based on MUs may be useful conservation tools.** Although MNWR was created as a sanctuary for migratory shorebirds, horseshoe crabs thrive in this area, and although they may not be dispersing into potentially overharvested areas during spawning season when horseshoe crabs are hand-harvested, they are susceptible to harvest by trawl when they enter Nantucket Sound, and therefore relieve some of the pressure of the Stage Harbor local population and other potential local populations within the metapopulation.
**TABLES**

Table 1. A comparison of daily detections in the two areas

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<tr>
<th>Tagging Location</th>
<th>Crabs</th>
<th>Total</th>
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<th>Node 2</th>
<th>Node 3</th>
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Table 2. The daily detections of horseshoe crabs in each node for animals tagged inside Stage Harbor (ISH).

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| Total   | 43 | 330 | 32 | 68 | 5 |
| Mean    | 1.3 | 9.7 | 0.9 | 2.0 | 0.1 |
Table 3. The daily detections of horseshoe crabs in each node for animals tagged in the MPAs of Monomoy National Wildlife Refuge (MNWR) and Cape Cod National Seashore (CCNS).

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<td>4.8</td>
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Table 4. Proportional flow matrices for a) horseshoe crabs tagged inside Stage Harbor \((n = 34)\) and b) horseshoe crabs tagged in the MPA \((n=24)\). Proportional flow matrices were calculated by dividing each value of directly observed movement events by the total number of movement events that occurred \textit{from} that node, including movement events into the array.

a. Horseshoe crabs tagged inside Stage Harbor

<table>
<thead>
<tr>
<th>from</th>
<th>Node 0</th>
<th>Node1</th>
<th>Node2</th>
<th>Node3</th>
<th>Node4</th>
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<tbody>
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<td>0.400</td>
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b. Horseshoe crabs tagged in the protected area

<table>
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<th>Node3</th>
<th>Node4</th>
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</thead>
<tbody>
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</table>
Figure 1. Map of the study area and horseshoe crab capture/tag/release locations. Harvesting of horseshoe crabs in the protected area (within the red delineation) is prohibited. Adult horseshoe crabs were tagged inside Stage Harbor \((n=40)\) along one spawning beach (yellow dots) and at various spawning beaches throughout the protected area \((n=35;\) red dots).
Figure 2. Female horseshoe crab (left) outfitted with an acoustic telemetry tag (red arrow) and a USFWS button tag (blue arrow).
Figure 3. Location of remote receivers VR2Ws (n = 20) used to examine the spatial ecology of horseshoe crabs. Red= Node 1: inside unprotected Stage Harbor; Yellow= Node 2: outside Stage Harbor, still unprotected; Blue= Node 3: Protected area North, intertidal sand flats; Green= Node 4 Protected area South, barrier beach.
Figure 4. Node location versus time for horseshoe crabs tagged in CCNS and MNWR (n=24). Circles indicate an animal’s presence.
Figure 5. Node location versus time for horseshoe crabs tagged inside Stage Harbor \((n=34)\). Circles indicate an animal’s presence.
Figure 6. Movement patterns of Crab ID 342. Star indicates tagging location, arrows are linear distances, and the chronological order of movement is indicated by letter. Crab ID 342 was tagged inside Stage Harbor on (A) 14 June 2010 and moved within the estuary from (B) 17 June 2010 to (C) 16 July 2010. Crab ID 342 was not detected again until (D) 28 October 2010, when she was detected almost continuously (with the exception of January, 2011), throughout the winter and early spring. In (E) May 2011, Crab ID 342 again moved up-estuary before being detected outside of Stage Harbor on (F) 30 June 2011. Crab ID 342 was detected in the MPA on (G) 21 July 2011.
Figure 7. Movement patterns of Crab ID 350. Star indicates tagging location, arrows are linear distances, and the chronological order of movement is indicated by letter. Crab ID 350 was tagged on (A) 29 June 2010 in the MPA and was next detected in the unprotected area on (B) 5 July 2010. She moved back into the MPA (C) the next day and was last detected in the unprotected area on (D) 3 August 2010.
Figure 8. Movement patterns of Crab ID 502. Star indicates tagging location, arrows are linear distances, and the chronological order of movement is indicated by letter. Crab ID 502 was tagged inside Stage Harbor on (A) 4 June 2010 and by (B) 14 June 2010 was detected ~ 6 km away. Crab ID 502 was not detected for 332 days until (C) 12 May 2011. She re-entered the harbor on (D) 14 May 2011 and remained within it until (E) 20 May 2011 when she was detected in the MPA. Crab ID 502 was last detected on (F) 9 June 2011.
Figure 9. Movement patterns of Crab ID 363. Star indicates tagging location, arrows are linear distances, and the chronological order of movement is indicated by letter. Crab ID 363 was tagged on a protected CCNS beach on (A) 13 June 2010 and by (B) 7 July 2010 had moved to the unprotected area. This individual was next detected on (C) 12 May 2011, 310 days later. She entered Stage Harbor the next day and remained within it until (D) 24 May 2011. Crab ID 363 was detected outside of the harbor until (E) 26 May 2011. She was then detected once on (F) 6 June 2011 before presumably leaving the array.
Figure 10. Inputs (red) and outputs (blue) of GLMMs performed in R. Note that the factors influencing model selection differ between the initial tagging location of a) inside Stage Harbor and b) the MPA.
Figure 11. Probability of movement out of each node for adult horseshoe crabs ($n=34$) tagged inside Stage Harbor. Red = Node 1; Green = Node 2; Dark Blue = Node 3; Light Blue = Node 4; Purple = Node 0. Circles indicate a movement event out of the node (at 1.0) or indicate that the horseshoe crab was next detected in the same node (at 0.0).
Figure 12. Probability of movement out of each node for adult horseshoe crabs ($n=24$) tagged in the MPA. Red = Node 1; Green = Node 2; Dark Blue = Node 3; Light Blue = Node 4; Purple = Node 0. Circles indicate a movement event out of the node (at 1.0) or indicate that the horseshoe crab was next detected in the same node (at 0.0).
BIBLIOGRAPHY


