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Horseshoe Crab (*Limulus polyphemus*) Movements Following Tagging in the Delaware Inland Bays, USA

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Abstract

The Delaware Bay region is the epicenter of horseshoe crab, *Limulus polyphemus*, activity, and despite the ecological and commercial importance of this species, few studies have examined the long-term movements of horseshoe crabs in this area and the amount of mixing that takes place between smaller coastal embayments within the region and the Delaware Bay proper, factors that are critical to effective management. To better understand these factors, 5568 crabs were tagged in the Delaware Inland Bays as part of the U.S. Fish and Wildlife Service's (USFWS) Cooperative Horseshoe Crab Tagging Program in 2002–2016. A high re-sight rate of 20.1% (1123 crabs) was reported to the USFWS. Re-sights suggest that the Delaware Bay population is distributed between coastal New Jersey (south of Barnegat Bay) and coastal Virginia (north of Chincoteague Inlet). There were 90 re-sights in the Inland Bays and 148 re-sights in Delaware Bay, with 320 days or more between tagging and re-sight, showing that substantial interchange between successive spawning seasons occurs. Distance analyses demonstrated that crabs can move between the Inland Bays and other Delaware Bay region waterbodies within a single year. The findings of this study support the current management strategy of splitting the harvest of Delaware Bay crabs between New Jersey, Delaware, Maryland, and Virginia and also demonstrate that the waterbodies within the Delaware Bay region are highly connected. This connectivity supports protecting spawning habitat within the smaller embayments of the Delaware Bay region and including spawning surveys from these systems in future stock assessments.

Keywords Horseshoe crab · Delaware · Tagging · Migration · Inland bays · *Limulus polyphemus* · Mid-Atlantic

Introduction

The Atlantic horseshoe crab (*Limulus polyphemus*) is important ecologically and commercially in Delaware and other states in the northeastern USA. Coastal waters between New Jersey and Virginia are home to the highest abundance of horseshoe crabs on the Northwestern Atlantic Continental Shelf, and the majority of these crabs are believed to belong to the Delaware Bay population (Shuster and Botton 1985; Botton and Ropes 1987). Previously harvested for fertilizer and livestock food during the late 1800s to early 1900s, horseshoe crabs are now harvested primarily by the bait and biomedical industries (ASMFC 1998, 2013). The importance of horseshoe crabs is not limited to services for humans, as numerous migrating birds rely heavily on the eggs of horseshoe crabs during migratory stopovers (Myers 1986; Castro and Myers 1993; Tsipoura and Burger 1999).

Because of the importance of horseshoe crabs to both humans and natural ecosystems, spawning populations of horseshoe crabs are monitored annually through statistically robust spawning surveys conducted by various organizations along the mid-Atlantic coast of the USA (Smith et al. 2002; Zimmerman et al. 2017). While the numbers of spawning crabs are documented annually, relatively few studies have examined adult horseshoe crab movements in the mid-Atlantic, fewer have examined long-term movements (> 3 years), and the exchanges amongst smaller embayments (the Delaware Inland Bays) within the Delaware Bay region, and Delaware Bay proper have never been quantified (Brousseau et al. 2004; Swan 2005; Smith et al. 2010;

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Beekey and Mattei 2015). Understanding the movements and extent of migration is critical for effective management.

Relatively long-term tagging studies that have been performed indicate the presence of regional horseshoe crab populations (Swan 2005; ASMFC 2013). Likewise, continuous tracking studies and genetic analyses have revealed resident and/or discrete populations in New England estuaries and the upper Chesapeake (Pierce et al. 2000; Moore and Perrin 2007; Schaller et al. 2010). The existence of discrete populations, along with differences in harvest pressures, provides support for management at the regional population level (Rutecki et al. 2004; ASMFC 2013). Critical to this management is an understanding of (1) where a regional population begins and ends (as accurately as possible), (2) how much mixing takes place between embayments within a region, and (3) the temporal and spatial aspects of travel within the region.

This study set out to understand these three factors by tagging 5568 crabs over a 15-year period (2002–2016) in the Delaware Inland Bays (Rehoboth Bay, Indian River and Bay, and Little Assawoman Bay), a network of shallow coastal embayments south of Delaware Bay and north of Ocean City, Maryland. The difference in time between tagging and re-sight, and the minimum distance each crab traveled, was calculated.

Table 1 Number of horseshoe crabs tagged each year of study

Year	*N* of crabs tagged	Sex		
		Females	Males	Unknown
2002	175	51	124	0
2003	99	19	80	0
2004	228	67	161	0
2005	192	48	144	0
2006	99	23	76	0
2007	264	73	184	7
2008	23	6	17	0
2011	209	89	120	0
2012	474	128	346	0
2013	1005	209	796	0
2014	800	203	595	2
2015	1000	152	848	0
2016	1000	170	830	0
Total	5568	1238	4321	9

Methods

Tagging

Tagging was done as part of the United States Fish and Wildlife Service's (USFWS) Cooperative Tagging Program. Tags were issued annually by the USFWS to the Delaware Center for the Inland Bays. The circular tags are ~2.54 cm in diameter and are printed with a telephone number to report the tag sighting, a website to submit electronically if that is preferred, and the tag number (unique to each crab). Tags were attached to the left posterior (rear) point of the prosoma using a household drill with a 0.39-cm diameter drill bit and a wine cork surrounding the bit, used as a stopper, to prevent the bit from completely puncturing the prosoma. A hole was drilled through the outermost layer of the prosomal wall, and the tag was inserted by hand into the crab. Sex, approximate age (young, mature, old), and prosomal width (widest point of the crab) were recorded, along with the GPS latitude and longitude, date, and responsible tagger. Volunteers performed the tagging and were trained annually by the Center for the Inland Bays, following an Environmental Protection Agency approved Quality Assurance Project Plan. Re-sights were reported to the USFWS–Maryland Fisheries Resources Office. In total, 5568 crabs were tagged in 2002–2016 (Table 1).

All tagging locations were in the Delaware Inland Bays (Fig. 1). Locations were primarily sandy beaches at sites used for the Inland Bays spawning surveys. A majority of crabs were tagged on nights coincident with spawning surveys, which occur May–June, with occasional dates in April or July, but a small number were tagged when staff were available at other times. Most of the tags for a given year were placed on crabs early in the spawning season, and this may have biased results towards quicker re-sights, as previous work has demonstrated that spawning crabs stay close to initial tagging sites over successive tides (Beekey and Mattei 2015), and spawning beaches are where the greatest amount of observer effort occurs. Tagging was primarily performed at night, while observations of tagged horseshoe crabs were biased towards the day, when beaches were more heavily used and tags were easier to see.

Determining Mixing Between Bays

All re-sight data were obtained from the USFWS. The difference in days between the initial tagging date and the re-sight date was calculated for each re-sight using R statistical software (version 3.4.0). Re-sights were also attributed to a waterbody (Delaware Inland Bays, Delaware Bay, New Jersey coastal bays, Maryland/Virginia waters, and others). The number of re-sights occurring in each waterbody was determined using the GPS location, and not the waterbody information provided in each re-sight report. Because re-sights are reported by members of the general public, it was found that the waterbody listed was not always accurate, and so each re-sight was examined using the GPS location, and the correct waterbody was determined from this.

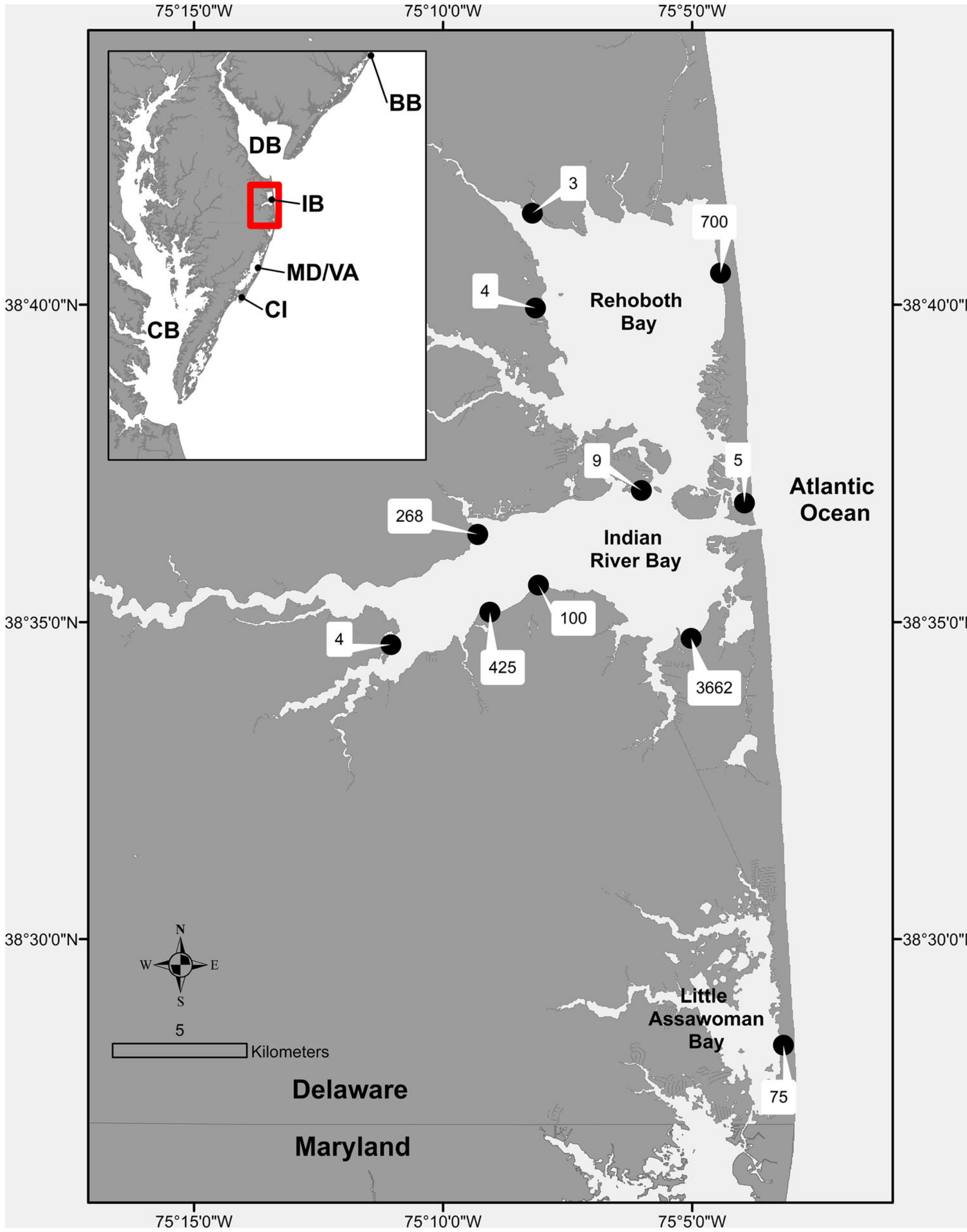

Fig. 1 Tagging locations in this study indicated by filled circles. Number of crabs tagged at each site listed next to site. Study area is highlighted by red square in inset map of Delmarva Peninsula. BB = Barnegat Bay, New Jersey, DB = Delaware Bay, IB = Inland Bays, Delaware, MD/VA = Maryland and Virginia bays, CI = Chincoteague Inlet, Virginia, CB = Chesapeake Bay. Image produced with ArcMap (ESRI, version 10.5)

Determining Distance Traveled

Assigning GPS Locations

To determine the minimum distance that each crab traveled, GPS locations had to be determined for re-sights that were reported without one. Of the 1123 re-sights of Inland Bays-tagged crabs, 717 were missing a GPS location. While these re-sight records indicated the beach or area where the crab was seen, some beaches are many kilometers in length, and therefore placing a re-sight point randomly, or at a specific end of the beach in these locations, would bias the results of the distance analyses. To prevent this, we attempted to assign a GPS location to as many of the 717 re-sights as possible. To standardize the placement of GPS locations, three rules were created for attributing an exact location to a re-sight. First, GPS locations for re-sights reported in inlets were positioned at the closest point on land, in the inlet, using the reported nearest city to dictate the side of the inlet on which to place the GPS point. Second, if only a beach was specified, the shore directly across from the entrance to the beach was used. If the beach had multiple entrances, the entrance closest to the tagging location was used. The exception occurred if the re-sight location could not be narrowed down using information provided in the report comments section or reported location column to < 804.67 m (an average beach length in the Inland Bays); in these cases, the re-sight was dropped from the analyses. This was done in an attempt to get the most accurate distances between tagging and re-sight as possible, without excluding data that were accurate to the average beach length within the Inland Bays. This may have introduced bias by favoring re-sights within the Inland Bays watershed as the author has better local knowledge of these locations and is therefore better able to interpret local names in the data records. Lastly, if only a marina or street was listed, the location was determined to be the area of water closest to the street or marina entrance. Using these rules, 471 re-sights were assigned a GPS location (65.6% of missing re-sights). In total, 877 re-sights were used for the analyses.

Spatial Analyses

In order to obtain the most accurate minimum distance traveled, linear distance between tagging locations and re-sight locations could not be used. Crabs do not travel over great distances on land, and therefore, using the linear distance was not appropriate. Travel between tagging and re-sight locations was restricted to estuaries and coastal waters. Shoreline layers were gathered from state GIS portals in order to create a land layer. All land layers were imported into ArcGIS 10.5 (ESRI), projected into WGS 1984 World Mercator, and merged into one land layer. This layer was converted to a raster (cell size 30 m), which was then resampled so that all land cells were given a cell value of NA, and all other cells (marine or estuarine cells) were given a value of 1. This raster was clipped to the smallest extent possible without infringing upon possible routes between re-sights and tagging locations. One re-sight in Connecticut was dropped because the raster size needed to keep this point in the analyses was too large to be computationally feasible on ordinary computers. This resulted in 876 re-sights used for distance calculations. Because re-sight and tagging locations are often reported from a beach (i.e., on land), but the analyses are restricted to travel through water only, all tagging locations or re-sight locations occurring on land were moved to the closest area of water. To do this, the raster was copied and resampled with a lower resolution (cell size 402 m) to facilitate further processing. This lower resolution raster was converted to a point layer in which each cell was represented by its midpoint. All re-sights occurring on land, and taggings occurring on land, were moved to the closest point in this layer for a maximum shift in distance of 201 m.

Re-sights were loaded into ArcGIS 10.5 (ESRI). At this point, 13 re-sights were dropped from the analyses because the difference in days between tagging and re-sight was < 0, indicating that one of the dates in the report was invalid. To calculate the minimum distance each crab traveled, we used the Cost Path Analysis Tool (ArcGIS 10.5, ESRI), which calculates the least costly (i.e., shortest) path between a point and all cells in the 30-m resolution raster. This was done individually for each tagging location, and the resulting distance raster values were extracted for all re-sight locations, resulting in the minimal distance between a re-sight and a tagging location when travel was restricted to water. One re-sight was dropped when it was determined that the crab in question could not have traveled > 98 km in a single day without the aid of human transportation. This resulted in 862 re-sights having valid distance calculations and differences between tagging and re-sight dates.

Results

Tagging Re-sights and Spatial Extent

A total of 5568 crabs were tagged from 2002 to 2016, 1238 females, 4321 males, and 9 unknown (Table 1). A total of 1123 re-sights (824 unique re-sights) were reported from 2002 to 2016, resulting in a recovery rate of 20.17% (Fig. 2). Live re-sights numbered 921 (82%), dead recoveries numbered 181 (16%), and unknown or unreported crab conditions numbered 21 (2%). The minimum time between tagging and re-sight was 0 d, the maximum difference in time was 4202 d (11.5 y) (dead) and 3014 d (8.25 y) (alive), and the mean difference in time was 216 d (Table 2).

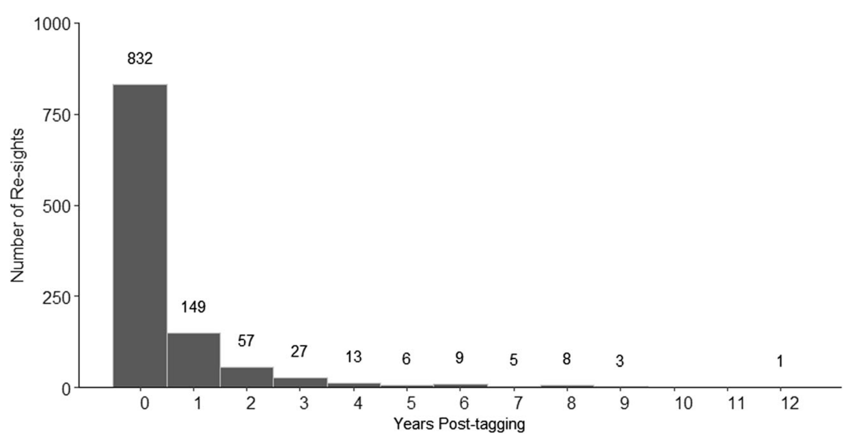

Fig. 2 Years elapsed between tagging and re-sight for all crabs with valid differences between tagging and re-sight. Total number of re-sights for each elapsed time period (i.e., re-sighted 1 y post-tagging, re-sighted 2 y post-tagging) displayed above bars

Table 2 Number of re-sights in each waterbody, number of re-sights after 320 d, minimum, maximum (alive re-sights only), and mean difference in time between tagging and re-sight for each waterbody

Waterbody	Re-sights	*N* after 320 d	Min diff re-sight time (d)	Max diff in re-sight time alive only, d (y)	Mean diff in re-sight time, d (y)
Inland Bays	915	90	0	3014 (8.25)	74
Delaware Bay	161	148	6	2900 (7.94)	871 (2.38)
NJ Coastal Bays	6	4	75	772 (2.11)	1531 (4.19)
MD/VA Coast	39	27	1	2977 (8.15)	583 (1.59)
Connecticut Coast	2	2	345	1181 (3.32)	763 (2.09)
All waterbodies	1123	271	0	3014 (8.25)	216

Of the 1123 re-sights, 13 had an invalid difference in time between tagging and re-sight. Seven hundred and ten occurred within 30 d of tagging, 181 occurred between 31 and 365 d, and 219 occurred > 1 y.

Of the 1123 re-sights reported, 915 (81.5%) occurred in the Inland Bays, 161 (14.3%) in Delaware Bay, 39 (3.5%) in Maryland or Virginia coastal waters, 6 (0.5%) in New Jersey coastal bays, and 2 (0.1%) in Connecticut (Table 2). A total of 1121 (99.8%) re-sights were reported between Chincoteague Inlet, Virginia, and Barnegat Bay, New Jersey, indicating that the vast majority of crabs remained within this area.

Mixing Between Embayments

After 320 d (approximate time between the last spawning survey date in late June and the first spawning survey date the following spring), there were 271 total re-sights. Of these, 90 (33%) re-sights occurred in the Inland Bays, 148 (54.6%) re-sights in Delaware Bay, 4 (1.4%) in New Jersey coastal bays, 27 (10%) in Maryland/Virginia coastal waters, and 2 (< 1%) in Connecticut (Table 2).

Distance Traveled

Of the 1123 re-sights, 862 had valid differences in time between tagging and re-sight and enough information to be analyzed for minimum distance traveled. Females traveled farther than males, as determined by a one-tailed Wilcoxon rank sum test ($W = 34{,}592$, $P = 0.001$). A total of 694 (80.5%) traveled < 2000 m between tagging and re-sight and 790 (91.6%) traveled < 20 km. Only 11 (1.2%) traveled > 100 km, indicating that migrations of this distance were uncommon. There were 441 re-sights within 5 d of tagging, and 440 (99.7%) of these re-sights occurred within 1 km of the tagging location, suggesting that crabs remain close to the tagging (spawning) beach for at least 5 d. Of the 223 re-sights occurring between 5-30 d (one month), 196 (87.8%) occurred within 1 km of the tagging location. For crabs re-sighted 31–365 d after tagging, 39% (41/105) occurred within 1 km of tagging, indicating that a majority of tagged crabs had dispersed from tagging beaches during this time.

Discussion

The 20.2% recovery rate reported in this study was substantially greater than some previous long-term tagging efforts (James-Pirri et al. 2005; Swan 2005), but similar to a more recent effort in Long Island Sound (Beekey and Mattei 2015). The difference in recovery rate may be partially explained by the areas where tagging was performed. The Inland Bays are more urbanized, densely developed, and are a much smaller area than the open waters Swan (2005) tagged in and the coastal embayments James-Pirri et al. (2005) tagged in. A more urbanized area would have a greater density of possible crab observers, which may also help explain the high re-sight rate Beekey and Mattei (2015) saw in Long Island Sound. Similarly, a smaller tagging area would also increase the chances of re-sight, particularly if crabs remained close to spawning beaches during the spawning season. The vast majority of re-sights occurred during the initial year after tagging, while crabs were still close to initial tagging locations (Fig. 2), which supports the idea that a smaller more densely developed area contributed to the higher recovery rate. Almost 94% of re-sights occurred < 3 y after tagging, though crabs were captured alive > 8 y after tagging, and dead 11.5 y after tagging (Fig. 2). These results are similar to the patterns seen in previous long-term tagging efforts (Swan 2005; Beekey and Mattei 2015) and suggest that crabs can survive for > 8 y after spawning.

Spatial Extent of Regional Population

With the exception of two crabs re-sighted in Connecticut, all crabs (99.8%) tagged in the Inland Bays remained between Barnegat Bay, New Jersey, to the north, and Chincoteague Inlet, Virginia, to the south. These spatial boundaries are similar to those reported by Swan (2005) and support the idea that the Delaware Bay population is primarily located within these northern and southern limits. Under the current Fisheries Management Plan and subsequent addenda (ASMFC 1998, 2012), the harvest quota for the Delaware Bay population is divided amongst four states (New Jersey, Delaware, Maryland, Virginia), and the spatial boundaries revealed in this study support this approach.

Long distance migrations (> 100 km) were very uncommon (1.27% of all re-sights analyzed for distance, 11 crabs total). This finding also echoes that of Swan (2005) who reported only 14 out of 2149 re-sighted crabs traveling > 100 km. Given that horseshoe crab larvae have a very limited capacity for long-range dispersal (Botton and Loveland 2003), any mixing that does occur between adjacent regional populations likely takes place amongst adults or older juveniles. Both this study and Swan (2005) demonstrated that long-distance migrations are uncommon, so it is natural to speculate on how much mixing takes place between adjacent regional populations. Botton and Ropes (1987) suggested that crabs in the New England area are relatively isolated from one another, and there is evidence for localized populations there (James-Pirri et al. 2005; Moore and Perrin 2007; Schaller et al. 2010). Work by Beekey and Mattei (2015) in Long Island Sound (crabs tagged in New York and Connecticut) also saw limited movement between Long Island Sound and populations to the south (New Jersey and Delaware). While Saunders et al. (1986) found few genetic differences between New England and mid-Atlantic populations when examining mitochondrial DNA, Riska (1981) found morphological differences between New England, Long Island Sound, and Delaware Bay horseshoe crabs. Pierce et al. (2000) looked at sequence variation in mitochondrial DNA of cytochrome oxidase I between Delaware Bay crabs and Chesapeake Bay crabs and found little evidence of gene flow, but King et al. (2005) examined 14 microsatellite DNA loci and found evidence of substantial gene flow between each regional population and its nearest neighbors. While the number of long-distance migrations reported by this study was low, it is important to remember that if the relationships reported in the present study hold true for the rest of the Delaware Bay population (estimated number 20 million crabs; Smith et al. 2006), then the numbers of crabs mingling with neighboring populations may be in the hundreds of thousands. Long-term, continuous tracking of crabs on the margins of regional populations (i.e., north of Barnegat Bay and south of Chincoteague Inlet) could clarify the degree of mixing at the margins between these populations.

Mixing Within the Region

Mixing between the Inland Bays and Delaware Bay was clearly evident. After 320 d post-tagging (approximate time between the last spawning survey date in late June and the first spawning survey date the following spring), there were more re-sights in Delaware Bay than the Inland Bays (Table 2), suggesting that considerable population mixing takes place between spawning seasons between the Inland Bays and Delaware Bay. Mixing was evident, but less common, between the Inland Bays and the Maryland/Virginia coastal bays, with 27 re-sights in Maryland/Virginia waters after 320 d. An alternate explanation of the lower numbers in Maryland/Virginia waters is that re-sights were biased towards more populous places. South of Ocean City, Maryland, the Assateague Island shoreline is relatively unused by humans for kilometers, and with fewer people there to spot crabs, re-sights were less common. Mixing between the Inland Bays and the New Jersey coastal bays was also observed, with six re-sights in the New Jersey coastal bays. Swan (2005) found that only two crabs tagged south of New Jersey migrated north of the Delaware Bay entrance and speculated that a combination of bottom currents and a deep (36 m) trench running south to south east out of Delaware Bay and to the continental shelf may be responsible for the low mixing observed. However, despite substantially fewer tagged crabs (5568 vs 13,137) in the present study, a total of 8 crabs (6 re-sights in New Jersey coastal bays, 2 re-sights in Connecticut) tagged within the Inland Bays were re-sighted north of the Delaware Bay entrance. While eight crabs are not enough to dismiss Swan's speculations, it does suggest that movements through (or around) the trench are perhaps more common than previously speculated.

The minimum times between tagging and re-sight for crabs re-sighted in Delaware Bay, in Maryland/Virginia waters, and in New Jersey coastal bays were all < 365 d, indicating that crabs can travel between embayments within the Delaware Bay region within a single year (Table 2). This study is the first to examine the amount of interchange between the Inland Bays and the Delaware Bay, Maryland/Virginia Bays, and New Jersey coastal bays and demonstrates that these systems are highly connected. This connectivity underscores both the need to conserve spawning habitat within the Inland Bays, Maryland/Virginia bays, and New Jersey coastal bays, as a loss of habitat in these systems would negatively impact the Delaware Bay population and also that spawning surveys in these coastal embayments should be taken into consideration by management agencies (if statistically robust).

Unfortunately, this study did not assess the percentage of crabs that remained in the Inland Bays over winter. Estimates from a previous study have suggested that as much as one third of the population may over-winter in Delaware Bay (Smith et al. 2006). Out of the 1123 re-sights in this study, 8 occurred in the months of November through March; 2 in Delaware Bay; 4 in the Inland Bays; 1 in Barnegat Bay, New Jersey; and 1 in Chincoteague, Virginia. While this number is biased due to less intensive use of coastal areas during the winter (fewer people to spot crabs), and over-wintering crabs likely limit movements during winter and primarily inhabit subtidal areas (Schaller et al. 2000; Moore and Perrin 2007), it does demonstrate that some overwintering occurs throughout the extent of the Delaware Bay regional population.

Distances and Spawning Behavior

From the distance analyses, it is clear that crabs remained close (< 1 km) to the beach on which they were tagged, for at least 5 d, likely to complete multiple spawning episodes. These findings are similar to those of Beekey and Mattei (2015) and demonstrate that within a single spawning season, there is some site fidelity; however, beyond a spawning season, based on re-sights occurring after 320 d, there does not appear to be site fidelity. Females have been shown to spawn four to five times in a season (Smith et al. 2010), and acoustic tracking in Delaware Bay has revealed that crabs spawn successively over two to five nights and then leave the area (Brousseau et al. 2004). Dispersion from the tagging beach became more and more common as time went on in this study as well, with < 40% of re-sights within 1 km of the tagging location after 1–12 months, compared to the 99.7% within 5 d. Females on average traveled farther than males, though the reasons for this are unclear. It may be that females search farther for and are more selective of spawning beaches; adult crabs appear to be capable of detecting beaches with preferred geochemical regimes (Botton et al. 1988). An alternative explanation is that because re-sights were biased towards quicker recaptures (as a result of tagging early on in the spawning season), and almost 80% of tags were placed on males, males had many more re-sights in the first few days after tagging, when they were still close to the initial tagging location. Perhaps if an equal proportion of males and females had been tagged, initial re-sights would have been more even between the two sexes and overall distances would have followed suit. Future tagging efforts should focus on tagging equal proportions if possible.

In summary, our data indicate that the Delaware Bay population is primarily distributed between Barnegat Bay, New Jersey, to the north, and Chincoteague Inlet, Virginia, to the south. These spatial boundaries are similar to previous tagging efforts and support the existing management strategy which splits the Delaware Bay horseshoe crab harvest amongst New Jersey, Delaware, Maryland, and Virginia. Our study, which was the first to examine mixing between the Inland Bays and the other embayments within the Delaware Bay region, suggests that a large amount of interchange occurs between the Inland Bays and the Delaware Bay, and to a lesser extent, the Inland Bays and the Maryland/Virginia and New Jersey coastal bays. The large amount of mixing demonstrated in this study stresses the need to protect spawning habitat in smaller embayments within the Delaware Bay region and also provides support for including spawning surveys from these smaller systems into future horseshoe crab stock assessments for the Delaware Bay region, as these systems combined account for a considerable amount of spawning habitat within the region. Lastly, crabs not only appear to stay close to spawning beaches for at least 5 d, a pattern seen in previous studies, but also appear capable of moving from one embayment to another within a single year, furthering the notion that the embayments within the Delaware Bay region are highly connected and should be managed as such.

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Compliance with Ethical Standards

The Delaware Center for the Inland Bays is a nonprofit organization and a National Estuary Program. It was created to promote the wise use and enhancement of the Inland Bays watershed by conducting public outreach and education, developing and implementing restoration projects, encouraging scientific inquiry and sponsoring needed research, and establishing a long-term process for the protection and preservation of the Inland Bays watershed.

Conflict of Interest The author declares that he has no conflict of interest.

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