

Articles

Striped Bass Movement in a Large Southeastern River System

Jason C. Doll,* Jason Marsik

J.C. Doll

Freshwater Ecology Center, Department of Biology, Francis Marion University, 4822 E. Palmetto Street, Florence, South Carolina 29506

J. Marsik

South Carolina Department of Natural Resources, 295 S. Evander Drive, Florence, South Carolina 29506

Abstract

Migratory behaviors of coastal Striped Bass *Morone saxatilis* are diverse and vary by latitude along the U.S. Atlantic Coast. Northern populations (e.g., north of Cape Hatteras, North Carolina) are anadromous, with spawning occurring in tidal freshwater/brackish rivers and adults leaving spawning locations during the winter to conduct north–south coastal migrations. The central Atlantic comprises a mixture of potamodromous and anadromous types, completing the natural continuum of behavioral modes along latitudinal ecotones. Southern populations (e.g., south of Cape Hatteras, North Carolina) are typically resident and potamodromous, completing full life cycles within 36river systems, and do not migrate along the Atlantic Coast. There are limited studies that have investigated daily movement of Striped Bass in the Southeast and no studies have documented movement of Striped Bass in the Great Pee Dee River, particularly with reference to spawning migrations. The objective of this study was to describe daily movement patterns and centers of attraction (e.g., spawning and resting stages) of Striped Bass in the Great Pee Dee River, South Carolina. We implanted 10 fish with hydroacoustic transmitters between 2013 and 2016. We describe daily movement and behavior using the state-space model with a two-dimensional spatial coordinate system. We recorded a total of 94,857 data points across all individuals and receivers. We observed two movement patterns. One group completed a seasonal migration (i.e., were recorded swimming upstream or downstream) that coincides with spring spawning season. A second group was present in the lower river section and Winyah Bay during the winter for 3 consecutive years but were never observed migrating up the Great Pee Dee River during the spring. One individual was documented swimming 80 river km north in the Atlantic Intracoastal Waterway, suggesting there are important overwintering locations outside their natal river. Additionally, there were significant gaps in observations for all individuals, particularly in the summer. It is possible that fish are leaving the main stem in search of thermal refuge within small tributaries. Identifying these overwintering areas and tributaries that serve as summer refuge is needed to determine stressors and fishing pressure of this important species.

Keywords: seasonal movement; migration; coastal fisheries

Received: January 2023; Accepted: August 2023; Published Online Early: April 2024; Published: December 2023

Citation: Doll JC, Marsik J. 2023. Striped Bass movement in a large southeastern river system. *Journal of Fish and Wildlife Management* 14(2):354–364; e1944-687X. <https://doi.org/10.3996/JFWM-22-073>

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* Corresponding author: jason.doll@fmarion.edu

Introduction

Movement of highly mobile species can make determining management regulations challenging, particularly when

the species cross political boundaries. Migratory and movement behaviors of coastal Striped Bass *Morone saxatilis* are diverse and vary by latitude along the U.S. Atlantic Coast. Northern populations (e.g., north of Cape Hatteras, North



Carolina) are typically anadromous, with spawning occurring in tidal freshwater/brackish rivers with adults leaving in the winter to conduct north–south coastal migrations (Carmichael et al. 1998; Secor et al. 2020B). Southern populations (e.g., south of Cape Hatteras, North Carolina) are typically resident and potamodromous, completing full life cycles within river systems, and do not migrate along the Atlantic Coast (Hill et al. 1989). The central Atlantic comprises a mixture of potamodromous and anadromous types, completing the natural continuum of behavioral modes along latitudinal ecotones.

Small- and large-scale migration patterns differ among Atlantic Coast Striped Bass. However, all Atlantic Coast Striped Bass spend at least a portion of their life cycle in coastal rivers and estuaries. Specifically, adults in southern populations are known to spend most of the summer in thermal refuges located in coastal rivers and spend winter months in coastal estuaries (Bjorgo et al. 2000). Transitions between these two locations occur during early spring spawning (Douglas et al. 2009). Some evidence exists that mixing across river populations does occur during these movement and migration events. A tracking study of adults in the Savannah River identified six migration events over a 3-y period. The migrations were to the Ogeechee River from the Savannah River and the majority occurred during spawning (Sibley 2020). Additionally, Bulak et al. (2004) used tag return data to evaluate migrations between systems and found some evidence of fish mixing between the Santee–Cooper and Pee Dee system (9 of 58 tag returns). These findings suggest that the philopatry paradigm that is currently accepted should be re-evaluated. Despite the findings of Bulak et al. (2004), the Great Pee Dee River population is believed to be primarily resident fish and it is unknown if large-scale migrations occur along the Atlantic Intracoastal Waterway (ICW).

Spawning activity and the timing of the spawning migration upstream and downstream have been linked to temperature (Carmichael et al. 1998; Bjorgo et al. 2000; Nack et al. 2019) and discharge (Rulifson and Manooch 1990; Andrews 2019) and vary by sex (Carmichael et al. 1998; Douglas et al. 2009). Bjorgo et al. (2000) tracked 30 adult Striped Bass in the Combahee River, South Carolina and found that their spring migration began when water temperatures ranged from 18 to 26°C. Striped Bass in the Roanoke River, North Carolina follow a similar pattern where they initiate migration when temperature of the lower reaches was 17 to 18°C (Carmichael et al. 1998). Sex-specific trends have varied; some have identified males beginning their migration earlier (Carmichael et al. 1998), whereas no differences between sex were found in a northern population in the Miramichi river (Douglas et al. 2009). River discharge has been linked to spawning duration, with an increase in discharge causing a decrease in water temperature, which stalls spawning (Rulifson and Manooch 1990).

Management of coastal riverine Striped Bass fisheries in the Southeast assumes no or minimal movement between systems (Rachels and Boggs 2021; Ricks and VanMiddlesworth 2022) where abiotic variables and angling pressure is localized to the system. Managing a system based on

the assumption of no movement can result in biased and uncertain recruitment and mortality estimates if the system is not closed to migration. Thus, not knowing the full extent of the migration patterns of coastal Striped Bass can impede successful management. First, stocking efforts in the Great Pee Dee River could be supplementing other coastal river populations (e.g., Cape Fear River or Santee River) rather than rebuilding the Great Pee Dee River population. Second, fish from other systems could be immigrating to the Great Pee Dee River, increasing the population at an unknown rate. Finally, overwintering locations outside the main river system (e.g., the ICW at Little River, South Carolina) could add fishing pressure to the Great Pee Dee River population.

The Great Pee Dee River watershed is 18,702 km² and flows across North Carolina and South Carolina. Approximately 327 km are located within North Carolina and are impounded in many sections to form seven reservoirs. The South Carolina portion runs 370 km where it converges with the Black River, Sampit River, and Waccamaw River to form Winyah Bay. Winyah Bay is the third largest estuary on the East Coast. The land use of the Great Pee Dee River is 33.4% agricultural, 25.7% forested, 27.9% forested wetland, 6.3% urban, 2.7% scrub/shrub, 2.6% water, 1.2% nonforested wetland, and 0.2% barren (SCDHEC 2015).

The Striped Bass population in the Great Pee Dee River consists of a mixed ancestry from the Cape Fear/Roanoke rivers and the Santee–Cooper system (South Carolina Department of Natural Resources [SCDNR], unpublished genetic analysis). The mixed ancestry is due to current and historical stocking strategies. Current stocking efforts consist of Santee strain brood because it has been determined that there is not a unique Great Pee Dee strain (Anderson et al. 2014). Striped Bass were stocked in the Great Pee Dee River in the mid-1990s and a new stocking program was initiated in 2019 in an attempt to rebuild the fishery. The current stocking rate is 25,000 to 30,000 152–203-mm fish (phase II fish) each winter. Adult Striped Bass sampling has been occurring in the Great Pee Dee River and Winyah Bay since 2012 to monitor genetic structure and abundance of this population (SCDNR, unpublished data). Although the Great Pee Dee River is free flowing in South Carolina, numerous impoundments are present in the North Carolina section of the river. Thus, the origin of the Roanoke River fish has been linked to upstream stocking in those North Carolina impoundments. Genetic analysis also indicates a varying proportion of fish designated as wild. The most recent genetic analysis of adult fish captured during spring electrofishing revealed that 60% ($N = 55$) were wild (SCDNR 2021, unpublished data). Wild fish are those that could not be linked to a specific hatchery and are assumed to be naturally reproduced.

The goal of this study was to describe movement patterns of adult Striped Bass in the Great Pee Dee River. The specific objective was to describe daily movement patterns and centers of attraction (e.g., spawning and resting stages) of individual fish. We hypothesize that Striped Bass will exhibit two centers of attraction on the basis of spawning and resting periods.

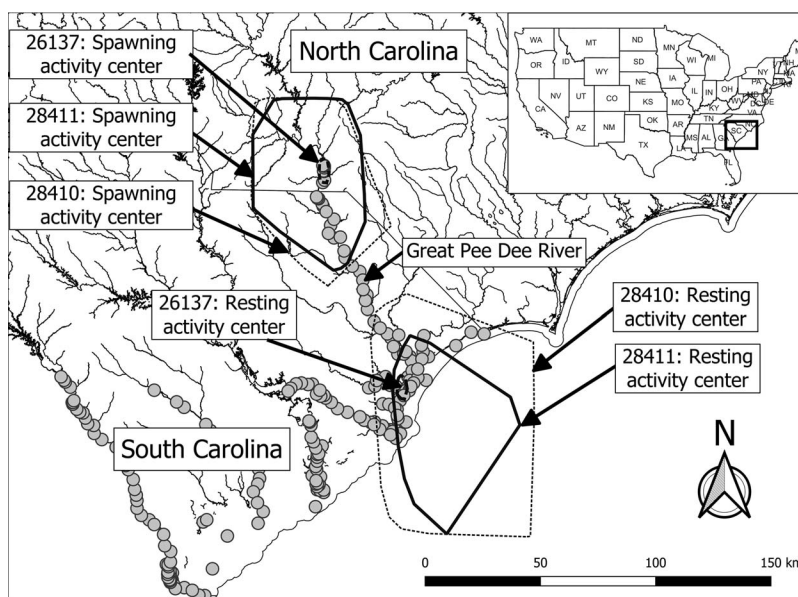


Figure 1. Map of Great Pee Dee River in South Carolina displaying the location of hydroacoustic receivers used between May 18, 2013 and June 22, 2019 and location of estimated spawning activity centers and resting activity centers. Shaded circles are locations of hydroacoustic receivers. Large dashed, solid, and small dashed outlines are spawning and resting activity centers for Striped Bass *Morone saxatilis* nos. 26137, 18411, and 28410.

Methods

Field collection

We collected all fish using boat electrofishing. We implanted 10 fish with transmitters between 2013 and 2016. We based number and timing of fish collections on field time and funding constraints. We implanted 5 of the 10 total fish with transmitters within the North Carolina section (34.981872, -79.867170) of the river and they ranged in length from 595 to 703 mm total length (TL; we recorded only a range of TLs). We implanted 2 of the 10 total fish (521 and 662 mm TL) with transmitters in April and June of 2015 in the lower Great Pee Dee River (33.468741, -79.268376). We implanted the final 3 fish of the 10 total (560, 655, and 665 mm TL) with transmitters in the lower Great Pee Dee River (33.468741, -79.268376) in April 2016. All tags were Vemco V16-4x tags. We programmed nine tags with high-output, 40–100-s delay; they had an expected life of 992 d. We programmed one tag with high-output, 50–130-s delay; it had an expected life of 1,262 d. The receiver array consists of a large distribution of Vemco VR-2W acoustic receivers (Figure 1; Data S2, *Supplemental Material*). The receiver array was deployed and was maintained by the SCDNR. Each receiver was suspended in the mid-water column and attached to a stainless-steel cable or high-tensile rope that was anchored to the bottom. A buoy was used to support the top of the cable and attached to a shoreline structure (e.g., bridge piling or tree). Distance between receivers was variable and ranged between 5 and 20 km apart (Figure 1). Specific locations were selected by the South Carolina diadromous fisheries section to monitor movement of Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* (Denison et al. 2023) and

Shortnose Sturgeon *Acipenser brevirostrum*. Data from receivers were obtained four times per year. All raw data are available in the online supplemental file (Data S1 and S2, *Supplemental Material*).

Movement model

We describe daily movement and behavior of individual fish using the state-space model described by Dora-zio and Price (2019), modified for a two-dimensional spatial coordinate system. This model is an individual-based model that describes single fish movement patterns, and we applied it to each fish separately. We restricted the two-dimensional spatial domain $B^{1,2} \in \mathbb{R}^{1,2}$ to include the minimum and maximum extent of the latitude and longitude in Universal Transverse Mercator. We used daily time periods for each individual fish monitored to describe their movement patterns. Let $\text{lat}_{-s_t} \in B^1$ and $\text{lon}_{-s_t} \in B^2$ denote the two-dimensional location at time t (for $t = 1, \dots, T$). The time bounds are unique to each fish and represent the first and last observations of an individual. We first specified the movement model with two centers of attraction. Centers of attraction define a location where an organism will spend a significant portion of its time. If a species does not migrate, then they are typically assumed to have one center of attraction. We used two centers of attraction here because coastal populations of Striped Bass exhibit predictable annual patterns where they rest in coastal estuaries and spawn upstream in freshwater sections of rivers. We modeled movement with a Gaussian autoregressive process along a two-dimensional spatial coordinate system (i.e., latitude and longitude). We based movement dynamics along each coordinate plane on one of two centers of attraction, μ_c , and the correlation between successive locations, ρ :

$$\text{lat } s_t | \text{lat } s_{t-1} \sim \text{normal}([1 - \rho_{\text{lat}}]\mu_{\text{lat},x_t} + \rho_{\text{lat}}s_{t-1}, \sigma_{\text{lat}}) \quad (1)$$

$$\text{lon } s_t | \text{lon } s_{t-1} \sim \text{normal}([1 - \rho_{\text{lon}}]\mu_{\text{lon},x_t} + \rho_{\text{lon}}s_{t-1}, \sigma_{\text{lon}}) \quad (2)$$

where μ_{lat,x_t} and μ_{lon,x_t} are the centers of attraction along the latitude and longitude spatial coordinates at the x_t location at time t ; ρ_{lat} and ρ_{lon} are the correlations between successive locations along the latitude and longitude spatial coordinates; and σ_{lat} and σ_{lon} are the standard deviation parameters that represent the amount of variation of the center of attraction along the latitude and longitude spatial coordinates. The study system is not closed, and it is possible for fish to leave the area or be harvested and not be detected by receivers. However, it is unlikely that fish would swim upstream or downstream and transition between states without being detected by at least one receiver. Maximum detection distance of the receivers used in this study has been found to range from 51 to 335 m in the Mississippi River under varying river stages (Casto-Yerty and Bettoli 2009). The Great Pee Dee River is generally between 75 and 200 m wide and has 40 receivers (not including receivers in other rivers in the system). Thus, it is unlikely that a single fish would go undetected if it swam upstream.

The center of attraction is a latent unobserved discrete random variable that represents one of two locations, where $x_t \in \{1, 2\}$. Equations (1) and (2) include the center of attraction indexed by x_t , which indicates the location or behavior of a fish during time t . We specified prior probability distributions (see prior probability distributions section below) so that zone 1 was near the resting locations (e.g., Winyah Bay) and zone 2 was near spawning locations (e.g., North Carolina/South Carolina border). We modeled changes in the behavior state with a hidden Markov model (Zucchini et al. 2016). The structure of this model was a first-order Markov process with transition probabilities $\phi_{kj} = \Pr(x_t = j | x_{t-1} = k)$. We specified the transition probability matrix as:

$$\Phi = \begin{pmatrix} \phi_{11} & \phi_{12} \\ \phi_{21} & \phi_{22} \end{pmatrix} \quad (3)$$

where each row sums to one. Changes in behavior state were dependent on the previous time and state:

$$x_t | x_{t-1} \sim \text{cat}(\phi_{x_{t-1}}) \quad (4)$$

where $\phi_{x_{t-1}}$ is the row of the transition matrix (equation 3) and cat represents the categorical distribution with vector of probabilities $\phi_{x_{t-1}}$. If the model did not converge then we attempted a simpler movement model with one area of attraction. This simplified model with one area of attraction eliminated equations (3) and (4) above and replaced equations (1) and (2) with:

$$\text{lat } s_t | \text{lat } s_{t-1} \sim \text{normal}([1 - \rho_{\text{lat}}]\mu_{\text{lat}} + \rho_{\text{lat}}s_{t-1}, \sigma_{\text{lat}}) \quad (5)$$

$$\text{lon } s_t | \text{lon } s_{t-1} \sim \text{normal}([1 - \rho_{\text{lon}}]\mu_{\text{lon}} + \rho_{\text{lon}}s_{t-1}, \sigma_{\text{lon}}) \quad (6)$$

Observation model

The observation data included a series of detections and nondetections at each acoustic receiver that was conditional on the individual's location during each period. We first separated time periods into hours and considered independent observations. For example, the receivers continuously recorded a fish being observed if it was stationary. If a fish was recorded as being present one or more times per hour it was designated as being present once in that hour. Observation intervals, t , were the sum of observations within a 24-h period. Thus, the total number of possible observations J of a single fish in 1 d was 24 and the observation model is parameterized as number of observations per day. We recorded observations as $y_{k,t}$ to represent the number of observations where a fish was detected by acoustic receiver k during time t . We modeled observed counts with a binomial distribution:

$$y_{k,t} | \text{lat } s_t, \text{lon } s_t \sim \text{binomial}(J, p_{k,t}) \quad (7)$$

where $p_{k,t}$ was the probability that a fish was detected by receiver k during time t . We modeled the probability of detection using the kernel of a Gaussian density function (Buckland et al. 2001; Dorazio and Price 2019) and assumed it decreased as an individual moved away from the receiver:

$$p_{k,t} = p_0 e^{(-1/2[\text{lat } s_t - \text{lat } x_k]^2 + [\text{lon } s_t - \text{lon } x_k]^2 / 2\sigma_p^2)} \quad (8)$$

where p_0 is baseline probability of detection when the location of an individual is exactly where the receiver is located; $\text{lat } x_k$ is the latitudinal coordinates of receiver k ; $\text{lon } x_k$ is the longitudinal coordinates of receiver k ; and σ_p^2 is the variance and represents the decline in detection probability with distance.

Model fitting

We used Bayesian inference to fit the movement and observation model (Doll and Jacquemin 2018). We conducted the analysis in R 4.2.2 (R Development Core Team 2022) with JAGS (Plummer 2003) and runjags 2.2.1-7 (Denwood 2016). Complete R code (Data S3, *Supplemental Material*) and JAGS code (Data S4, *Supplemental Material*) for fitting the model are available in the online supplemental material. We used three concurrent Markov chain Monte Carlo chains; each chain consisted of 10,000 total iterations, thinning every 10 steps, and we discarded the first 5,000 steps. We assessed convergence using visual inspections of trace plots and the Gelman–Rubin statistics. Chains are considered to have converged when the Gelman–Rubin statistics of each parameter are close to one. Gelman–Rubin statistic values less than 1.10 indicate that the chains have converged. We also assessed the model using posterior predictive checks (Gelman et al. 2004; Chambert et al.

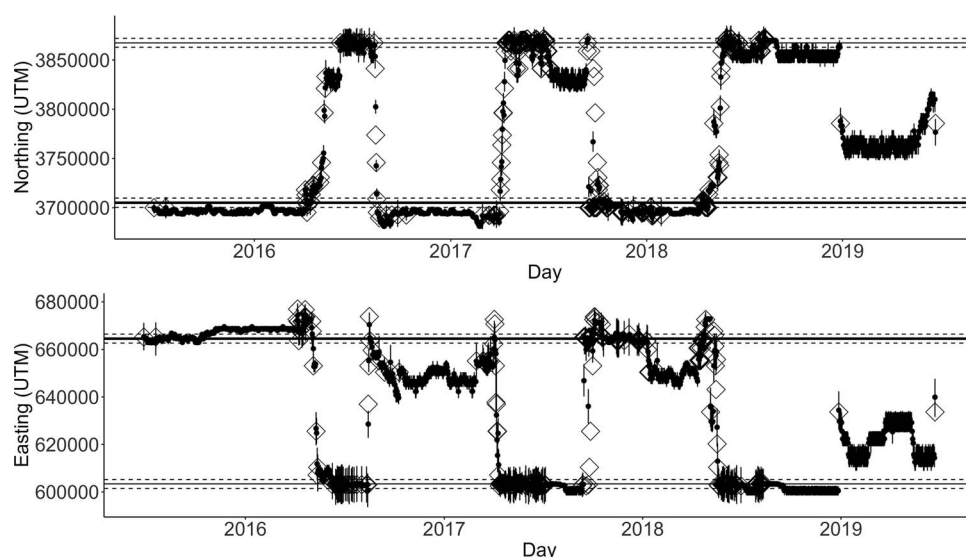


Figure 2. Northing and easting location of Striped Bass *Morone saxatilis* no. 26137 by day from June 27, 2015 to June 22, 2019 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median and 95% posterior probability intervals of resting activity center (thick solid horizontal line with dashed upper and lower lines) and spawning activity center (thin solid horizontal line with dashed upper and lower lines).

2014). We generated posterior predictive distributions for each individual at a location during each time step (equations 1 and 2). Posterior predictive checks produce a series of replicated data (e.g., latitude and longitude) that we compared with observed data. We made graphical comparisons to identify any systematic deviations of model predictions from observed data.

Prior probability distributions

We divided easting and northing (Universal Transverse Mercator) values by 10,000 to improve convergence. We used weakly informative prior probabilities, when possible, to enforce restrictions and permit identifiability. Centers of attractions are generally predictable on the basis of known spawning locations (e.g., limited by dams) and overwintering locations (e.g., limited by the ocean). We used a weakly informative prior probability distribution to specify these two locations. We used a normal distribution for $\mu_{lat,x_{i,t}}$ with a mean of 370 ($\mu_{lat,1}$) and 386 ($\mu_{lat,2}$) with standard deviation (SD) = 1,000. Similarly, we used a normal distribution for $\mu_{lon,x_{i,t}}$ with mean = 67 ($\mu_{lon,1}$) and 61 ($\mu_{lon,2}$) and SD = 1,000. The prior probability distribution for the logit-scaled correlation between successive locations, $\text{logit}(\rho_{lat})$ and $\text{logit}(\rho_{lon})$, was a normal distribution with mean = 0 and SD = 1.5. We gave the logit-scaled baseline detection probability, p_0 , a normal prior probability distribution with mean = 0 and SD = 1.5. We gave prior probability distributions for all standard deviations (σ_{lat} , σ_{lon} , and σ_p) a positive-sided half-normal prior probability distribution with mean = 0 and SD = 2.5. We specified all SD values as precision (1/SD) in the model because JAGS was used to fit the model. Thus, SD = 1,000 is equivalent to a precision of 0.001.

Results

Ten fish were recorded by at least one receiver between May 2013 and June 2019. A total of 94,857 data points was recorded across all individuals and receivers. Days between the first and last recording per individual ranged from 71 to 1,456, with an average of 623. All individuals that were at large for 1 y or more had significant periods where they were not observed. There was not a consistent trend in unobserved periods and fish were missing when they were in coastal and near spawning areas (Figures 2 and 3; Figure S1, *Supplemental Material*).

Movement was variable across individuals (Figures S1–S8, *Supplemental Material*). However, there were two groups with similar movement. First, one group completed a seasonal migration that coincided with spring spawning season (March through May; Figure 2; Figures S1, S2, S4, S6–S9, *Supplemental Material*; fish nos. 26133, 26134, 26137, 28409, 28410, 30555, 28411, and 28412). These seasonal migrations include upstream movement in the early spring to areas where spawning activity is thought to occur on the basis of time of the year, followed by downstream movement in late summer to overwintering areas near the coast. However, only three fish had distinct activity centers (Figure 2; Figures S7 and S8, *Supplemental Material*; fish nos. 26137, 28410, and 28411). The postspawning migrations between activity centers began in April and May when they transitioned from coastal areas, upstream toward the North Carolina border. The postspawning downstream migration period was not consistent across individuals within this group. The two activity centers located in the lower Pee Dee River watershed and at the North Carolina/South Carolina border show high uncertainty of fish nos. 28410 and 28411 (Figure 1). The resting activity centers extend into

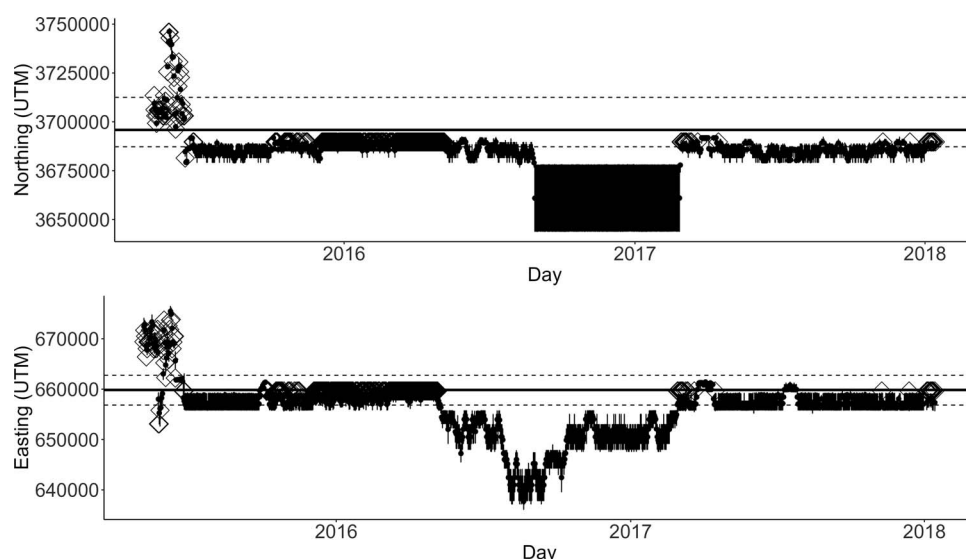


Figure 3. Northing and easting location of Striped Bass *Morone saxatilis* no. 26135 by day from May 6, 2015 to January 14, 2018 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median and 95% posterior probability intervals of activity center (thick solid horizontal line with dashed upper and lower lines). The large black box in upper figure represents an extended period where the model predictions are consistent, resulting in points and error bars that are overlapping.

the Atlantic Ocean for these fish, although no records of Striped Bass have been recorded in the ocean off the South Carolina coast. Similar uncertainty was observed in the spawning activity center of these two fish. The weekly persistence transition probability (i.e., probability of staying in their current center between weekly time steps) was generally high (Table 1). The lower 95% probability interval for transition probability to stay in center of attraction zone 2 was 0.70 or greater for the three fish. Five individuals were not observed for a significant amount of time in the summer after spawning (Figure 2; Figures S2, S5, S7, and S8, *Supplemental Material*; fish nos. 26134, 26137, 28410, 28411, 28412) and one individual was not detected during the winter before spawning (Figure S1, *Supplemental Material*; fish no. 26133). In contrast, one fish (Figure S6, *Supplemental Material*; fish no. 30555) appeared to stay in the main channel and was periodically observed within the Great Pee Dee River during the summer. This fish was also observed in the upper river during July.

A second movement pattern was present where two fish (Figure 3; Figure S3, *Supplemental Material*; fish nos. 26135 and 26136) were observed in the lower river

section and Winyah Bay during the winter over 3 consecutive years but were never observed migrating up the Great Pee Dee River during the spring. Fish no. 26135 was observed over a 3-y period in the lower river section during the winter (Figure 3). The other fish (no. 26136) traveled north in the Atlantic ICW near the North Carolina border during winter of 2017 and 2018 (Figure S3, *Supplemental Material*).

Detection probability for a fish that is immediately next to the receiver was very low (Table 2). The upper 95% probability interval of detection probability from six fish was lower than 0.05. Only two fish had a lower 95% probability interval of detection probability that was above 0.28. Sigma (determines how quickly p declines with distance, with larger values indicating a slower decline) is inversely related to p ; when detection probability is low, sigma is generally high (Table 2).

Table 2. Baseline daily detection probability (p_0) and Sigma (σ) for all Striped Bass *Morone saxatilis* tagged in the Great Pee Dee River and tracked between May 18, 2013 and June 22, 2019. Results are summarized with Bayesian 95% posterior probability intervals (2.5% and 97.5%) and medians (50%).

Fish	Baseline detection probability			Sigma		
	2.5%	50.0%	97.5%	2.5%	50.0%	97.5%
26133	0.011	0.013	0.015	0.372	0.398	0.427
26134	0.087	0.106	0.125	0.180	0.191	0.204
26135	0.289	0.317	0.347	0.140	0.144	0.145
26136	0.038	0.044	0.050	0.169	0.177	0.186
26137	0.005	0.005	0.006	0.786	0.819	0.855
28409	0.133	0.155	0.178	0.333	0.352	0.371
28410	0.009	0.011	0.014	0.363	0.410	0.461
28411	0.027	0.031	0.036	0.428	0.456	0.488
28412	0.333	0.431	0.537	0.127	0.134	0.142
30555	0.019	0.025	0.032	0.495	0.575	0.661

Table 1. Persistence probability for spawning activity center (Figure 1) of three Striped Bass *Morone saxatilis* tagged in the Great Pee Dee River and tracked between August 13, 2013 and June 22, 2019. Results are summarized with Bayesian 95% posterior probability intervals (2.5% and 97.5%) and medians (50%).

Fish	2.5%	50.0%	97.5%
26137	0.94	0.97	0.98
28410	0.70	0.88	0.97
28411	0.72	0.89	0.96

Discussion

Our results revealed variability in Striped Bass movement at the individual level. A subset of the individuals followed the philopatric paradigm, which is consistent with what is known about adult Striped Bass in south-eastern rivers (Dudley et al. 1977; Bjorgo et al. 2000); another subset was not consistent with this paradigm. Additionally, migration events supported two centers of attraction that were distinctly identified for three fish. However, a total of eight fish exhibited seasonal upstream/downstream movements. The two centers of attraction identified in this study corresponded to suspected spawning locations upstream and resting/feeding locations near coastal estuaries. It is possible the five fish where centers of attraction could not be estimated made shorter seasonal upstream migrations and were spawning in the lower sections of the river or skipped spawning. Spawning in the lower and upper sections of the Great Pee Dee River would be consistent with behavior of Striped Bass in the Hudson River where Secor et al. (2020A) identified two geographic centroids that were separated by approximately 100 km. Further, the uncertainty in the spatial size of the resting and spawning activity areas is generally large. The estimated activity centers imply that Striped Bass are going to the Atlantic Ocean or in tributaries outside of the main Great Pee Dee River. This is due to the uncertainty in the data and the nature of a riverine system. Striped Bass have never been documented in the ocean in this location and it is unknown if spawning is occurring in tributaries of the Great Pee Dee River.

Seasonal migration is common among all Striped Bass populations in the Atlantic Coastal Plain (Carmichael et al. 1998; Bjorgo et al. 2000; Nack et al. 2019). Striped Bass movement in this study generally followed a seasonal pattern and was consistent with populations in the nearby Combahee River in South Carolina where fish moved downstream during the fall and upstream during the spring (Bjorgo et al. 2000). However, there were periods during the summer when fish were not detected in the main stem of the Great Pee Dee River or Winyah Bay. One potential explanation for the long periods of nondetection is that fish could have found thermal refuges in spring-fed tributaries where there are no receivers and waited until the main stem cooled (Van Den Avyle and Evans 1990). It is also possible that these fish left the system entirely. Although daily detection probability was low for a single receiver, we suggest it is unlikely a fish left the system without being detected by receivers in coastal South Carolina rivers. If they did leave, the undetected fish could have migrated north along the Atlantic ICW to North Carolina where there was no active receiver array during the study period. However, this path would have taken fish past two receivers in the South Carolina portion of the ICW.

We observed that two of the adults in this study did not have an upstream migration during the spring but rather disappeared in the spring. These fish either skipped spawning or were not mature. Skipping spawning has been observed in other studies (Bradley et al. 2018). A study in the Neuse River, North Carolina reported that 27

of 61 tagged adult fish did not make upriver migrations (Bradley et al. 2018). However, it is possible some of the fish in the Neuse River were immature and thus did not make a spawning migration. The fish in the Neuse River study ranged in size from 349 to 923 mm TL. In our study, the fish that did not make an upstream migration were 662 and 665 mm TL at tagging. Maturation stage at tagging was not determined in our study or in Bradley et al. (2018). However, Will et al. (2002) reported that Striped Bass <750 mm were generally not sexually mature in the Savannah River. In contrast, a study in the Roanoke River revealed that 44% of age-3 females (fork length = 465–550 mm) were sexually mature and all females were mature by age 6 y (fork length = 575–736 mm; Olsen and Rulifson 1992). Maturation at age or length is not known for the Great Pee Dee River fish. On the basis of the size at tagging, it is likely the two fish in this study that did not make a spawning migration were mature but spawned elsewhere or skipped spawning. This is further supported by the three fish for which two centers of attraction could be estimated being <703 mm at tagging. Fish no. 26137 was 560 mm at tagging on April 4, 2016 and started its seasonal migration the following spring. Understanding maturity schedules of this population is needed to fully describe these seasonal migrations.

Most fish in this study stayed within the Great Pee Dee River and Winyah Bay. However, one fish (no. 26136) was periodically observed during three consecutive winters in the Atlantic ICW near the North Carolina/South Carolina border. This is approximately 80 river km from Winyah Bay, where most fish overwinter. This large movement outside of the main river system is made possible by a man-made connection (the ICW). The overwintering population near the North Carolina/South Carolina border does support an active fall/winter fishery (personal observation) but it is unknown how large this population is. It is also unknown where the overwintering population originates. The Cape Fear River is approximately 65 river km north of the Little River location and it is possible that this population is also using the ICW in the winter. Transient behavior of coastal Striped Bass is supported by other studies where this behavior has been observed during spawning migrations in the Savannah River (Sibley 2020). More information is needed about the overwintering population near Little River to determine potential population mixing and extent of large-scale movements.

Daily detection probability was low for all individuals. The low detection probability is due to the large gaps in observations for most individuals. The timing of the gaps was not consistent across individuals (i.e., some were missing during the winter; others were missing during the summer). It is unknown what caused these large gaps but it is possible that fish were not moving or were outside of the receiver array system. Daily detection probability of six fish had an upper 95% posterior probability that was ≤ 0.05 . However, it is important to note that a daily detection probability of 0.05 is equivalent to a monthly detection probability of 0.79 (McCallum 2005).

Variation in migration patterns across individuals in this study and results of Sibley (2020) suggest that there

is a need to better understand coastal Striped Bass movement, particularly at the population level. It is important to note that sample size in this study was low ($n = 10$) and 6 of 28 tracked fish in the Sibley (2020) study migrated between rivers; thus, inference can only be restricted to the individual level. Nevertheless, our data support the need for a more robust tracking study in the Great Pee Dee River. If there is significant migration between systems, then a regional management approach could be necessary. Describing the extent of this mixing because of movement among tributaries across coastal rivers could help inform variation in recruitment patterns and ultimately population stability. We recommend a larger sample size (e.g., >50), and water temperature, river discharge, and fish size should be incorporated as covariates predicting movement patterns in future studies.

Supplemental Material

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Data S1. Raw data of Striped Bass *Morone saxatilis* observations collected from receivers in the Great Pee Dee River system between May 18, 2013 and June 22, 2019. Date and time of each recorded Striped Bass location, receiver number, animal identification tag number, receiver station name, and latitude and longitude are included.

Available: <https://doi.org/10.3996/JFWM-22-073.S1> (14.855 MB XLSX)

Data S2. Latitude and longitude of each hydroacoustic receiver located in the Great Pee Dee River system that was used in this study between May 18, 2013 and June 22, 2019.

Available: <https://doi.org/10.3996/JFWM-22-073.S2> (4 KB XLSX)

Data S3. Complete R code for fitting the daily movement and behavior model of individual Striped Bass *Morone saxatilis* using a two-dimensional spatial coordinate system. We used code to analyze Striped Bass movement data from the Great Pee Dee River system collected between May 18, 2013 and June 22, 2019. The code loads data from Data S2, sets parameters needed to fit the model using JAGS, and saves the posterior probability distribution.

Available: <https://doi.org/10.3996/JFWM-22-073.S3> (15 KB R File)

Data S4. Complete JAGS code to fit the daily movement and behavior model of individual Striped Bass *Morone saxatilis* using a two-dimensional spatial coordinate system that is described in equations (1)–(8). The code analyzed Striped Bass movement data from the Great Pee Dee River system collected between May 18, 2013 and June 22, 2019.

Available: <https://doi.org/10.3996/JFWM-22-073.S4> (3 KB TXT)

Figure S1. Northing and easting location of Striped Bass *Morone saxatilis* no. 26133 by day from July 24,

2015 to June 18, 2016 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S5> (364 KB PNG)

Figure S2. Northing and easting location of Striped Bass *Morone saxatilis* no. 26134 by day from April 9, 2015 to March 18, 2016 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S6> (470 KB PNG)

Figure S3. Northing and easting location of Striped Bass *Morone saxatilis* no. 26136 by day from April 6, 2015 to September 16, 2018 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S7> (427 KB PNG)

Figure S4. Northing and easting location of Striped Bass *Morone saxatilis* no. 28409 by day from May 18, 2013 to July 28, 2013 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S8> (376 KB PNG)

Figure S5. Northing and easting location of Striped Bass *Morone saxatilis* no. 28412 by day from October 10, 2013 to March 27, 2015 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S9> (423 KB PNG)

Figure S6. Northing and easting location of Striped Bass *Morone saxatilis* no. 30555 by day from April 7, 2018 to June 30, 2018 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median (thick solid horizontal line) and 95% posterior

probability intervals of activity center (dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S10> (363 KB PNG)

Figure S7. Northing and easting location of Striped Bass *Morone saxatilis* no. 28410 by day from October 25, 2013 to December 14, 2015 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median and 95% posterior probability intervals of resting activity center (thick solid horizontal line with dashed upper and lower lines) and spawning activity center (thin solid horizontal line with dashed upper and lower lines).

Available: <https://doi.org/10.3996/JFWM-22-073.S11> (453 KB PNG)

Figure S8. Northing and easting location of Striped Bass *Morone saxatilis* no. 28411 by day from October 13, 2013 to November 17, 2014 in the Great Pee Dee River. Diamonds are observed locations, solid circles and error bars are median and 95% posterior probability intervals of model predicted location, horizontal lines are the estimated median and 95% posterior probability intervals of resting activity center (thick solid horizontal line with dashed upper and lower lines) and spawning activity center (thin solid horizontal line with dashed upper and lower lines).

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Acknowledgments

We thank James Bulak and Jason Bettinger for designing the tagging study and tagging the fish. We also thank Bill Post and Ellen Waldrop for providing the tracking data and maintaining the hydroacoustic array. Funding for J.C.D. was provided by Francis Marion University Summer Research Stipend program for faculty. Funding for J.M. was provided by the U.S. Fish and Wildlife Federal Aid in Sportfish Restoration program and the SCDNR. We appreciate the recommendations from the reviewers and editors. This manuscript was greatly improved with their suggestions.

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