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ARTICLE

Coastal Migration and Homing of Roanoke River Striped Bass

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Abstract

Anadromy in Roanoke River Striped Bass *Morone saxatilis* has been documented; however, the specifics of the ocean migration and the degree of homing in this population remain unstudied and would greatly benefit the management of this economically important species. To this end, we telemetered and released 19 large Roanoke River Striped Bass (750–1,146 mm TL) on their spawning grounds during the springs of 2011 and 2012. Data from a large-scale acoustic telemetry array along the U.S. Atlantic coast (480 total receivers, including the Roanoke River) were used to evaluate the seasonal migration and distribution of telemetered fish, their degree of homing and skipped spawning, their migration speeds, and the environmental drivers of migration timing. We found that large Roanoke River Striped Bass (>900 mm TL) rapidly emigrated (~59 km/d) after spawning to distant (>1,000 km) northern ocean waters (New Jersey to Massachusetts), where they spent their summers. They then migrated southward in the fall to overwintering habitats off Virginia and North Carolina and completed their migration circuit the following spring by returning to the Roanoke River to spawn. Our results showed no evidence of straying or skipped spawning, as all migrants successfully returned (homed) to the Roanoke River the next spring to spawn. Cooler ocean water temperatures in 2013 delayed the spring spawning run by nearly 3 weeks relative to a year of average spring temperatures (2012). Our study provides novel information that aids the management of Striped Bass at both small (e.g., setting of fishing seasons in the Roanoke River) and large spatial scales (e.g., stock identification of Roanoke River fish in the mixed-stock ocean fishery) and more broadly highlights the utility of large-scale cooperative telemetry arrays in studying fish migration.

Many fish undertake migrations during some stage of their life. Migration has been defined as "those movements, often nonrandom or directed, that result in an alternation between two or more separate habitats, occur with a regular periodicity and involve a large fraction of the population" (Northcote 1978, 1984). Migrations occur at various spatial and temporal scales and are related to activities such as feeding, seeking environmental refugia or shelter, and reproduction (Wootton 1998). From an evolutionary perspective, migration is favored when the benefits of moving to a different habitat outweigh the costs of this behavior and therefore positively impact fitness (Gross 1987; Hendry et al. 2004).

Anadromy is a specific type of migration in which fish are born in freshwater and subsequently emigrate to ocean habitats, where they spend most of their lives (feeding and overwintering), but return to freshwater environments to reproduce

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(McDowall 1987; McDowall 2001). Most anadromous species are believed to exhibit a strong "homing" behavior, or the ability to return from distant ocean waters to the same freshwater system (river) in which they previously spawned or were born. Direct evidence of homing in anadromous fishes is largely restricted to the well-studied salmonids of the Pacific coast (Hartman and Raleigh 1964; Quinn 1993; Candy and Beacham 2000; Quinn et al. 2006) and also American Shad *Alosa sapidissima* (Melvin et al. 1986; Hendricks et al. 2002). However, even in those studies the extent of ocean migration is unknown, mainly due to the difficulty of tracking the movements of individual organisms over vast expanses of the ocean or along its coastline. The knowledge of ocean migration distances is important because "homing" generally implies that fish move considerable distances away from their spawning habitats and therefore must invoke some type of guidance mechanisms (e.g., orientation to celestial bodies or geomagnetic fields, olfaction) to return "home" (Leggett 1977; Dittman and Quinn 1996). To qualify as homing, the extent (distance) of ocean migration should be such that it allows for potential straying into other known spawning systems and should not be locally restricted to nearshore ocean waters just outside the mouth of the natal estuary (sensu Huntsman 1937).

Striped Bass *Morone saxatilis* is a common species along the Atlantic coast of the USA that exhibits variation in its migration behavior (degree of anadromy) both among and within populations. Striped Bass populations to the south of Cape Hatteras, North Carolina, are believed to be nonanadromous riverine residents (Raney 1952; Dudley et al. 1977), whereas populations to the north of Cape Hatteras exhibit anadromy and originate from four principal spawning systems including the Hudson River, Delaware River, Chesapeake Bay, and Roanoke River (Boreman and Lewis 1987; Waldman et al. 1997; Welsh et al. 2007; Able et al. 2012; Callihan et al. 2014; Kneebone et al. 2014). Within these populations, the degree of anadromy has been shown to vary as a function of fish size (Waldman et al. 1990; Dorazio et al. 1994; Callihan et al. 2014) and year-class strength (i.e., density-dependent movement; Merriman 1941; Dunning et al. 2006). Additionally, intrapopulation variability in lifetime migration behaviors (e.g., resident versus anadromous) irrespective of fish size or sex has been found in Striped Bass, particularly the Hudson River population (Secor and Piccoli 1996; Secor et al. 2001; Zlokovitz et al. 2003); this strategy is thought to promote population resiliency (the contingent hypothesis: Clark 1968; Secor 1999). Relative to other spawning populations, the occurrence of anadromy in Roanoke River Striped Bass has only been recently documented in the primary literature (Callihan et al. 2014), and the details of this migration are poorly understood and warrant further investigation.

Roanoke River Striped Bass exhibit a strong, size-dependent ocean emigration pattern after spawning. Spawning occurs in the upper Roanoke River from river kilometer (rkm) 195 (measuring from its confluence with the Albemarle Sound) to just below the fall line (rkm 209) once water temperatures reach 18°C in the spring (Hassler et al. 1981; Rulifson 1990; Carmichael et al. 1998). The Roanoke River spawning run consists of mature adults; that is, females > age 4 (>450 mm total length [TL]) and males > age 3 (>350 mm TL) (Trent and Hassler 1968; Olsen and Rulifson 1992; Boyd 2011). Based on tag returns of adult Striped Bass captured and released on the Roanoke River spawning grounds across an 18-year period (1991–2008), Callihan et al. (2014) found it was predominantly the large adults (>900 mm TL) in the population that emigrated to distant ocean waters (>1,000 km north of the release site). The smallest adults (<600 mm TL) were mainly recaptured in the Albemarle Sound estuary, and an intermediate size-group of 700–850 mm TL appeared to emigrate from freshwater and utilize nearby North Carolina ocean waters during the summer (Callihan et al. 2014).

While Callihan et al. (2014) provided convincing evidence of size-based ocean emigration, their study lacked the resolution needed to evaluate more specific details of the coastal migration of large Roanoke River Striped Bass. Multiple relocations of fish throughout the year are necessary to address questions such as the degree of homing, variability among the migration trajectories of individual fish, and environmental drivers of migration timing. However, these questions cannot be addressed with conventional tagging alone because multiple recaptures are rare and therefore only two data points (tagging and recapture) are available for most fish (Pine et al. 2003). Passive acoustic telemetry is an evolving technology that provides unique data on fish migration that can complement and expand upon the more coarse information obtained with conventional tagging studies. In particular, the scalability of this technology and relative ease of sharing detection data among researchers has promoted the development of large-scale cooperative telemetry arrays (Grothues et al. 2009; Welch et al. 2009; Pautzke et al. 2010; Welch et al. 2011; Wood et al. 2012; Kneebone et al. 2014) that constitute an unprecedented means to study fish migration.

In this 3-year study (May 2011–June 2014), we used data from the Atlantic Cooperative Telemetry (ACT) Network, which includes our local receiver array in the Roanoke River, to investigate the migration and homing behaviors of the migratory component of the Roanoke River Striped Bass population (fish > 900 mm TL) identified by Callihan et al. (2014). Specifically, we examined the seasonal migration and distribution, degree of homing, effect of temperature on the timing of the spring spawning run, and postspawning migration speeds of large Roanoke River Striped Bass. We also estimated the degree of "skipped spawning" in large Striped Bass, which is defined as the extent of nonannual spawning by mature fish (Rideout et al. 2005). These new data inform the management of this economically important species at both smaller spatial scales, when fish are concentrated on the spawning grounds and highly vulnerable to exploitation (state-level jurisdiction), as well as at larger spatial scales, when Roanoke River Striped

Bass contribute to mixed-stock ocean fisheries during the nonspawning period (multistate and federal-level jurisdictions).

METHODS

Fish Tagging

A total of 19 Striped Bass (750–1,146 mm TL; mean = 1,032 mm TL) were captured, telemetered, and released on the Roanoke River spawning grounds (Figure 1) during the spring spawning seasons of 2011 (May 2; $n = 6$ fish) and 2012 (April 19; $n = 13$ fish). Striped Bass were captured on the spawning grounds with a boat-mounted electrofisher (Smith-Root 7.5 GPP; 1,000 V of direct current, 4–5 A) operating at a pulse rate of 60 pulses/s. Netted fish were transported (<2 km) in a live well to the tagging vessel, sexed via expression of gonadal products, surgically implanted with a Vemco V13-1 L acoustic transmitter, and immediately released at the site of tagging. All fish > 900 mm TL ($n = 17$; 939–1,146 mm TL) were females, and the two smallest fish (750 and 873 mm TL) were males. The transmitters we used in 2011 had an average delay (the time between successive transmissions) of 60 s and a manufacturer-estimated battery life of 632 d. The transmitters we used in 2012 had an average delay of 90 s and an estimated battery life of 890 d, with the exception of two transmitters that were used from the previous year and implanted into fish F6 and F7 (the estimated battery lives for these transmitters were adjusted for shelf time between the 2011 and 2012 tagging events). Striped Bass were also externally tagged with an internal anchor tag (Floy Model FM-84) that indicated a US$100 reward would be given to fishers who reported information on recaptured fish (e.g., date, time, location of capture).

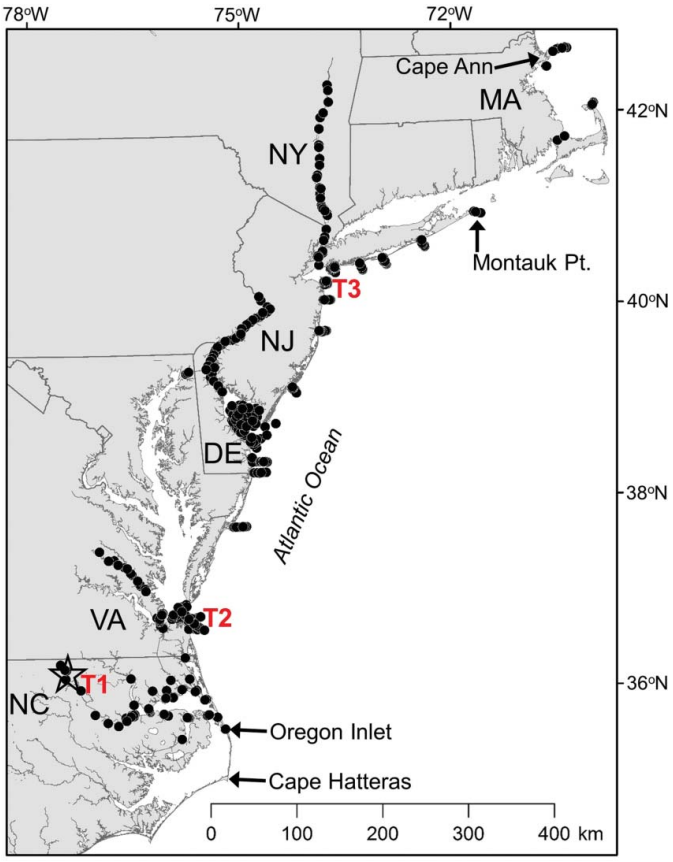

FIGURE 1. Map of the study area, showing the U.S. Atlantic coast from the Oregon Inlet, North Carolina (NC), to Cape Ann, Massachusetts (MA). Adult Striped Bass were captured, telemetered, and released on the upper Roanoke River spawning grounds (star on map) in May 2011 and April 2012. Black circles indicate the locations of acoustic receivers ($n = 480$) from which detection data were available; these receivers are part of the Atlantic Cooperative Telemetry Network. The T1, T2, and T3 (red text) denote the locations of water temperature stations in the upper Roanoke River (U.S. Geological Survey gauge 0208062765), along coastal Virginia (VA) (National Oceanic and Atmospheric Administration Buoy 44099), and along coastal New York (NY) (National Oceanic and Atmospheric Administration Buoy 44065), respectively. Additional abbreviations are as follows: NJ = New Jersey and DE = Delaware.

The lack of smaller adults (350–750 mm TL) in our study was due to the targeted sampling of large Striped Bass (>900 mm TL) on the Roanoke River spawning grounds. A major advantage of tagging fish on the spawning grounds is that the spawning population (stock) being studied is known (Waldman et al. 1988; Callihan et al. 2014). The fish we telemetered on the spawning grounds were part of a larger study on mortality and reporting rates of Striped Bass in the Roanoke River and Albemarle Sound (Harris and Hightower 2014). In that study, electrofishing on the spawning grounds was found to be the most effective method to capture large Striped Bass, presumably because this is where fish were concentrated and exhibited more restricted movements. All smaller Striped Bass ($n = 142$ fish ranging in size from 445 to 695 mm TL; mean = 517 mm TL) telemetered by Harris and Hightower (2014) were captured and released in western Albemarle Sound prior to the spawning season. Although the spawning population of those individuals could not be confirmed (because they were not captured on the spawning grounds), it is interesting to note that none of these smaller fish were detected outside of Albemarle Sound (mean time at liberty = 7.5 months). One larger fish (a 905-mm female) that was released in western Albemarle Sound did emigrate to the ocean 3 weeks postrelease but did not appear to be part of the Roanoke River spawning population as it was intermittently detected off the coast of Long Island, New York, for a period of 1.5 years, from May 2011 through October 2012.

Receiver Arrays

Our receiver array in the Roanoke River ($n = 19$ receivers) is part of the collaborative ACT Network along the U.S. Atlantic coast (http://www.theactnetwork.com/). This program involves data-sharing of detections from acoustically tagged organisms released by researchers from Georgia to Maine. For the purposes of our study, detection data (from the Striped

TABLE 1. Summary of receiver deployment and operation history during the study period: May 2, 2011, to July 8, 2014. The number of receivers that were operational in each detection area (see Figure 2 for area definitions) at the start of the study is provided, and as some receivers were added to the coastal arrays during the second year of this study, the deployment dates for these "partial" receivers are also provided. If receivers in a given array were not operational year-round, their seasonal dates of operation are listed, as is the period for which detection data were available from each array. Abbreviations are as follows: NA = not available, NC = North Carolina, NJ = New Jersey, and NY = New York.

Array	Number of receivers operational at start of study	Number of receivers added to array in year 2	Deployment dates for partial receivers	Operational year-round?	Detection data availability
Roanoke River, NC	16	3	Mar 15, 2012	Yes	May 2, 2011→Jul 8, 2014
Albemarle Sound, NC	61	NA	NA	Yes	May 2, 2011→May 1, 2014
Chesapeake Bay	NA	68	Dec 1, 2012	Yes	Dec 1, 2012→Feb 28, 2014
Delaware coast	12	27	Jan 1, 2012	Yes	May 2, 2011→Dec 31, 2013
Delaware Bay and River	94	18	Jan 1, 2012	Yes	May 2, 2011→Dec 31, 2013
NJ–NY coast	21	101	Jan 7, 2012	Yes	May 2, 2011→Jun 30, 2014
Hudson River	12	21	Apr 1, 2012	No (Apr–Oct)	May 2, 2011→Dec 31, 2013
Massachusetts coast	26	NA	NA	No (Apr–Oct)	May 2, 2011→Dec 31, 2013

Bass we released on the Roanoke River) and receiver operation data were available from other researchers' arrays (461 receivers; Vemco VR2 and VR2W receivers) deployed from Albemarle Sound, North Carolina, northward to Cape Ann, Massachusetts (Figure 1; Table 1). Most of these arrays were deployed and active before our first tagging event in spring 2011, with the exception of the Chesapeake Bay array, which was deployed in December 2012 (Table 1). Receivers were added to some arrays during the second year (2012) of our study (Figure 2; Table 1). Most notably, 101 receivers were added to the New Jersey–New York coastal array, which was expanded in January 2012 both northward (to Montauk Point) and southward (along the coast of New Jersey) from the western end of Long Island, where 21 receivers were initially deployed in 2011 (Figure 2; Table 1). Most arrays were operational year-round, except the two northernmost arrays in Massachusetts and the Hudson River, which were seasonally operational from April to October (Table 1). Although the occasional loss of individual receivers occurred in all arrays, rarely were entire receiver lines lost or compromised. The one exception was during winter 2013 (December 2013–February 2014), when only 4 of 21 receivers offshore of the mouth of Chesapeake Bay were operational due to receiver loss or failure (water damage) during the previous summer and fall. Detection data were available from all arrays north of North Carolina from May 2011 through at least December 2013; data were available from Chesapeake Bay and the New Jersey/New York coast through February 2014 and June 2014, respectively (Table 1).

Due to the wide geographic (multiple habitats) and temporal (years) scope of our study, it was difficult to define an "average" detection range for acoustic receivers. The theoretical maximum range, in calm ocean waters, for the transmitters we used (power output = 147 dB re 1 μPa at 1 m) is 539 m for VR2 and VR2W receivers, which operate at a frequency of 69 kHz (http://vemco.com/range-calculator/). However, the detection range is generally higher in freshwater than in marine habitats (Pincock et al. 2010; Pincock and Johnston 2012) and also strongly dependent on sea state (Lembo et al. 2002; Mathies et al. 2014) and turbidity (Callihan 2011).

Processing of Telemetry Data

We screened raw detection data for false detections prior to data analyses. Typically, detections that are isolated in space and time (e.g., a single detection at a given receiver in a 24-h period or less) are flagged as potential false positives in fish telemetry studies (Heupel et al. 2006; Dagorn et al. 2007; Pincock 2012). However, due to the rapid movements of Striped Bass in our study (see Results), it is entirely possible that a telemetered fish could pass by a receiver or receiver line and emit only one transmission before the fish is out of detection range. Therefore, instead of using a rigid criterion to identify false detections, we viewed animations of the successive detection locations of each fish in ArcMap (version 10.1; using time-enabled shapefiles) to ensure there was a logical sequence of detections. In a few instances, a fish was detected at two geographically disparate locations (>200 km) at essentially the same time (<1 h apart). In these situations, the false detection was easily identified as that which did not agree spatially with prior and subsequent detections of the fish being examined (see Video S.1 in the supplemental file for an example animation). Using this rationale, we deemed 0.14% of the 55,762 total raw detections as false and excluded them from analyses.

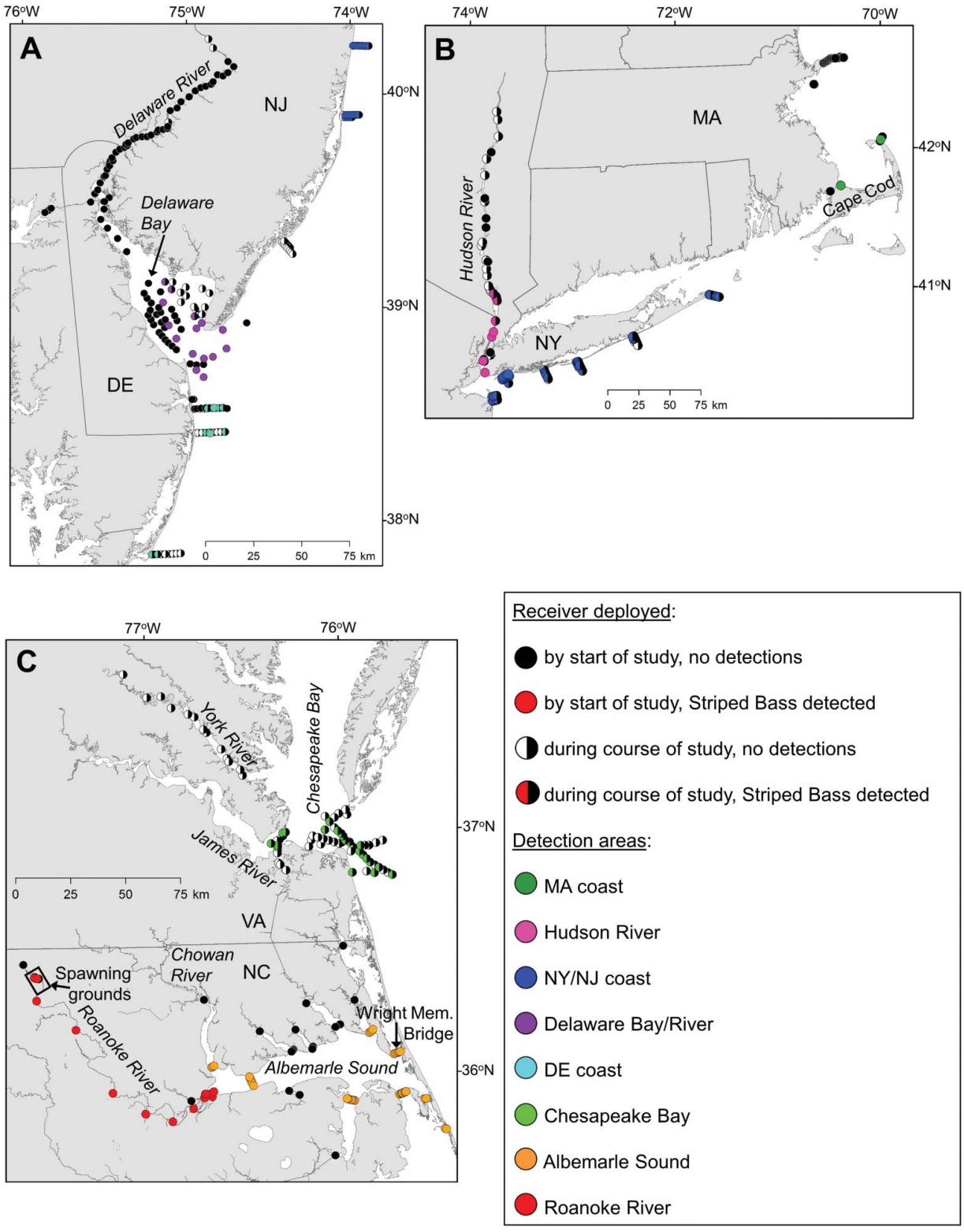

FIGURE 2. Receiver deployment and Striped Bass detection locations in **(A)** the Delaware (DE)–New Jersey (NJ) coastal region and Delaware Bay and River, **(B)** coastal New York (NY)–Massachusetts (MA) and the Hudson River, and **(C)** North Carolina (NC) to lower Chesapeake Bay. As indicated in the legend, fill patterns of circles (i.e., completely filled with any color versus half black) are used to denote whether receivers were deployed and operational by the start of the study (May 2011) or deployed during the course of the study (after May 2011); the different fill colors represent the detection areas used to illustrate movement patterns in Figure 3. Table 1 provides additional information on the dates of receiver deployments in each area and their operation seasonality. The black rectangle in the upper Roanoke River in panel (C) encompasses the spawning grounds of Roanoke River Striped Bass.

Data Analyses

Homing.—We calculated the homing rate as the percentage of "migrant" Striped Bass known to be alive through the next spring (April–May) that were detected on the Roanoke River spawning grounds. Migrant Striped Bass were those fish that moved to (were detected in) ocean waters between spawning events. Four fish were last detected more than 9 months before the start (April 1) of the next spawning season, and we assumed these fish died and therefore did not have the chance to home. Three of these fish appeared to be in route to the ocean as they were last detected at the Wright Memorial Bridge (F1, F9) and mouth of the Roanoke River (F8) in May after migrating downriver postspawning; the other fish (F10) was last detected off the coast of New York in June. In addition, two fish were reported as being harvested by fishers prior to the following spring and were therefore excluded from homing analyses. All other Striped Bass were detected at least 13 months postrelease and were therefore eligible for the homing analysis (i.e., were available for detection through the following spring).

In addition to providing information on homing, the acoustic monitoring of all major spawning systems of migratory Striped Bass permitted an evaluation of skipped spawning. We assumed Striped Bass skipped spawning in a given year if they were not detected in any spawning system (Roanoke River, Chesapeake Bay, Delaware River, or Hudson River) during the spring (April–May) after their release. We only included in this analysis fish known to be alive (detected) through the end of the next spawning season (late May).

Timing of the spawning run.—To examine interannual differences in the timing of the spawning run, we used detection patterns to quantify and compare (among years) the dates Striped Bass arrived and departed from the Roanoke River. For these analyses, we only included fish that made the complete spawning run (i.e., detected in the Albemarle Sound or ocean waters both before and after spawning). We considered the "arrival date" as the day Striped Bass were initially detected in the Roanoke River and the "departure date" as the date of last detection in the river. Due to low sample sizes ($n = 5$ fish per spawning year), a two-sample Wilcoxon exact test was used to test for differences in arrival and departure dates between spawning years (2012 versus 2013). Only one male (M1) was available for these analyses. Therefore, we performed statistical tests with and without this individual to account for its potential bias (sex effects) on results.

Postspawning migration speeds.—We estimated the migration speeds of Striped Bass during their postspawning migration from the Roanoke River to northern ocean waters. We focused on this northern leg of the coastal migration because fish were detected more frequently there than on the southern leg (see Results), thus providing more accurate estimates of migration speeds. The starting and ending points of the "postspawning migration" for each fish were as follows: (1) the date and location of the last detection on the Roanoke River spawning grounds and (2) the date and location of the first detection on a coastal receiver outside of North Carolina, respectively. We estimated the distance between these endpoints using Google Earth and ArcMap. Nonlinear distances in the river were more easily measured in Google Earth; the river kilometers we estimated closely matched, within 1–3 km, published values for the few sites ($n = 3$ U.S. Geological Survey gauges) for which river kilometers were available (Wehmeyer and Wagner 2011) for the exact locations where we deployed receivers in the Roanoke River. Straight-line measurements in ArcMap were sufficient to estimate distances across the open waters of Albemarle Sound and along the Atlantic coast. Migration speeds (km/d) were estimated for each fish by dividing the total distance between the start and end points of the postspawning migration by the time it took to complete this migration (i.e., the time between the last detection on the spawning grounds and the first detection in ocean waters). Migration speeds were also standardized to body lengths per second (BL/s) to facilitate comparisons of our results to other studies.

In calculating migration speeds, we assumed all fish exited the Albemarle Sound through the Oregon Inlet. While only 1 of 14 migrants was detected at the pair of receivers at Oregon Inlet, this was likely due to the low detection efficiency and occasional receiver loss in this high-energy environment (M. Loeffler, North Carolina Division of Marine Fisheries, personal communication). The nearest alternative exit point to ocean waters was Hatteras Inlet, 67 km south of Oregon Inlet. Therefore, if any fish entered the ocean through Hatteras Inlet, our migration speeds would be slightly underestimated.

To test for an effect of body size on postspawning migration speeds, we used least-squares linear regression with migration speed as the response variable and fish length (mm TL) at release as the explanatory variable. Some fish were at liberty for more than 1 year and engaged in postspawning migrations in consecutive years. For these individuals, we only estimated migration speeds for the first spring and summer after their release because lengths at tagging were the most reflective of the size during the migration. We also excluded one fish that did not undergo a postspawning migration until its second year at liberty (fish F5, see Results). We removed as outliers any observations with Cook's distance (Cook's D) values exceeding $4/n$ (where n = the number of observations; Bollen and Jackman 1990) and with studentized residuals $> |2|$, as recommended by Belsley et al. (1980).

RESULTS

Detection Summary

A total of 55,762 valid detections were logged from the 19 Striped Bass released in the Roanoke River in the springs of 2011 and 2012. Detection locations ranged from the upper

Roanoke River, North Carolina, to Cape Cod, Massachusetts, a distance of ~1,200 km. Most Striped Bass (13 of 19, or 68%) were detected more than 1 year (≥390 d) after being released; three of these fish (M2, F16, and F17) were detected more than 2 years postrelease (Figure 3). Of the other six fish, three were last detected ~2 months (59–66 d) postrelease, and three were last detected just 11–21 d after release. Two of the fish detected for ~2 months (F11 and F12) were reported as being harvested by recreational and commercial fishers in coastal Massachusetts and Albemarle Sound, respectively (Figure 3). The three fish detected for only a short period (≤21 d) appeared to survive the tagging process as they all moved downriver and were detected at the mouth of the Roanoke River. Two of these individuals (F1 and F9) moved across Albemarle Sound and were last detected at the Wright Memorial Bridge (Figure 2C) and possibly moved into the ocean.

Coastal Migration

Large Striped Bass (>900 mm TL) exhibited a strong seasonal migration pattern along the U.S. Atlantic coast. After emigrating from the Roanoke River spawning grounds in May, fish migrated northward to ocean waters off northern New Jersey and New York, where they resided during the summer (June–September) (Figure 4). Only two fish were detected north of Montauk Point, New York, in the vicinity of Cape Cod; there were no detections to the north of Cape Cod on the Cape Ann receiver line (Figure 2B). A southward fall migration began in October as indicated by the progression of detections, New York–New Jersey to Delaware to Virginia, from October to December (Figure 4). Although detections during winter were sparse, especially in 2013, fish appeared to overwinter off the coasts of Virginia and North Carolina as there were no detections north (Figure 4) or south of this area

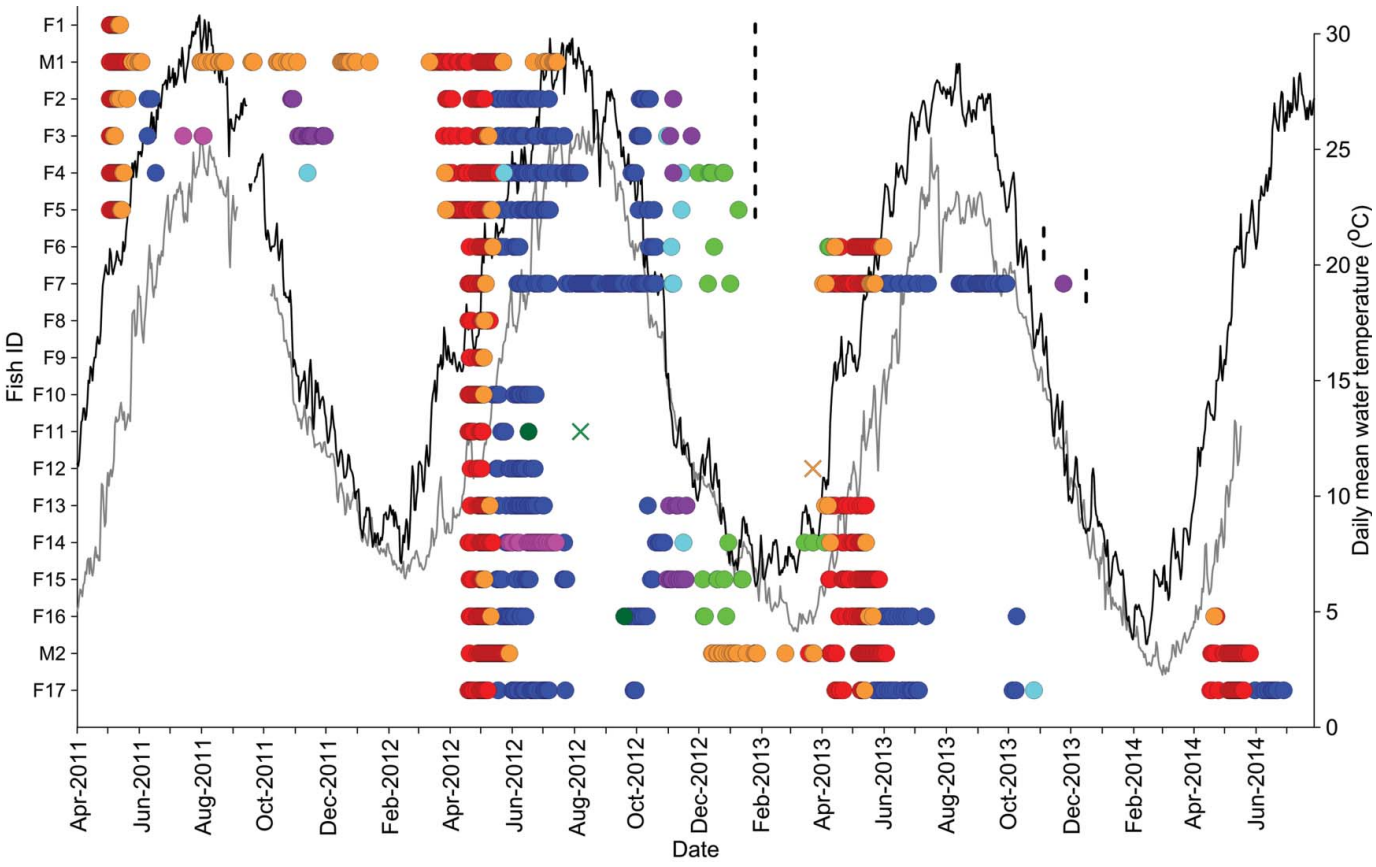

FIGURE 3. Detection histories of individual Striped Bass telemetered and released on the upper Roanoke River in the springs of 2011 (May 2; $n = 6$ fish; 873–1,104 mm TL) and 2012 (April 19; $n = 13$ fish; 750–1,146 mm TL). The fish IDs preceded by an "F" are females; "M" prefixes denote males. Detection locations are color coded by the geographic areas in Figure 2; if a given fish was detected at any receivers within a specific area, a color-filled circle for that area (e.g., orange for the Albemarle Sound) is shown for that day. The vertical dashed line to the right of the detection history for each fish represents the estimated expiration date of the transmitter battery provided by the manufacturer; lack of a dashed line indicates that the transmitter for that individual was projected to be active beyond the end of the study (July 8, 2014). An "X" denotes Striped Bass that were reported as being harvested by fishermen and are color coded to the geographic area (Figure 2) in which harvest occurred. The black and gray lines represent the mean daily water temperatures for the upper Roanoke River, North Carolina, and coastal waters off New York, respectively (see Figure 1 for locations of temperature stations; also note that temperature data was unavailable off New York after May 17, 2014).

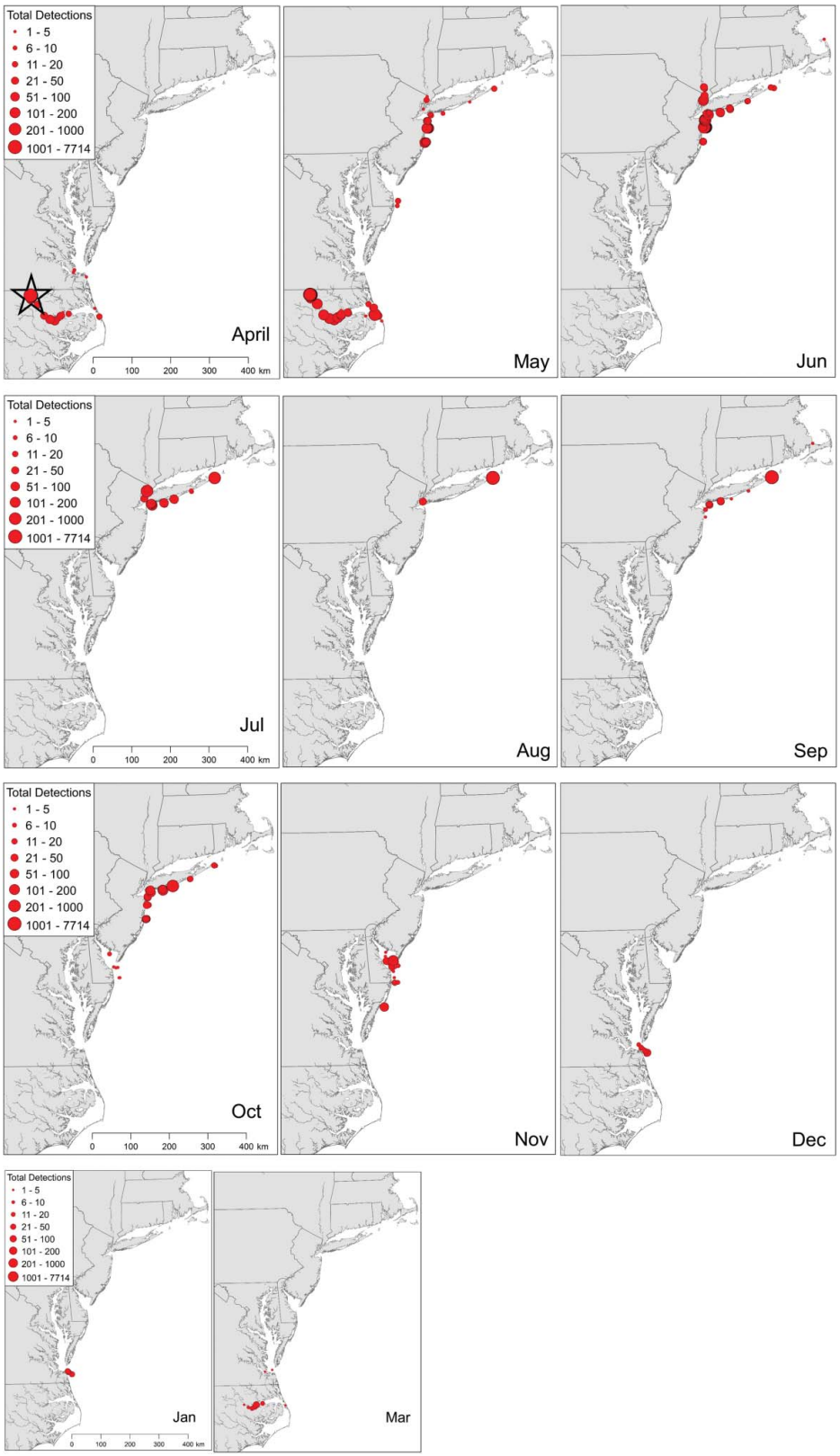

FIGURE 4. Monthly detections of Striped Bass > 900 mm TL ($n = 17$ females) telemetered and released in the upper Roanoke River (star on map) on May 2, 2011, and April 19, 2012. The detection data were pooled across fish and years (May 2011 to July 2014); bubble sizes are positively scaled to the total number of monthly detections at each receiver station as indicated in the legend. Note there were no detections in February.

from December to March. Receiver arrays were deployed year-round (2011–present) in coastal rivers and nearshore areas of South Carolina ($n = 47$ receivers; Santee–Cooper River) and Georgia ($n = 120$ receivers; Altamaha River), but the Striped Bass released in our study were not detected by these arrays (B. Post, South Carolina Department of Natural Resources, personal communication; D. Peterson, University of Georgia, personal communication). During late March and April, Striped Bass completed their migration circuit and returned to the Roanoke River from ocean waters to spawn (Figures 3, 4).

The seasonal migration pattern revealed in our study was remarkably consistent across fish. All Striped Bass > 900 mm TL that were known to be at liberty for at least 1 year ($n = 11$) engaged in a similar seasonal, coastwide migration pattern (Figure 3), regardless of their release year (2011 or 2012). Moreover, the two females at liberty for more than 2 years (F16 and F17) repeated the same seasonal migration pattern in consecutive years (Figure 3).

Although the two smallest fish in our study, males of 750 and 873 mm TL, did not appear to migrate to northern ocean waters, their detection pattern suggests that they left the Albemarle Sound after spawning. Both males (M1 and M2) moved down the Roanoke River in late May and crossed the Albemarle Sound in 2–3 d as they were detected at the Oregon Inlet (M1) and Wright Memorial Bridge (M2) and not detected thereafter for 59 and 198 d, respectively (Figure 3). Given the lack of detections on coastal arrays to the north and south of North Carolina, these males likely utilized nearshore ocean waters off North Carolina during the summer (which lacked receivers, Figure 1). Male M1 was sporadically detected at Oregon Inlet from August to January. Both males (M1 and M2) were detected in the Albemarle Sound during winter and made the spawning run in the Roanoke River the following spring (Figure 3).

Homing and Skipped Spawning

Roanoke River Striped Bass exhibited a high degree of homing. The estimated homing rate was 100% as all fish ($n = 11$) that migrated to distant northern ocean waters and were alive through the following spring returned to the Roanoke River spawning grounds that spring (2012 or 2013). There were no detections in the Delaware River, and the two fish (F3 and F14) detected in the Hudson River were detected at locations (lower river, higher salinity; Figure 2B) and times (summer, June–August; Figure 3) at which spawning does not occur. Although two fish (F6 and F14) were detected at the mouth of the Chesapeake Bay during early April, these fish were detected 4–5 d later in Albemarle Sound (Figure 3), then made the > 200-km spawning run up the Roanoke River.

We found no evidence of skipped spawning. All Striped Bass known to be alive through the next spawning season ($n = 13$) participated in the spring spawning run up the Roanoke River. Interestingly, the three fish (F16, F17, and M2) available for detection during two successive spawning seasons after their release made the spawning run in consecutive years (2013 and 2014; Figure 3).

Timing of the Spawning Run

The spring spawning run occurred later in 2013 than in 2012. On average, Striped Bass arrived in the Roanoke River 19 d later in 2013 (April 13) than in 2012 (March 25). This difference in arrival dates was significant regardless of whether male M1 was included in analyses (exact Wilcoxon tests: $P = 0.008$ with male, $P = 0.016$ without male). Striped Bass did not enter the river until the ocean waters off of Virginia warmed to and remained above 9–10°C, which occurred 1 month later in 2013 (April 8) than in 2012 (March 8) (Figure 5). Upon reaching the spawning grounds, Striped Bass did not leave until river temperatures reached at least 18°C, which occurred on May 1 in 2012 and May 11 in 2013 (Figure 5). Most fish (70%, or 7 of 10) left the spawning grounds < 6 d after this temperature threshold was reached (Figure 5). However, a few fish ($n = 3$, including male M1) remained on the spawning grounds for longer periods and did not emigrate downriver until 15–17 d after temperatures reached 18°C. Striped Bass exited the Roanoke River 1 week earlier in 2012 (mean departure date = May 12) than in 2013 (mean departure date = May 19), but the difference in departure times was only significant, albeit marginally so, when male M1 was excluded from the analyses (exact Wilcoxon tests: $P = 0.08$ without male, $P = 0.24$ with male).

Postspawning Migration Speeds

Northward migration speeds ranged from 23.8 to 79.6 km/d, or 0.26 to 0.80 BL/s. Estimates of migration speeds during 2011 (range = 23.8–26.9 km/d; mean = 25.5 km/d; $n = 3$ fish) were more than two-fold lower than in 2012 (range = 31.9–79.6 km/d; mean = 59.3 km/d; $n = 9$ fish). We considered the 2011 data biased low given the similarity in fish size and water temperature between years and therefore excluded the 2011 data from the regression analysis. In addition, one observation from 2012 (24.8 km/d) had a Cook's D value of 0.60 (greater than the cutoff of 0.40) and a studentized residual of −2.5 and was therefore considered an outlier and removed from the analysis. Despite the relatively small size range of fish examined (939–1,146 mm TL), migration speeds showed a strong ($r^2 = 0.78$) positive relationship ($P = 0.002$) with fish length (Figure 6). The fastest migration speed of nearly 80.0 km/d was achieved by the largest fish in the study, an 1,146-mm female (F15) that migrated from the Roanoke River spawning grounds to coastal New Jersey (off Shark River Inlet), a distance of 837 km, in just over 10 d.

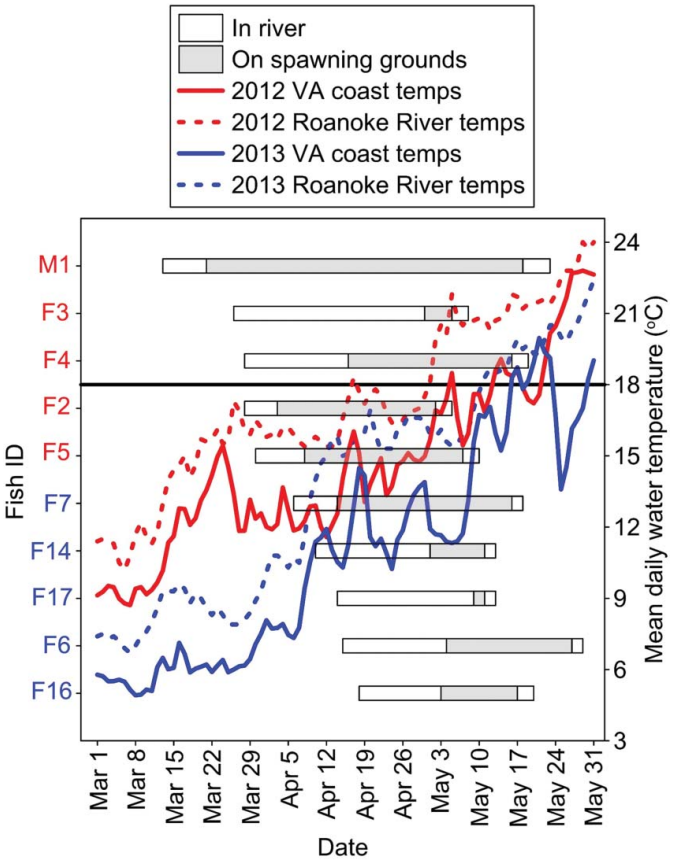

FIGURE 5. Timing of the Roanoke River spawning run of Striped Bass (>873 mm TL) in relation to spring water temperatures in the upper Roanoke River and along coastal Virginia (VA) (see Figure 1 for locations of temperature stations). Detection patterns in the Roanoke River were used to determine the periods of upriver and downriver migration (white portions of the horizontal bars) and when fish resided on the spawning grounds (the gray-filled portions of the bars). The thick black line indicates the minimum spawning temperature of Roanoke River Striped Bass (18°C) determined by Rulifson (1990). The fish IDs in red represent fish released in 2011 that made the 2012 spawning run, and the fish IDs in blue denote fish released in 2012 that made the 2013 spawning run. The fish IDs preceded by "F" indicate females and "M" indicates males. Data are only included for Striped Bass known to enter and subsequently exit the Roanoke River (i.e., those fish detected in coastal waters or the Albemarle Sound prior to entering the river and also detected in either of those regions following their exit from the river).

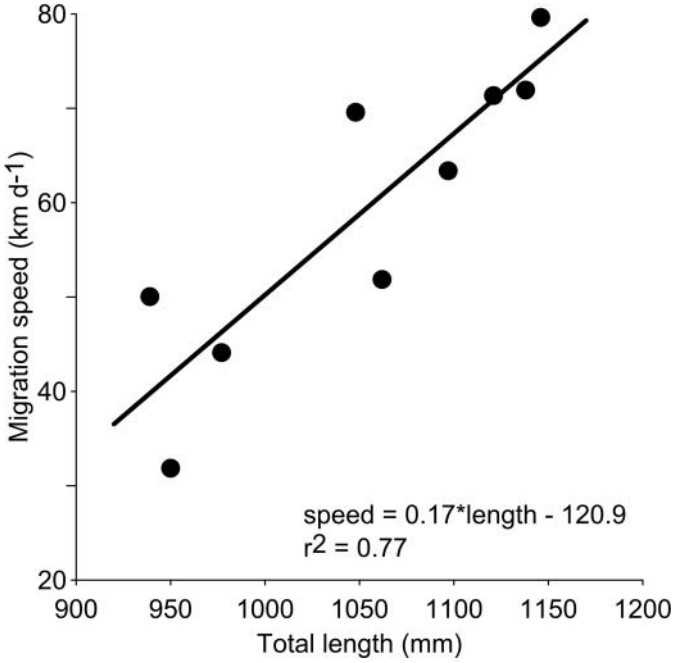

FIGURE 6. Relationship between migration speed and fish length during the 2012 postspawning migration of Striped Bass from the Roanoke River, North Carolina, to northern ocean waters off New Jersey and New York. Migration speeds were estimated for each fish by dividing the distance between their last detection on the spawning grounds and first detection in ocean waters off New Jersey or New York by the time between these detections.

DISCUSSION

Our study provides novel information on the life history of Roanoke River Striped Bass. Most notably, our study is the first to document homing in this population. We demonstrated that large Striped Bass (>900 mm TL) emigrate rapidly from the Roanoke River spawning grounds to northern ocean waters from New Jersey to Massachusetts, where they spend their summers. Then they migrate southward in the fall to overwintering habitats offshore of North Carolina and Virginia and subsequently return to the Roanoke River to spawn the next spring (there was no evidence of skipped spawning). Furthermore, we found that temperature had a strong effect on the timing of the Roanoke River spawning run, as entry to the Roanoke River from ocean habitats occurred almost 3 weeks later in a cold year (2013) relative to a year of average spring temperatures. Our results inform the management of this economically important species at both small (state-level) and large (U.S. Atlantic coast) spatial scales and also provide impetus for future research avenues.

Coastal Migration and Homing

The movement patterns of Roanoke River Striped Bass revealed by our study typify migration. First, movements were rapid and directed (i.e., nonrandom). After release, telemetered Striped Bass migrated rapidly (mean = 59.3 km/d; maximum = 79.6 km/d) to northern ocean waters (there were no detections to the south of Oregon Inlet), and fish successfully returned (homed) to the Roanoke River to spawn the next spring. The strong directionality of postspawning movements was also observed by Callihan et al. (2014), who noted that tag returns of large Roanoke River Striped Bass (>900 mm TL) occurred exclusively to the north of Oregon Inlet. The migration speeds estimated in this study (0.39–0.80 BL/s) fall within the range of sustained swimming speeds (0.4–1.5 BL/s) reported for the active migration phases of other anadromous fishes including salmonids, shads (family Clupeidae), and sturgeons (family Acipenseridae) (Beamish 1978; Bernatchez and

Dodson 1987; Quinn 1988), further confirming the migratory behavior of Roanoke River Striped Bass. Dingle and Drake (2007) noted that another characteristic of migration is its preemptive nature, namely that "habitats are abandoned before their quality has declined too seriously." Inshore water temperatures in North Carolina routinely approximate 30°C in midsummer (Figure 3); these temperatures are especially unsuitable for Striped Bass > 900 mm TL (Coutant 1985) due to the increased metabolic demand posed by a large body size (Hartman and Brandt 1995). Therefore, the rapid postspawning migration of large Striped Bass to cooler ocean waters to the north, which is preemptive and occurs well in advance of midsummer (by nearly 2 months), likely provides a metabolic reprieve and places fish in a more ideal environment for growth (Callihan et al. 2014). Northcote (1978, 1984) also stated that migration involves a large fraction of the population. Although the coastal migration of Roanoke River Striped Bass mainly involves fish > 900 mm TL, this size-group has comprised nearly 20% of the mature female population in recent years (Callihan et al. 2014) and likely contributes substantially to reproductive output in the population. Finally, the migration of Roanoke River Striped Bass clearly involves an alteration between habitats (ocean for feeding and freshwater habitats for spawning) that occurs with a regular periodicity (on a seasonal basis).

An effect of water temperature on the timing of the spawning run (cooler temperatures delayed the 2013 spawning run of Roanoke River Striped Bass) has been previously demonstrated in Striped Bass and other anadromous species. Peer and Miller (2014) analyzed 25 years of gill-net catch data for the Chesapeake Bay spawning grounds (upper Chesapeake Bay and Potomac River) and found that females occurred on the spawning grounds later in cooler years. Furthermore, Douglas et al. (2009) determined via acoustic telemetry that adult Striped Bass arrived on the spawning grounds in the Miramichi River, Canada, about 1 week later in the spring of 2005 (cooler year) versus 2004. A negative relationship between the timing of the spawning run (day of year) and water temperature (i.e., warm water causes earlier spawning) has also been documented in American Shad (Leggett and Whitney 1972; Quinn and Adams 1996). Interannual variability in water temperature has a greater effect on run timing in anadromous species such as American Shad and Striped Bass, whose progeny experience environmental conditions similar to those of adults during the spawning run due to their much shorter hatching times than salmonids, whose run timings are less plastic and primarily under genetic control (Quinn and Adams 1996). Based on these findings, it appears reasonable to conclude that cooler water temperatures were the primary cause for the delayed spawning run of Roanoke River Striped Bass in 2013 versus 2012, especially given the similar size of telemetered Striped Bass participating in the run those years (2012: 873–1,104 mm TL; 2013: 939–1,146 mm TL). Warming ocean temperatures likely act as a cue for Roanoke River Striped Bass to enter the Albemarle Sound estuary from their offshore wintering grounds and subsequently move upriver to spawn. It should also be noted that no fish left the spawning grounds until river temperatures reached 18°C, which is the minimum reported spawning temperature for this population (Rulifson 1990).

Our study is the first to document homing in Roanoke River Striped Bass, and in general, our results agree with genetic studies of this species along the U.S. Atlantic coast. The subsequent recapture of tagged fish in the same spawning system they were previously released in cannot be taken as true evidence of homing because the location(s) of tagged fish during the interim (i.e., between spawning events) is unknown. The Striped Bass telemetered in our study not only returned to the same river they previously spawned in (were released in) but in the interim underwent an extensive coastal migration (>1,000 km) past other major spawning systems (Chesapeake Bay, Delaware River, Hudson River), which they did not enter for the purposes of spawning (i.e., no spawning runs were made in those systems). The strong tendency of Roanoke River Striped Bass to return to their river of previous spawning should result in reproductive isolation of this population, which has been confirmed by genetic studies. Gauthier et al. (2013) genetically analyzed young-of-the-year Striped Bass from each major spawning system along the U.S. Atlantic coast, including the Roanoke River as well as the Chesapeake Bay, Delaware River, and Hudson River. They found significant genetic divergence among samples from these major spawning systems (Gauthier et al. 2013) indicating a high degree of, but not "perfect," homing of adults to their natal system (Bielawski and Pumo 1997). Gauthier et al. (2013) concluded that most of the limited, contemporary gene flow that does occur is from the large spawning population of the Chesapeake Bay into other systems and that migratory Striped Bass originating in other systems, including the Roanoke River, return exclusively to their natal rivers to spawn, as we found.

Waldman et al. (2012) hypothesized that the latitudinal limits of the coastal migration of Striped Bass were related to population origin in a manner that minimized migration costs but still placed fish in a favorable environment for growth (i.e., migratory Striped Bass from more southerly populations do not migrate as far north in summer and those from more northerly populations do not migrate as far south in winter). While their results (genetic-based stock compositions) were equivocal and did not conclusively support this prediction, they recommended further testing of their hypothesis (Waldman et al. 2012). In our study, Roanoke River Striped Bass, which are believed to be the southernmost migratory (anadromous) population along the U.S. Atlantic coast (Boreman and Lewis 1987), were not detected north of Cape Cod, which provides some support for the hypothesis of Waldman et al. (2012). However, conventional tagging data indicate that Roanoke River Striped Bass occasionally use coastal waters north

of Cape Cod based on tag returns from this area, the farthest being from Sheepscot Bay, Maine (1,350 km from the Roanoke River release site) (J. L. Callihan, unpublished data). Future data collected by the ACT Network should provide further insight into this research question.

Receiver Operation Histories

While large-scale acoustic telemetry arrays can provide novel information on fish migration, two of our findings highlight the utility of evaluating receiver operation histories when analyzing such data. First, postspawning migration speeds were more than two-fold lower in 2011 than 2012, despite the fact that telemetered Striped Bass were of similar size between years (2011: mean size = 1,054 mm TL; 2012: mean size = 1,053 mm TL). The disparity in migration speed estimates between years was likely due to the reduced spatial coverage of the New Jersey–New York array in 2011 ($n = 21$ active receivers) relative to 2012 ($n = 122$ active receivers). After reaching their summer foraging grounds (which appear to be in the vicinity of Long Island for Roanoke River Striped Bass), fish likely make reduced movements. Therefore, by the time Striped Bass were in the vicinity of the 2011 receivers (a small cluster on the western end of Long Island), they were probably already in foraging mode, whereas in 2012 fish were first detected farther south (in New Jersey) while they were still in transit to the foraging grounds, thus providing more accurate estimates of sustained swimming speeds during active migration. This finding clearly highlights the implications of receiver array design and location on the accuracy of migration speed estimates. When the 2011 data were removed from the regression analysis, a strong positive relationship was observed between fish size and migration speed, as has been shown in many fish species; this is due primarily to the fact that larger fish have a greater stride length, or the distance moved with one tail beat (Bainbridge 1958; Sambilay 1990). Secondly, there were no detections off the mouth of Chesapeake Bay in winter 2013, possibly implying that Striped Bass overwintered farther offshore that year, which seems plausible given that ocean temperatures were cooler in 2013. However, the lack of detections could also be attributed to the reduced receiver coverage ($n = 4$ operational receivers) in that region during winter 2013. Therefore, an interannual difference in overwintering distribution cannot be inferred from these detection data because of the potential confounding effect of reduced receiver coverage.

Management Implications

The high degree of homing demonstrated by Roanoke River Striped Bass could aid fishery managers in determining the stock composition of the mixed-stock ocean fishery along the U.S. Atlantic coast during the nonspawning period (summer to winter). By releasing telemetered Striped Bass on feeding or overwintering grounds and determining what river they returned to for spawning, managers could identify the composition of the migratory mixed stock. Additional data from fish tagged as part of the United States Fish and Wildlife Service Cooperative Tagging Program (ASMFC 2013) would also help identify the composition of the migratory stock. This "river of return" method could also complement genetic-based stock identification tools to further investigate if and how the stock composition of migratory Striped Bass varies across space (e.g., coastal sampling location) and time (e.g., sampling year) (sensu Waldman et al. 2012).

Our results on the effect of water temperature on the run timing of Roanoke River Striped Bass inform local-scale management within North Carolina. Since 2008, the North Carolina Wildlife Resources Commission has used a fixed open season, March 1 to April 30, in the Roanoke River to control fishing effort and limit the number of females that are harvested before they have a chance to spawn. Females have been shown to arrive on the spawning grounds about 10–14 d later (early May) than males (mid to late April) (Carmichael et al. 1998), hence the seasonal closure of the fishery on April 30. Long-term water temperature data were available for the upper Roanoke River, in the vicinity of the spawning grounds (Figure 1), for 14 of the past 15 years (1999–2013, except 2007). Based upon these data, the mean day on which river temperatures exceeded the 18°C minimum spawning temperature was May 2. During most years (79%, or 11 of 14 years) this threshold was reached by the first week of May and in some years (50%) as early as the latter half of April. Therefore, in most years, females likely arrived in the Roanoke River well before the season was closed. For example, in 2012, a year of average spring temperatures (18°C by May 1), the four telemetered females that participated in the spawning run arrived in the lower Roanoke River during March 26 to March 30. There are regulations in place to protect large, prime-spawning females (e.g., only 1 of 2 fish allowed to be kept each day during the open season can exceed 686 mm TL); however, temperature could be used as an adaptive cue to further manage female harvest if deemed necessary in the future.

Large Roanoke River Striped Bass do not appear to exhibit skipped spawning. Accordingly, estimates of spawning stock biomass made from adult collections on the Roanoke River spawning grounds should not need to be adjusted upwards to account for skipped spawning (Jørgensen et al. 2006; Rideout and Tomkiewicz 2011; Skjæraasen et al. 2012), at least for this segment of the population (fish > 900 mm TL). Secor and Piccoli (2007) found that although skipped spawning in Chesapeake Bay Striped Bass was minimal overall, younger adults were more likely to skip spawning than older (larger) fish based on lifetime otolith microchemistry profiles. Therefore, skipped spawning warrants further investigation in smaller adult Roanoke River Striped Bass before it can be discounted for the entire population.

In closing, our study demonstrated the utility of large-scale and long-term acoustic telemetry arrays for examining fish migration. When accompanied with receiver operation data, such studies can provide robust and novel data on the migration dynamics of fishes. For instance, our study advanced the current knowledge of Roanoke River Striped Bass life history by providing the first direct evidence of homing in this population. Furthermore, our telemetry-based results have important and immediate implications for management, including stock identification, the setting of fishing seasons, and the effect that skipped spawning has (or does not have in our case) on population biomass estimates. As acoustic telemetry technology and the network of researchers using this approach continue to evolve, we are likely to learn much more about the migration and movements of fish and other aquatic organisms that can enhance their management and conservation.

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