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Telemetry reveals migratory drivers and disparate space use across seasons and age-groups in American horseshoe crabs

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Abstract. Identifying mechanisms that underpin animal migration patterns and examining variability in space use within populations is crucial for understanding population dynamics and management implications. In this study, we quantified the migration rates, seasonal changes in migratory connectivity, and residency across population demographics (age and sex) to understand the proximate cues of migration timing in American horseshoe crabs (*Limulus polyphemus*). Juvenile ($n = 25$) and adult ($n = 70$) horseshoe crabs were tracked with acoustic telemetry techniques for a 3-yr period in Moriches Bay, NY. Connectivity metrics and residency probability were quantified through spatial network analysis and empirically derived Markov Chain models (EDMC), respectively. The migratory probability of adult horseshoe crabs between Moriches Bay and the Atlantic Ocean was estimated to be 41.0% (95% CI: 34.0–59.8); in contrast, only 8% (95% CI: 1.2–31.6) of juveniles migrated into the ocean. Migration timing was influenced by the interaction of photoperiod and temperature, revealing seasonal differences in migration timing and a 50% narrower range of photoperiod and temperature over which fall migrations occurred compared to spring. Sex-specific differences in space use and connectivity within each season were largely absent; however, centralized habitats were important for maintaining connectivity across all seasons. EDMC results revealed that when standardized to the number of horseshoe crab detections on each receiver, the centrally located habitats in Moriches Bay and Inlet accounted for >50% of the total relative residency probability within most seasons, indicating these areas may be preferred by adult horseshoe crabs. Ontogenetic differences in maximum spatial extent, space use, and connectivity were observed in the bay, as juveniles exhibited lower linkages between locations ($n = 4$) relative to adults ($n = 13$) during the same temporal period. Our work highlights the application of novel quantitative approaches for addressing the movement dynamics of horseshoe crabs that can be readily applied to other taxa in the context of wildlife conservation.

Key words: acoustic telemetry; horseshoe crabs; migratory connectivity; movement ecology; network analysis; partial migration; residency; space use.

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INTRODUCTION

Quantifying animal movement and migratory connectivity across spatiotemporal scales is vital to understand population dynamics in a holistic context; yet, this knowledge is often limited for many species (Patterson et al. 2008, Morales et al. 2010). Movement is largely influenced by a combination of internal factors, such as physiological condition, foraging state, and resting mode, and external factors, including temperature, habitat suitability, presence of predators, and anthropogenic disturbances that interact differently across a variety of geographic and temporal scales (Nathan et al. 2008, van Beest et al. 2016). Understanding the interaction of these factors on animal movement in coastal marine environments is often challenging (LaMontagne et al. 2002, Lotze et al. 2006, Nathan et al. 2008, Rochette et al. 2010, Barkley et al. 2018). However, it is imperative to examine the underlying migratory structure identify migratory drivers, and quantify spatiotemporal variability in migratory connectivity to assess the habitat requirements needed for a population's persistence (Chapman et al. 2012, Papastamatiou et al. 2013, Walther and Nims 2015). For example, partial migration can be a result of ontogenetic shifts in resource use or may be mediated by reproduction purposes, and can result in demographic-specific differences in susceptibility to perturbations, such as dredging, and habitat fragmentation (Chapman et al. 2012, Walther and Nims 2015). Additionally, determining the cues that underpin migration timing can provide insight into the intricacies of animal movement dynamics. For instance, photoperiod can serve as an annual cue for seasonal migrations, whereas the specific date of annual migration is commonly associated with temperature (Shaw 2016). Alterations in annual migration phenology have become more prevalent across many taxa as a result of temperature changes from anthropogenic climate change (Anderson et al. 2013, Crear et al. 2020, Shaw 2020). Therefore, a comprehensive understanding of dominant migratory cues and factors that influence animal movement is critical for predicting shifts in distributions and associated ecological consequences, especially for vulnerable species that are susceptible to multiple threats.

The American horseshoe crab is an iconic coastal marine arthropod and is currently listed as vulnerable on the IUCN Red List (Smith et al. 2016). In recent decades, horseshoe crabs have experienced declines in several regions presumably from exploitation from commercial industries (biomedical and commercial fishing) coupled with habitat loss, and this pattern has raised conservation concerns for the species (Berkson and Shuster 1999, Smith et al. 2016, 2017). Despite their vulnerable status, there is limited information on seasonal changes in subtidal habitat use, migration timing, and the distribution of horseshoe crabs in many regions. Although acoustic telemetry techniques have been successfully employed to observe adult horseshoe crab breeding patterns (Brousseau et al. 2004), daily locomotion rhythms (Watson et al. 2016), partial migration (James-Pirri 2010, Schaller et al. 2010), and seasonal changes in activity (Watson et al. 2016), these studies had limited spatial and temporal resolution and neglected to examine horseshoe crab space use across interannual scales, sex, and age-groups. In addition, seasonal spatial distributions and movement patterns of larger juvenile horseshoe crabs (80–170 mm prosomal width) remain limited due to their elusive behavior and essential nursery areas have yet to be categorized (Botton 2009). Seasonal distribution data of both adult and juvenile age-groups are currently scarce within estuaries, particularly outside of Delaware Bay (Able et al. 2019), and have primarily focused on horseshoe crab exchange between the estuaries and ocean. There is some evidence that adult crabs may utilize different habitats within estuaries outside of the spawning season in summer (Lee 2010), and trawl data suggest the elusive juvenile age-group may be fairly mobile given they are found on the continental shelf in the Mid-Atlantic Bight in the fall (Able et al. 2019). However, a thorough evaluation of the estuarine habitats linked by horseshoe crab movements through time for adults and juveniles is lacking, and thus, a rigorous analysis of migratory connectivity is required to understand the ecological and conservation implications of their movement dynamics (Cohen et al. 2018, Gao et al. 2020).

Despite some horseshoe crab populations exhibiting partial migration, it remains unclear

which environmental factors influence their timing and frequency of migratory activity (Smith et al. 2009). For example, temperature is correlated with horseshoe crab activity in temperate horseshoe crab populations because they become inactive when temperatures fall below 10°C, and recent studies suggest that seasonal spawning may be influenced by a combination of photoperiod and temperature (Watson et al. 2009, 2016, Brockmann and Johnson 2011). Recent evidence indicates horseshoe crabs have endogenous circalunidian clocks that mediate peak spawning activities around new and full moons and may also influence migration activities (Smith et al. 2002, Ehlinger and Tankersley 2003, Chabot et al. 2011). Migratory horseshoe crabs predominantly exhibit oceanic to estuarine migrations in the spring to spawn in estuarine beaches and seaward migrations in the fall to prepare for overwintering on the continental shelf (Botton and Ropes 1987, Swan 2005, Smith et al. 2009, Able et al. 2019). However, the degree of migration varies throughout their current geographic range (Yucatan, Mexico to Maine, USA) and may differ between sexes. In the mid-Atlantic, the majority of horseshoe crabs exhibit seasonal migration (Smith et al. 2009, Able et al. 2019); conversely, New England populations predominantly consist of residents in local estuaries that exhibit limited seasonal migratory exchange between the continental shelf and estuaries (James-Pirri 2005, 2010, Moore and Perrin 2007, Schaller et al. 2010). Additionally, females are hypothesized to migrate at higher proportions than males, given their abundances have been documented to be higher on the continental shelf in some areas (Rudloe 1980). Despite extensive tagging efforts, the proportion of migratory individuals and the impacts of environmental factors on migration timing remain to be quantified for populations throughout the Mid-Atlantic Bight and between sexes.

Our goals in this study were to utilize acoustic telemetry to (1) quantify the variation in migration timing and identify environmental drivers of migration in adult horseshoe crabs, (2) quantify the proportion of migratory vs. resident individuals, and (3) examine differences in horseshoe crab migratory connectivity and residency patterns in Moriches Bay, NY, among seasons, and between sex and age-groups. We expected adults

to exhibit the greatest dispersal and experience the highest amount of unique location linkages outside of the spawning season relative to other seasons. Additionally, we expected males to exhibit lower connectivity and dispersal relative to females during the spawning season, because they are known to spend more time near spawning beaches (Penn and Brockmann 1992). We predicted that adults would exhibit higher residency near spawning beaches during the spring and summer and low residency in the bay in the fall. We also expected juveniles to have high residency year-round in locations with lower adult residency patterns. Lastly, we predicted the spatial extent and migratory connectivity to be lower for juveniles relative to adults over the same time periods. This study provides insight into the complexity of horseshoe crab spatiotemporal movement patterns that can be used to improve the understanding of subtidal space use and inform conservation efforts for horseshoe crabs throughout the U.S. East Coast.

METHODS

Study site and acoustic telemetry array

Deployment of acoustic telemetry receivers and all horseshoe crab tagging activities were carried out in Moriches Bay and in the Atlantic Ocean near Moriches Inlet (Fig. 1). Moriches Bay is a shallow estuary centered at 40°47'22" N, 72°42'56" W. It is part of the South Shore Estuarine Reserve, which is composed of a series of interconnected estuarine lagoons in Long Island, NY. Peak horseshoe crab spawning activity in Moriches Bay occurs in late May–early June (Sclafani et al. 2009). A maximum of 28 passive (fixed-station) acoustic telemetry receivers (69kHz VR2AR, VR2W, and VR2Tx, VEMCO Ltd., Halifax, Nova Scotia, Canada) were deployed in the spring–fall seasons from 2017 to 2019 (Fig. 1 and Appendix S1: Fig. S1). Additional information on the study site, acoustic receiver array, transmitter programming, justifications for seasonal durations, and attachment methods is included in the Appendix S1.

To quantify the transmitter detection probability by acoustic receivers, we conducted a range test on V8, V9, and V13 transmitters across seven distances ranging from 75 to 508 m from the test transmitters in Moriches

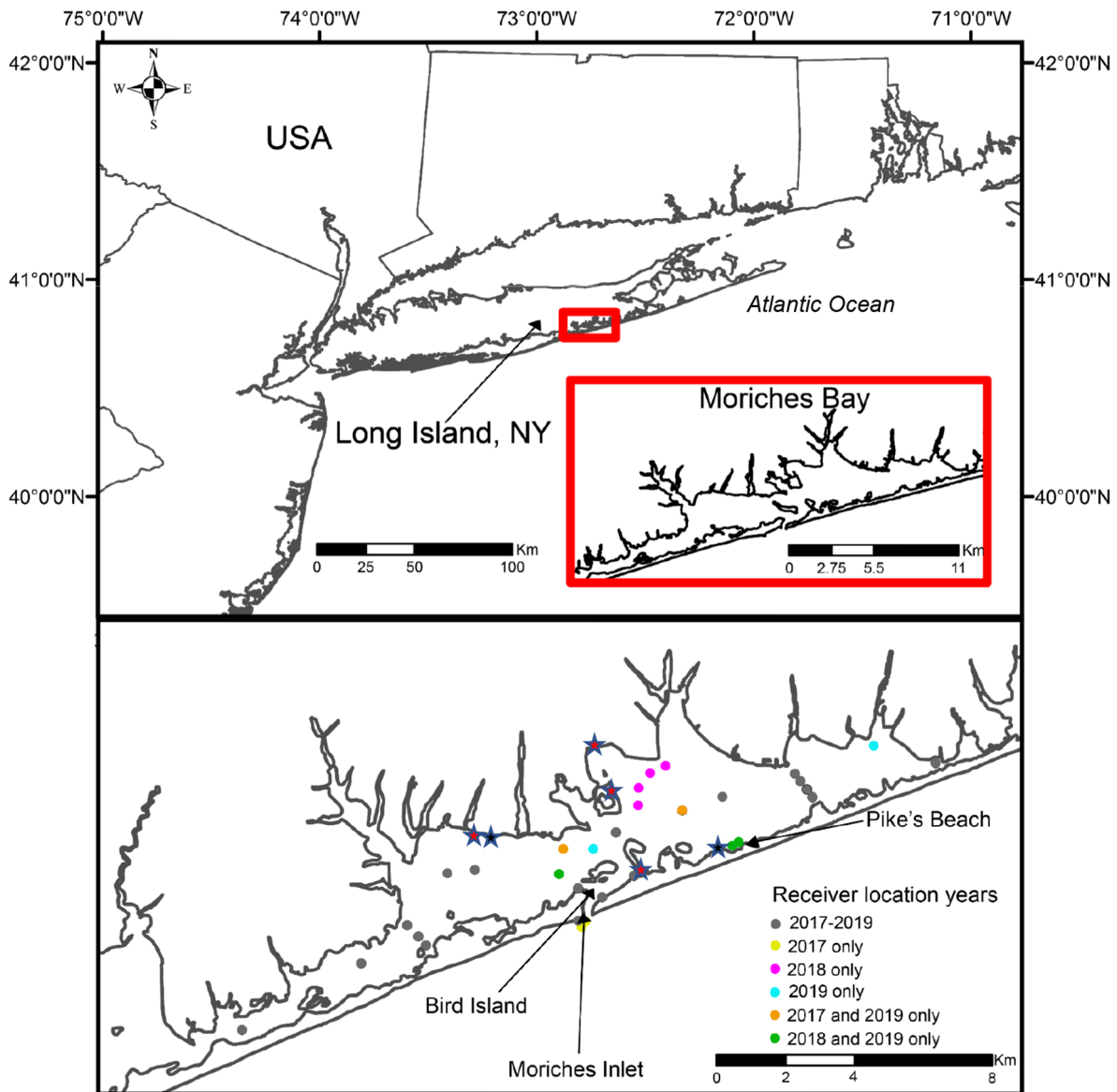


Fig. 1. Map showing the study area Moriches Bay, in Long Island, NY, USA (top) and acoustic receiver locations (bottom). Acoustic receiver locations from 2017 to 2019 in Moriches Bay and Moriches Inlet represented by circles. Years in which receivers were deployed are outlined in the legend. Receivers deployed across all years are represented in black. Red stars denote juvenile, and black stars denote adult tagging release locations in 2017 (bottom panel).

Bay from 8 August to 15 August 2019 (see Appendix S1: Table S2 for receiver distances). All receivers used for the range test were oriented in a linear array, and the transmitters were fixed facing the range test array. To minimize transmitter collisions and loss of data,

each transmitter was activated 20 s apart from each other and each transmitter had a pinging interval of 60 s. Range test results were used to determine the probability of receiver overlap in our gated arrays and inlet receiver overlap with the inlet jetties (Appendix S1: Table S2).

Horseshoe crab capture and tagging

Adult horseshoe crabs ($n = 70$; 208.8 ± 2.4 mm PW) were captured by hand and tagged at two spawning beaches during 15–24 June 2017 (Fig. 1). Juvenile and sub-adult horseshoe crabs ($n = 25$; 131.9 ± 5.4 mm PW) were captured with a modified crab dredge from September–October 2017, and tagged individuals were released at four locations (Fig. 1; see Appendix S1: Table S1 for size ranges). Juveniles were tagged in the fall to minimize the chance that individuals would lose their tags by undergoing their annual molt, because juvenile molting likely occurs in late-August to early-September each year when water temperatures peak (Estes et al. 2015). To ensure we did not tag individuals prior to molting, we tagged individuals that had blue-green carapaces with a fresh mucous layer and no characteristics of molting (i.e., split flange). Individuals that exhibited physical damage or abnormal behaviors were not tagged. Before tagging, all horseshoe crabs captured were submerged in a fish tote filled with seawater. Individuals had their blotted dry weight (g), sex, and prosomal width (mm) recorded. For adults, sex was determined externally based on the presence or absence of modified pedipalps (Smith et al. 2009, 2010). In juveniles, sex was determined by gonopore (genital pore or slit) structure (Hata and Berkson 2003). Details regarding the acoustic transmitter tagging process (see Brousseau et al. 2004) and transmitter battery life can be found in Appendix S1.

Data analyses

Before conducting formal analyses, false detections were identified and removed from the data set following criteria from Pincock and Johnston (2012) using the GLATOS package in R (Binder et al. 2016, Holbrook et al. 2016) (See Appendix S1). All data manipulation, formatting, and statistical analyses were conducted in R version 3.2.2 (R Core Development Team 2020).

Migration.—An animal was designated as migratory if it had at least three consecutive acoustic detections on an inlet receiver (<300 m from Inlet Jetties). The probability of migration and 95% confidence intervals, assuming binomial errors, was estimated for adult and juvenile horseshoe crabs separately based on the total number of tagged individuals in each group. All

migration events from 2017 to 2019 were incorporated in the analysis. The Inlet receivers were deployed from April–December in 2017–2018 in efforts to maximize the detection of immigration and emigration events (see Appendix S1 for deployment duration details).

To determine whether horseshoe crabs exhibited a preference for migrating under specific lunar phases, we used Rao's spacing test, a circular statistics method where the null hypothesis assumes that the underlying distribution is uniform (Bergin 1991). Rao's spacing test is more robust relative to other circular statistical tests and is capable of handling data with multimodal distributions. All lunar phase data were obtained from the Lunar package (Lazaridis 2014) in R. All phases (8) of the moon were matched to each individual's corresponding migration date from 2017 to 2018. To analyze migration data with circular statistics, each lunar phase value was converted into circular degree angles.

Migration frequency distributions were compared between the fall and spring seasons for temperature and photoperiod regimes in 2017 and 2018, because the total number of migration events in 2019 was small ($n = 8$). Photoperiod was calculated with the *geosphere* R package (Hijmans et al. 2017). To examine seasonal differences in the distributions of migration timing in relation to photoperiod and temperature, empirical cumulative distribution functions (ECDF) were constructed allowing for visual inspection of the entire range of environmental variable values when horseshoe crabs migrated. ECDFs were compared using two-sample bootstrap Kolmogorov-Smirnov tests in the *Matching* R package (Sekhon 2011). Bootstrap Kolmogorov-Smirnov tests were appropriate to use because they do not assume normally distributed errors, do not require a continuous distribution, and allow for the presence of ties (Sekhon 2011).

A generalized linear mixed-effects model (GLMM) was used to examine intrinsic and environmental drivers that influenced the migration timing in adult horseshoe crabs. Only migration data from the summer and fall of 2017 were used in the GLMM because this period was observed to have the highest number of migration events and tags at liberty in the array, compared to subsequent years. The date of migration was the response variable,

and dates were converted to the Julian calendar day of the year. In the model, a Gamma distributed error structure with a log-link was used, as the Gamma distribution was well suited for the non-zero, continuous, positive data of the response variable (Zuur et al. 2009). For the explanatory variables, individuals were considered to be random effects, whereas temperature, photoperiod, age-group (factor), sex (factor), and prosomal width were considered as fixed effects. An interaction term for photoperiod and temperature was also included in the model to determine whether migration timing was affected non-additively by these two external factors, as is the case with other seasonal migration patterns (Ingram et al. 2019). Model selection was carried out by using the dredge function in the *MuMIn* R package to compare the fits of all potential model combinations (Barton and Barton 2015). The small sample size-corrected Akaike information criterion (AIC_c) was used to determine the best model given the data (Burnham and Anderson 2002). Following criterion from Burnham and Anderson (2002), inference was derived from model variants with $\Delta AIC_c < 3$. All GLMMs were fit in the *lme4* R package (Bates et al. 2015).

Network connectivity.—Prior to calculating spatial network connectivity metrics and residency probabilities, all receivers were grouped into distinct geographical receiver states, a requirement for both network and empirically derived Markov Chain analyses (Stehfest et al. 2015). Receiver groups that were observed to have overlapping detection ranges ($n = 7$ receivers) were designated as one geographical state to avoid a potential bias from simultaneous detections across two or more individual receivers. Both network analysis and EDMC models require transition matrices, although the details of their construction differ as described below and in the Appendix S1. Separate transition matrices were created for each season, adult sex, and age-group (adults and juveniles). Detection data were split into approximately 2-month periods for each season, and hereafter, each season will be designated as spring (25 May–14 July during 2018 and 2019), summer (24 June–16 August 2017; 15 July–16 September 2018–2019), and fall (17 August–11 November 2017; 17

September–11 November 2018–2019). Ideally, we would have preferred to have year-round receiver coverage, but receiver deployment was constrained temporally by USCG buoy deployments and logistical constraints (i.e., delayed receiver shipments).

Spatial network analysis was used to quantify seasonal patterns in migratory connectivity for sex and age-groups to identify important population-level habitat linkages within the study area. Weighted and directed unipartite spatial networks were constructed from transition matrices within each season for each sex and age-group. Each transition matrix enumerated the number of transitions between receiver states within the array and ignored consecutive detections at each receiver state to examine only movement between receiver states. From the transition matrix, edges (movement between a unique receiver pair) were constructed by using relative interaction data (RID). RID were calculated from the proportion of movement events made between a specific pair of nodes (receiver locations) divided by the total number of edges in the network (Jacoby et al. 2012). It should be noted that network metrics are constrained by our receiver array configuration, and therefore, do not represent all potential movement paths of horseshoe crabs within the bay.

Two metrics, degree and eigenvector centrality, were used to quantitatively assess the strength of habitat linkages and their relative influence in the network structure (Lookingbill et al. 2010, Jacoby et al. 2012, Ledee et al. 2015). Degree centrality is the number of direct connections to a node and can be calculated as the number of movement connections into a node, out of a receiver node, or as a total for both directions (Jacoby and Freeman 2016). The latter was used in the present study. Degree centrality can be perceived as a proxy of important connection centers within a network.

Eigenvector centrality quantifies the relative influence a location has on overall habitat connectivity in the network. Eigenvector centrality assigns a score to each receiver relative to other receiver locations based on its own degree centrality and the degree centrality of each receiver connected to it (Stehfest et al. 2015, Newman 2018). Eigenvector centrality was calculated as the dominant eigenvector of the transposed

transition matrix using the power method (Newman 2018). It is a proxy of preferred space use by organisms (Stehfest et al. 2015).

Average path length was measured for each individual crab in each season to measure the efficiency of horseshoe crab movement among habitats (Rayfield et al. 2011, Ledee et al. 2015). Average path length was measured as the average number of nodes an individual passed through in moving from one location to another (Ledee et al. 2015). If the average path length was high, then an individual visited a high number of receivers in a given route, and suggests movement is not patchy or fragmented between locations (Rayfield et al. 2011).

Two-way ANOVAs were employed to determine whether the variation in network connectivity metrics (degree centrality, eigenvector centrality, and average path length) was driven by sex and season. Because of different annual receiver configurations, separate ANOVA models were constructed for each year. Type I sum of squares (SS) was used for the degree centrality and eigenvector centrality ANOVA models since the data were balanced. For the average path length metric, Type III SS was applied given the design was unbalanced. To minimize violations of normally distributed errors and homogeneity of variance, an extended Box-Cox analysis was carried out on the network metrics prior to running ANOVAs (Box and Cox 1964, Sokal and Rohlf 2012). This extended Box-Cox procedure employed maximum likelihood to find the power transformation of the data that optimized normality and homogeneity likelihoods (Sokal and Rohlf 2012). The analysis suggested that a log transformation was indicated; network metrics were $\ln(x + 0.001)$ transformed with the small constant added because of the presence of zeros in the response variable. Residuals were visually checked following ANOVA to ensure the normality and homogeneity assumptions were met. A Tukey's HSD pairwise comparison test was used to examine factor levels in significant fixed effects using the *stats* R package (R Core Development Team 2020).

Residency period.—An empirically derived Markov chain model (EDMC) was employed to quantify residency probabilities of horseshoe crabs during each season for each sex and age-group. This analysis included all detection data

(transitions and consecutive resident detections at a receiver location). Residency probabilities for each receiver location and intermediate state between locations were obtained from the dominant eigenvector of the transition matrix. The dominant eigenvector was calculated using the power method (Stehfest et al. 2015). The resulting steady-state vector values represent residency based on the observed transition matrices. To obtain relative detection probabilities for each receiver, we standardized the residency probabilities at observed receiver locations to sum up to 1 by taking each receiver residency probability and dividing it by the total residency probability at all receiver locations. Relative residency probability was estimated for each season, and additional information on the EDMC setup is available in the Appendix S1.

RESULTS

Detection summary

According to range test results, adult horseshoe crabs had a 65.5% (SD = 25.7) average detection probability for V13 transmitters in the Moriches Inlet, provided the closest receiver to land was <290 m away from the farthest jetty (Appendix S1: Table S2) and was consistently retrieved each year. Juvenile detection probabilities were 55.8% (SD = 25.0) (Appendix S1: Table S2).

Throughout the study, 62 (88%) adults and 20 (80%) juveniles were detected in at least one annual deployment period (May–November) (Appendix S1: Table S1). For adults released in 2017, 53% were consistently detected in 2018, while 33% of adults were detected during in both 2018 and 2019. The number of detected adult crabs declined through time with 60, 33, and 25 of the 70 tagged adult horseshoe crabs detected in 2017, 2018, and 2019, respectively. Overall, 80% ($n = 20$) of tagged juveniles were detected in the 2017–2018 receiver deployments, with five individuals detected in 2017 and 15 individuals detected in the spring and summer of 2018. When detections were standardized per individual, adults (4914 detections per individual; 344,019 total detections) were detected 3× more often than juveniles (1812 detections per individual; 45,318 total detections). The average number of detections for adults and juveniles was

5460 ± 770 and 2578 ± 841, respectively. Cumulative days at large (DAL) in the array across the entire study period for all individual crabs ranged from 0 to 439 d, and the maximum DAL was 192 within a given year (Appendix S1: Table S1). Most juveniles ($n = 16$; 64%) were only detected in the spring to early summer of 2018 and were not detected after 14 July.

Migration

The frequency of migration varied among individuals and with age-group, but not by sex (Table 1). In 2017, 63% ($n = 15$) of the emigration ($n = 22$) events out of the bay occurred in the fall from 26 September to 14 November. In spring 2018, 92% ($n = 12$) of all immigration events ($n = 13$) from the ocean occurred from 22 April to 16 June. During April–November 2019, 7 adult crabs migrated (one-way) in total between Moriches Bay and the Atlantic Ocean and 2 of these individuals were observed to migrate for the first time. Of the adult migratory contingent (29 out of 62 detected crabs), 62% ($n = 18$) migrated one year, 31% ($n = 9$) migrated 2 yr, and 7% ($n = 2$) migrated during all three years. From 2017 to 2019, 9 (41%) individuals from the migratory group were observed to return to the bay in the spring (2018), and 3 (14%) were not detected in 2018 but returned to the bay in 2019. The average migration probability exhibited by adults was 41% (95% CI: 34.0–59.8). Juveniles exhibited a higher proportion of resident individuals than adults, with only 8% (95% CI: 1.2–31.6) of tagged juveniles (1 male and 1 female) migrating out of the bay into the ocean in November 2017. No migratory juvenile was observed to return to Moriches Bay.

Horseshoe crabs showed a heterogeneous migration pattern (Rao's spacing test of uniformity, $U = 282.16$, $p < 0.01$), but preferentially migrated (emigration and immigration) during the new moon phase (Fig. 2). Using 2017 and 2018 data, migration was observed during all moon phases with the greatest number of migration events (both into and out of the bay) during the new moon ($n = 9$; 26%). The lowest number of migrations was observed during full moons ($n = 2$; 5%).

Seasonal migration out of Moriches Bay in the summer–fall and into Moriches Bay in the spring–summer differed with respect to temperature regimes (Kolmogorov-Smirnov test, $D = 0.44$, $p = 0.03$). In 2017, >75% of migrations occurred before temperatures fell below 15°C in the fall (Fig. 3A). Conversely, >65% of individuals returned to the bay from the continental shelf before temperatures exceeded 15°C in the spring of 2018. The coldest water temperature observed during migration was 7.5°C (an individual immigration event), and the warmest water temperature observed during any migration event was 22.6°C (an individual emigration event).

Migratory frequency also differed with photoperiod regimes (Kolmogorov-Smirnov test, $D = 0.64$, $p < 0.01$) (Fig. 3B). During emigration into the ocean during the summer–fall 2017, adults migrated at day lengths ranging from 14:9 to 10:0 hours (median = 11.5 h). In contrast, the day length range for immigrations into the bay during spring–summer 2018 was 15.1 to 12.7 h (median=14.5 h), roughly half the time range as observed for emigration.

After model selection, the best GLMM model for migration timing included temperature, photoperiod,

Table 1. Total number of horseshoe crabs tagged, detected, and migrating during 2017–2019 for each age and adult sex class.

Age-group	Sex	Total tagged	Total individuals detected	No. individuals migrating	Migration probability (%)
Adults	Males	31	28	13	42 (27.5–66.1)
	Females	39	34	16	41 (29.7–64.8)
	Total	70	62	29	41 (34.0–59.8)
Juveniles	Total	25	20	2	8 (1.2–31.6)

Notes: Migratory individuals are those that moved between Moriches Bay and the Atlantic Ocean at least once throughout the study duration. The migratory probability is presented with 95% confidence intervals in parentheses. The average migration probability was based on the number tagged.

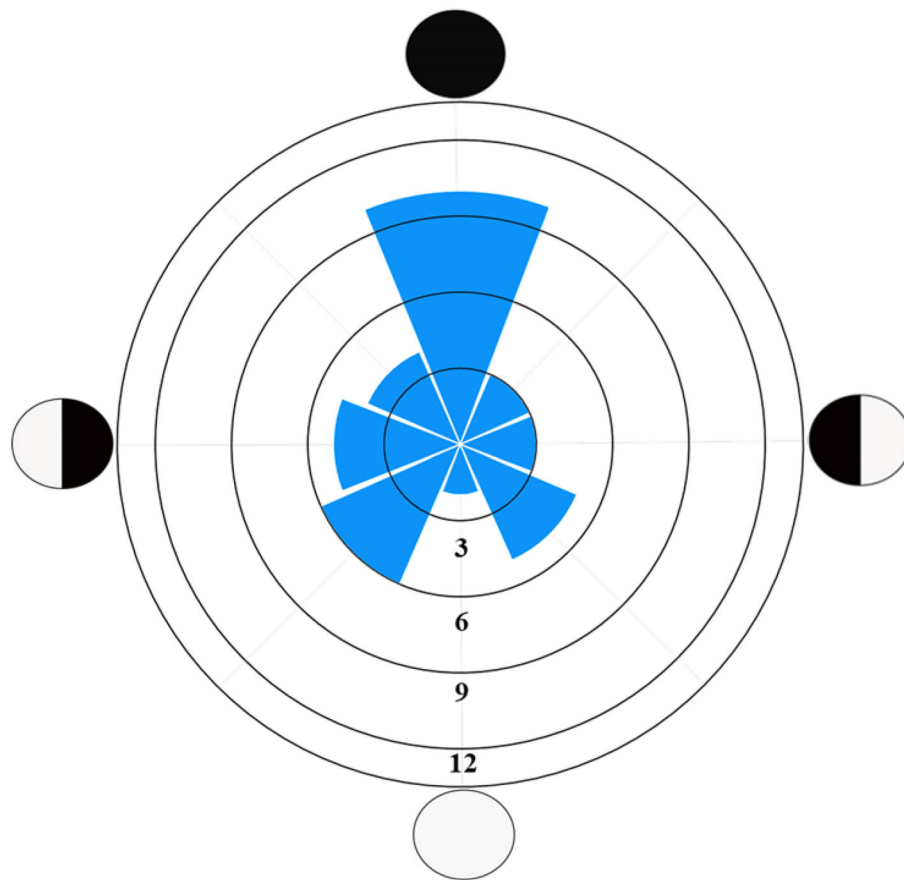


Fig. 2. Rose plot representing frequency of migration with moon phase for adult horseshoe crabs from 2017 to 2018 data sets. Quarterly moon phases are indicated by shading with black representing the new moon and white representing full moon.

and the interaction term between temperature and photoperiod (Table 2 and Appendix S1: Table S3). The best model had strong support given the Akaike weight was >0.85 , the ΔAIC_c of the second model was >5 , and the evidence ratio of the top model relative to the second model was 21.5 (Appendix S1: Table S3).

Network connectivity

There was substantial evidence for degree centrality (number of unique location linkages) variation by year, season, and sex (Fig. 4, Table 3). The interaction term (season:sex) was significant in 2018 ($F_{2,102} = 4.58$, $p = 0.01$) and 2019 ($F_{2,102} = 3.09$, $p < 0.05$), but no significant interaction or main effect was present in 2017 (Tables 3 and Appendix S1: Table S4), likely due to lack of available data in spring 2017. In 2018, females

exhibited higher degree centrality in the spring compared with summer (Tukey HSD, $M = 4.37$, $p < 0.01$), whereas males were observed to have higher degree centrality in the spring ($M = 4.04$, $p = 0.01$) compared with the summer and fall. In 2019, seasonal differences in degree centrality occurred in males ($M = 4.43$, $p < 0.01$), but not females, and were greater in the spring relative to the fall and summer (Appendix S1: Table S4). Males and females exhibited differences in degree centrality in the summer months of 2018 and 2019 (Table 3). During the spring seasons, adult horseshoe crabs made connections to nearly all receiver locations relative to other seasons. In contrast, most location connections in the bay were concentrated within the central section around Bird Island and the Moriches Inlet with little movement in the Eastern or Western

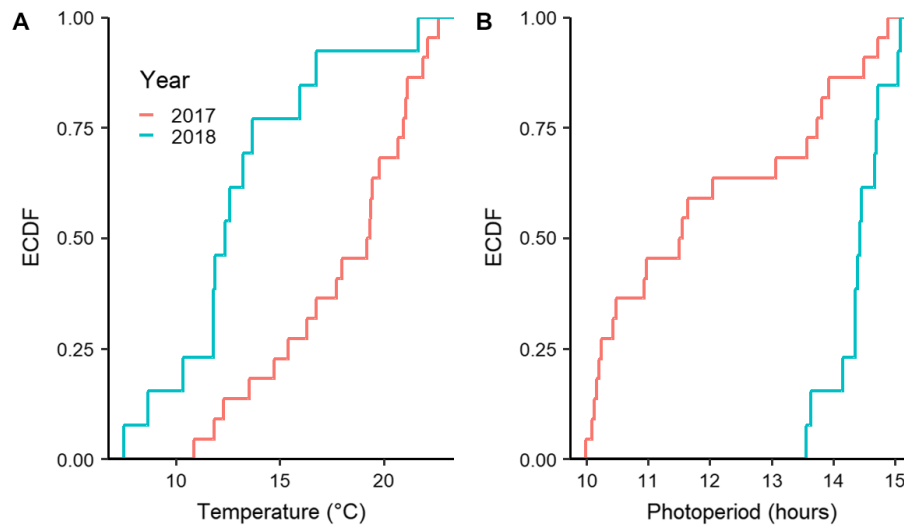


Fig. 3. Empirical cumulative distribution functions (ECDFs) of adult horseshoe crab migrations between Moriches Bay and the Atlantic Ocean over temperature (A) and photoperiod (B). Summer–fall 2017 (red line) migration observations ($n = 22$) represent movement to the Atlantic Ocean from Moriches Bay. Spring–summer 2018 (blue line) migration observations ($n = 15$) represent movement from the Atlantic Ocean into Moriches Bay.

Table 2. Results for the best generalized linear mixed-effects model (GLMM) for migration timing of adult horseshoe crabs from the bay to the Atlantic Ocean in the fall 2017.

Fixed effects	Estimate	SE	t	p
(Intercept)	7.0936	0.170	41.538	<0.001
Temperature	-0.0128	0.008	-1.554	0.120
Photoperiod	-0.1396	0.016	-8.376	<0.001
Temperature: photoperiod	0.0017	<0.001	2.241	0.025

Notes: Temperature:photoperiod represents the interaction of temperature and photoperiod. Intercept and slope estimates, standard error (SE), t , and p are presented. For the random effect (individual ID), the variance was 0.0001 with a standard deviation of 0.0103. See Appendix S1: Table S3 for GLMM candidate set.

locations during the summer and fall seasons (Fig. 5).

Eigenvector centrality (strength of location linkages) also indicated year, season, and sex variability but was not as variable as degree centrality. In 2017, there were no significant main effect or interaction terms present (Appendix S1: Fig. S4, Table 3). In 2018, season was significant ($F_{2,102} = 6.17$, $p = <0.01$) but not sex ($F_{1,102} = 0.45$, $p = 0.50$). Horseshoe crabs, regardless of sex, had higher eigenvector centrality in the spring

compared with the summer (Tukey HSD, $M = 1.63$, $p = 0.02$) and spring relative to fall ($M = 1.88$, $p = <0.01$). In 2019, the interaction of season and sex influenced eigenvector centrality ($F_{2,102} = 5.69$, $p = <0.01$). Only females exhibited seasonal differences with higher eigenvector centrality in the spring ($M = 3.19$, $p = <0.01$) and summer ($M = 2.65$, $p = 0.04$) relative to fall. Locations in the center portion of Moriches Bay around Bird Island had the highest eigenvector centrality scores consistently across season for both sexes throughout the duration of the study, except for males in spring 2018 (Appendix S1: Fig. S4).

More than 96% of all juvenile detections occurred in spring 2018, and thus, juvenile habitat connectivity patterns were only analyzed during this period. Juvenile horseshoe crabs made transitions only between two pairs of receivers (degree centrality <3) and primarily restricted their movements to the north-central section of the bay (Fig. 5). Juveniles exhibited a 12-fold lower number of unique location linkages ($n = 4$) compared with adults ($n = 48$) during the spring period in 2018 (Figs. 4 and 5), with 20% ($n = 5$) juveniles observed to make transitions between available receiver states.

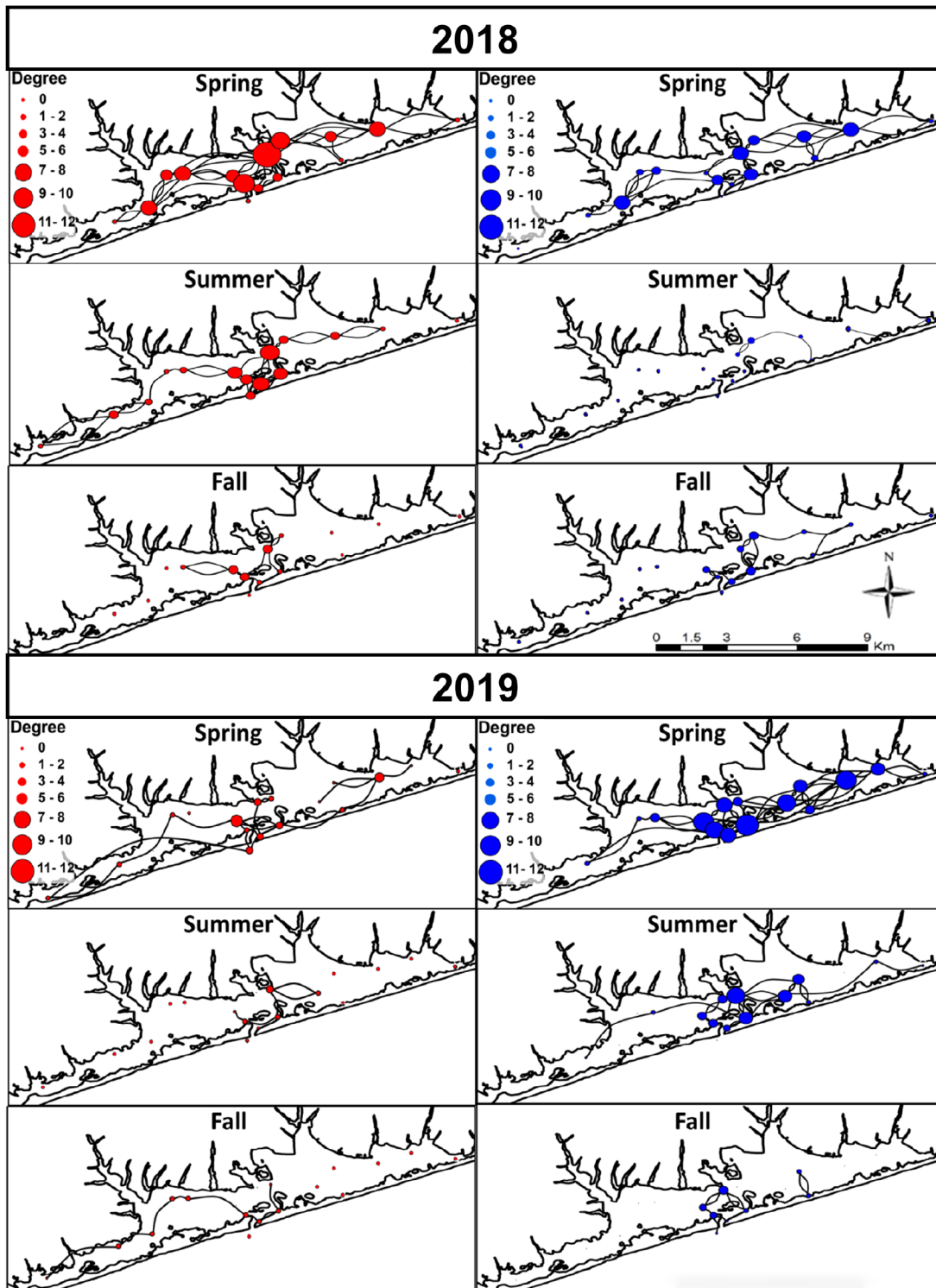


Fig. 4. Network maps denoting degree centrality for each acoustic receiver by season, sex, and year (2018 and 2019). Males are denoted in red and females are represented by blue. Years represented are as follows. No pairwise differences in degree centrality for 2017 were found (see Appendix S1: Fig. S3).

Table 3. Two-way ANOVA results for the network analysis metrics (eigenvector centrality and degree centrality) for 2017, 2018, and 2019.

Variable	Degree centrality					Eigenvector centrality				
	df	SS	MS	F	p	df	SS	MS	F	p
2017										
Season	1	19.50	19.46	1.06	0.30	1	8.90	8.903	0.97	0.32
Sex	1	4.40	4.37	0.23	0.62	1	0.01	0.007	<0.01	0.97
Season:sex	1	0.70	0.65	0.03	0.85	1	0.20	0.223	0.02	0.87
Residuals	56	1027.80	18.35			56	509.70	9.102		
2018										
Season	2	231.20	115.61	8.93	<0.01	2	75.20	37.61	6.17	<0.01
Sex	1	32.80	32.84	2.53	0.11	1	2.70	2.74	0.45	0.50
Season:sex	2	118.40	59.20	4.57	0.01	2	24.50	12.27	2.01	0.13
Residuals	102	1319.20	12.93			102	621.00	6.09		
2019										
Season	2	189.30	94.65	6.99	<0.01	2	64.20	32.11	4.39	0.02
Sex	1	50.60	50.56	3.73	0.05	1	0.02	0.01	0.00	0.96
Season:sex	2	83.60	41.79	3.09	0.05	2	83.10	41.57	5.68	<0.01
Residuals	102	1379.50	13.52			102	745.70	7.31		

Note: Season:sex denotes the season and sex interaction.

Sex and season did not significantly affect the average path length of adult horseshoe crabs in any year based on two-way ANOVA results. Path length in juveniles was not analyzed given the low number of observed transitions (five individuals made transitions) in 2018.

Residency probabilities

Of the horseshoe crabs detected, individuals spent 34.8–98.3% of their time outside of the acoustic receiver array coverage areas during the periods of receiver coverage, but Bird Island and Moriches Inlet receivers were the most probable detection regions in the study area (Fig. 6). These results are consistent with eigenvector centrality metrics generated from network analyses. Adults did not occupy the easternmost and westernmost habitats (0% relative residency probability in all seasons) (Fig. 6). Overall, most location states with the highest eigenvector centrality scores in the network analysis also had the highest residency probability estimates from the EDMC model for each year, season, and sex (Appendix S1: Fig. S4 and Fig. 6).

Several differences in preferred residency locations were observed between sexes within seasons. In fall 2017, spring 2018, and spring 2019, females had up to 8 times greater relative probability of being detected in the inlet compared with males (Appendix S1: Fig. S5 and Fig. 6). In

fall 2017, females had only two locations with non-zero relative probabilities, while males had 3 times as many habitats with non-zero relative probabilities (Appendix S1: Fig. S5 and Fig. 6). In 2018, the number of locations with relative residency probabilities > 0 did not differ substantially within a season between males and females (Fig. 6). In 2019, males had 2 times greater relative residency probability relative to females in most locations north of Bird Island and Pike's Beach in the spring. This residency trend was reversed between sexes in the summer and fall of 2019.

Juvenile residency probability was 2 times greater in the northeast habitats of Bird Island in spring 2018 compared with their adult counterparts. Juveniles also had nearly 3 times less locations with relative residency probabilities > 0 in the bay in spring 2018. Overall, it should be noted that juveniles were detected across a short duration (spring 2018 only) due to limited battery life, and thus, inferences regarding juvenile horseshoe crab seasonal connectivity and residency are limited compared with adult counterparts in this study.

DISCUSSION

Migration patterns

Similar to many migratory taxa (Shaw 2016), we found evidence of partial migration in the

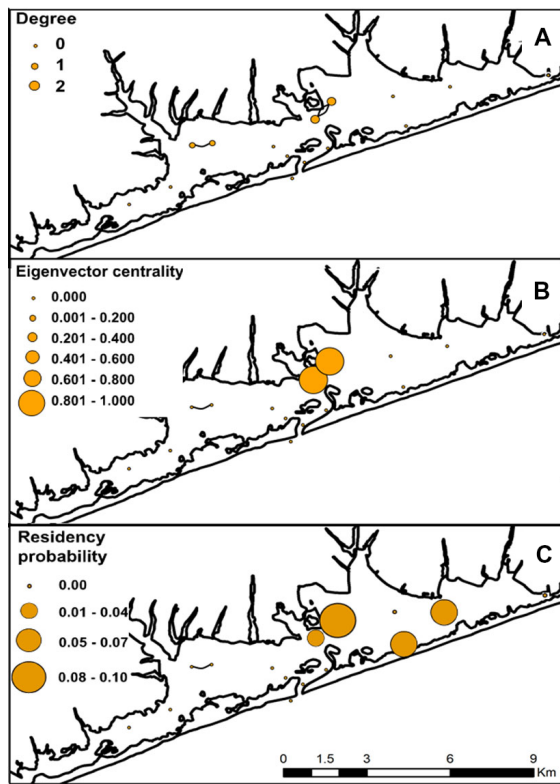


Fig. 5. Juvenile horseshoe crab spatial network metric maps for the spring of 2018. Degree centrality (A), eigenvector centrality (B), and residency probability (C) are graduated by circle size. Residency probability for juvenile horseshoe crabs from empirically derived Markov chain (EDMC) models during spring 2018.

Moriches Bay, NY, horseshoe crab population, with the majority of individuals remaining as residents within the bay. Partial migration can enhance population stability because both resident and migratory contingents may play important roles in regulating population dynamics. For example, migrant individuals may capitalize on additional resources that are unavailable to resident individuals and reduce intra-specific competition at the expense of increased physiological cost (i.e., energy expenditure) or heightened predation risk. Resident counterparts may experience reduced energy expenditure by exploiting local resources with potentially greater variability in availability but can buffer population declines (Skov et al. 2011, Chapman et al. 2012). As a result, preserving partial migration is perceived to be an important conservation objective in

many populations because migratory traits may optimize resource utilization, enhance reproductive success, and provide exchange of energy among systems (Dingle and Drake 2007, Bauer and Hoyer 2014, Lennox et al. 2016). For example, Norwegian spring-spawning herring, *Clupea harengus*, are responsible for transporting 1.3×10^6 tons of biomass annually from the ocean to the coast from eggs and milt, which likely represents the world's largest influx of energy from a single species population (Varpe et al. 2005). For horseshoe crabs, it is estimated that 13.2 million out of 20 million adult crabs migrate from the Atlantic continental shelf into the Delaware Bay estuary to spawn and as many as 16–62% of eggs can be exhumed into estuarine waters from the sand (Smith et al. 2006, Jackson et al. 2020). Thus, horseshoe crabs may be important vectors of energy transfer between estuarine and continental shelf ecosystems in regions where a large fraction of horseshoe crabs are migratory.

We observed no differences in the migratory proportions between adult sex groups in this study (Table 1), contrary to our expectations given adult male crab reproductive tactics and the 2:1 M:F sex ratio on spawning beaches (Bopp et al. 2019). Consequences of alternative reproductive tactics in males, in part, may affect male migration rates. Adult male horseshoe crabs have two reproductive modes: (1) directly attached to females in amplexus (2) unattached as satellites that surround spawning pairs (Brockmann and Penn 1992). Satellite males are often more numerous (up to eight males per female) relative to attached males and have been observed to have superior foraging abilities relative to attached males throughout the spawning season (Smith et al. 2002, 2013). Therefore, one would potentially expect satellite males to exhibit higher migratory frequency compared with females given they may be in a better energetic state and may need to travel long distances to search for females. Satellite males, however, may be older and in poorer condition than attached males, making them more likely to remain resident in local estuaries than attached males (Brockmann and Penn 1992; Brockmann et al. 1994). Furthermore, although attached males are often younger and in better condition, their strategy may be more energetically taxing because they may search or remain attached extensively

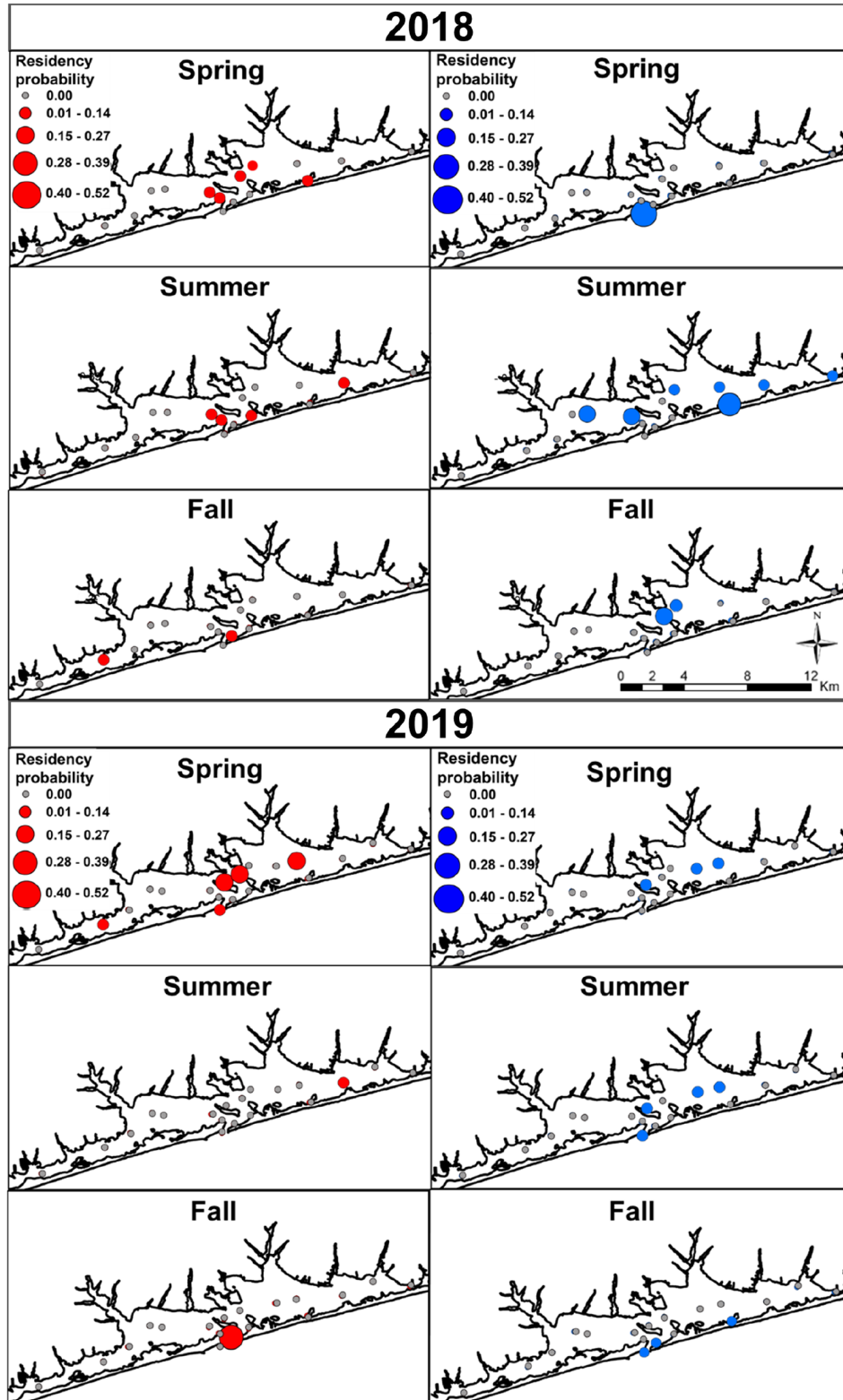


Fig. 6. Relative residency probabilities obtained for each year, season, and sex estimated from the dominant

(Fig. 6. *Continued*)

eigenvector derived from empirically derived Markov chain (EDMC) models. Males are denoted by red colors, and females are represented by blue. Receiver locations with relative probabilities <0.01 are denoted on the scale as gray circles. Years are as follows: 2018 (top) and 2019 (bottom).

to females throughout the year outside of the spawning season at the expense of sustained periods (weeks to months) of chronic starvation (Smith et al. 2013, 2017). These results may partially explain why males did not have higher migration rates relative to females. Further investigation on the impact that physiological condition has on horseshoe crab migration status is recommended considering condition influences the individual migration status in other aquatic species (Brodersen et al. 2008).

The qualitative migration pattern of adult horseshoe crabs in this study mirrored the seasonal migration structure (partial migration) of mid-Atlantic counterparts (Botton and Ropes 1987, Swan 2005, Smith et al. 2006, Able et al. 2019). From a quantitative perspective, the proportion of migratory individuals for Moriches Bay (41%, 95% CI: 34.0–59.8) was lower than the percentage of the migratory contingent within Delaware Bay, which is estimated to be about 66% (Smith et al. 2006). These findings, coupled with the previous horseshoe crab movement findings for New England populations (James-Pirri 2010, Schaller et al. 2010, Watson et al. 2016, Able et al. 2019), corroborate previous observations that migratory propensity in adult horseshoe crabs decreases outside of the Delaware Bay region, which could be an artifact of varying geographic population densities. In the United States, the Delaware Bay boasts the highest population densities of horseshoe crabs, while Long Island, New England, and Florida populations can comprise spawning densities that are 2–400 times lower relative to Delaware Bay (Cohen and Brockmann 1983; Ehlinger and Tankersley 2003; Mattei et al. 2010; Bopp et al. 2019). In some taxa that exhibit partial migration, high population densities confer higher rates of migration to reduce local resource competition among conspecifics and bolster population fitness (Deutsch et al. 2003, Mysterud et al. 2011). Recent studies have also suggested that the migratory status of a population may be determined from underlying

genetic variation or may be caused by a combination of genetic and environmental interactions (Pulido 2011, Chapman et al. 2012). Although the underlying mechanisms of partial migration activities in horseshoe crabs are not known, the impacts of migratory status on individual fitness should be examined to determine whether migration is solely strategic or driven by extrinsic factors (i.e., resource availability) and to better understand the ecological implications of migration propensity throughout *L. polyphemus*'s range (Hegemann et al. 2019).

Drivers of migration

Understanding the factors that underpin migration timing is imperative because migration is often sensitive to local environmental conditions and alterations in migration timing can potentially affect survival (English et al. 2005), reproduction (Gienapp and Bregnballe 2012), and foraging patterns (Beard et al. 2019) in myriad species (Kovach et al. 2013). The interaction between temperature and photoperiod appeared to influence adult horseshoe crab migration timing (Table 2), but the temperature and photoperiod regimes in which horseshoe crabs emigrated and returned to the bay varied considerably between seasons. More than 50% of individuals migrated out of Moriches Bay before ocean temperatures were below 15°C (7 November 2017). Conversely, the return to the bay occurred at cooler temperatures where more than 50% of migratory events occurred before ocean temperatures surpassed 15°C (Fig. 3). These results generally support observations made by Watson et al. (2016), who found that temperate horseshoe crabs experience greater locomotor activity when temperatures are above 10°C; however, two individuals in our study migrated when temperatures were below this threshold in the spring of 2018. It is worth noting that migrations were recorded while crabs were in transit, and given the incomplete spatial coverage of our receiver array, we could not determine when crabs initiated migration. Interestingly,

horseshoe crabs migrated across a twofold wider range of day lengths in the fall compared with spring, suggesting that photoperiod may have a stronger influence on migration timing in the spring. In some migratory marine species, such as in Atlantic Salmon (*Salmo salar*), migration cannot occur by temperature cues alone in the absence of photoperiod cues, suggesting that photoperiod may serve as the primary circannual driver of migration with temperature acting as a secondary phenological cue in response to photoperiod (Zydzlewski et al. 2014). For example, photoperiod responses are typically mediated by the neuroendocrine system or circannual endogenous clocks in many taxa, but locomotive activity may be triggered by temperature in response to an organism's metabolism (Mathes et al. 2010, O'Brien et al. 2012). On a finer temporal scale, lunar periodicity appeared to influence the migration timing of adult horseshoe crabs as a plurality of crabs underwent migration during new moons (Fig. 3) and supported recent evidence of circalunidian clocks influencing horseshoe crab locomotion activity (Chabot et al. 2016).

Space use and migratory connectivity

In contrast to expectations that horseshoe crabs would remain close to spawning beaches, adult horseshoe crabs generally exhibited the greatest migratory connectivity and widespread spatial distributions in the spring seasons in Moriches Bay compared with summer and fall (Appendix S1: Fig. S4). Spring (April–June) is when adults exhibit peak spawning activity on low-energy estuarine beaches within the mid-Atlantic (Smith et al. 2002, Brousseau et al. 2004). During the breeding season, both sexes have been observed to repeatedly spawn on local beaches, and they tend to remain <800 m from shore between spawning bouts (Penn and Brockmann 1994; Brousseau et al. 2004). The relative residency probability at Pike's Beach was also quite low within the spring, indicating that adults spend limited amounts of time near this major spawning beach (Fig. 6) which is consistent with previous studies (Penn and Brockmann 1994, Brousseau et al. 2004). Dispersive behavior by adults in the spring could represent a searching behavior for suitable spawning habitats. Outside of the spring-spawning season, adults exhibited lower levels of connectivity between habitats, especially in the fall, and they primarily

restricted their movements to the centrally located areas around Bird Island and Moriches Inlet. This reduced migratory connectivity may be partially a result of adults intensively foraging during high tides in intertidal flats after the breeding season and into the fall to take advantage of high benthic productivity in intertidal habitats (Lee 2010). Further investigation is required to identify the processes that drive these seasonal distribution patterns in horseshoe crabs.

The only clear sex-specific differences within a season occurred for degree centrality during summer 2018 and 2019 (Table 3). The summer patterns were inconsistent between years, with degree centrality greater for males in 2018 and for females in 2019. These results suggest that sex-specific differences in movement patterns are possible but may have been influenced by different receiver configurations between 2018 and 2019. Additionally, the time period within a season when crabs of each group were near receivers may have differed, giving rise to apparent differences in connectivity. Network metrics do not preserve the temporal sequence of detections (Stehfest et al. 2015, Jacoby and Freeman 2016), so they cannot be used to check time-dependent behaviors. The EDMC analysis suggests that females were more widely distributed than males during the summer of both 2018 and 2019. Thus, network degree centrality may not be accurately portraying behavior in the summer of 2018. In any event, it is imperative to consider the effects of receiver array designs, sample size, and the fine temporal behavior of a species or group of interest on connectivity because they can influence the interpretation of ecological data and resulting management applications (Ellis et al. 2019, Novak et al. 2020).

Horseshoe crabs also showed considerable differences in space use patterns between age-groups within Moriches Bay. Adults made more dispersive movements and utilized nearly all habitats in the bay during the spring 2018, presumably a result of adults conducting a broad array of behaviors associated with spawning (Watson et al. 2009, Lee 2010, Able et al. 2019); in contrast, juveniles utilized less than a third of observable locations in the bay, predominantly restricted their distribution to the northcentral section of Moriches Bay and were six times less

likely to migrate to the ocean relative to adults (Table 1). This pattern is similar to observations in Great Bay, NH, where intermediate sized juveniles (80–150 mm prosoma width) were observed to exhibit burial behaviors in subtidal mudflats adjacent to spawning beaches and restricted occupancy to one half of the bay; in contrast, adults exhibited dispersed movements and occupied nearly all sections of the Great Bay Estuary (Cheng 2014). Disparate habitat preferences and requirements are likely a product of differences in ontogenetic space use patterns in horseshoe crabs (Gillanders et al. 2003, Grol et al. 2011). Cheng (2014) speculated that fine-grained environments may be preferred by juveniles given that it may be easier for them to excavate for foraging and resting behaviors than in coarse-grained areas. Additionally, mature adults require intertidal beaches for reproduction (Penn and Brockmann 1994) and foraging post-spawning (Lee 2010) in the spring and summer months, whereas juveniles have no reproductive habitat requirements and remain strictly within shallow subtidal areas (<6 m depth). Differences in foraging preferences are an unlikely driver of this disparate space use between the age-groups monitored during this study because stable isotope ($\delta^{15}\text{N}$) values from these age-groups overlapped within the one trophic level range in Pleasant Bay, MA (Carmichael et al. 2004).

Conservation implications

Quantifying habitat connectivity of animals is a primary guiding principle for conservation planning and is necessary for improving the representation of population connectivity among areas with heterogeneous management regulations (Engelhard et al. 2017). In the case of horseshoe crabs, examining their migratory connectivity and space use is necessary to determine the current efficacy of conservation measures. For example, bycatch from benthic and demersal commercial fisheries is thought to be an important source of adult horseshoe crab fishing mortality throughout the United States (ASMFC 2020) and understanding their spatiotemporal distributions can help prioritize protections for essential habitats. Additionally, multiple protected areas throughout the U.S. East Coast exist for horseshoe crabs and other species, including the Gateway National Recreation Area within the NY area and the Carl N. Shuster

Jr. Horseshoe Crab Reserve; therefore, understanding regional movement patterns is critical for examining the integrity of spatially oriented management strategies, especially between state jurisdictions (Kerr et al. 2010). The limited dispersal observed in most subtidal juvenile horseshoe crabs also has potential conservation implications for local horseshoe crab populations. Juveniles may be more susceptible to habitat loss and localized disturbances than adults in subtidal habitats (Munday 2004, Coates et al. 2013). Physical disturbances from ground fishing gear could result in reduced prey availability for juveniles in coastal estuaries where trawling is prevalent (Hiddink et al. 2011). These factors coupled with the slow intrinsic growth rate of horseshoe crabs (age at maturation: 8–11 yr) may hinder juvenile horseshoe crab recruitment into the adult stock (Le Pape et al. 2007; Courrat et al. 2009). Conversely, by limiting their spatial extent to smaller areas and strictly subtidal habitats, larger juveniles (80–150 mm prosoma width) could avoid factors that impose greater physiological stress and increased risk of mortality in adult crabs, such as stranding or predation during spawning in intertidal areas and allocating energy reserves for reproduction (Botton and Loveland 1989, Smith et al. 2017). This study highlights the application of complementary modern quantitative tools that can be readily applied to rigorously assess space use and migration patterns across many taxa.

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DATA AVAILABILITY STATEMENT

Data are available from the Mid-Atlantic Acoustic Telemetry Observation System: <https://matos.asascience.com/project/detail/166>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3811/full>