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ARTICLE

Residence, Habitat Use, and Movement Patterns of Atlantic Tripletail in the Ossabaw Sound Estuary, Georgia

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Abstract
Atlantic Tripletails *Lobotes surinamensis* support a popular recreational fishery along the coast of Georgia; however, Atlantic Tripletail residency and movements within Georgia estuaries have not been studied. Our objective was to describe estuarine movements and residency of Atlantic Tripletails in the Ossabaw Sound Estuary, Georgia. During summer in 2010 and 2011, large juvenile and adult Atlantic Tripletails ($n = 32$; 42.1–71.0 cm TL) were captured with traditional angling methods and received surgically implanted ultrasonic transmitters. Tagged individuals were detected within the estuary via a stationary array of acoustic receivers that monitored the estuary continuously from June 2010 through May 2012. Manual tracking was conducted with a portable hydrophone and homing. Atlantic Tripletails were detected in the estuary during March–November at sustained water temperatures above 21°C; tagged fish were not detected by the stationary array during any other period. Movements were highly correlated with tidal stage; 100% of the tagged fish moved upstream with flood tides and returned to the sound with the ebbing tide on a daily basis. Atlantic Tripletails were observed as far upstream as river kilometer 33. Our results from acoustic telemetry provide the first information on spatial and temporal habitat use by Atlantic Tripletails within the South Atlantic Bight and suggest that these fish (1) exhibit a high degree of residency in Georgia estuaries and (2) use a large portion of the estuary during their daily movements. Although estuarine habitat use appeared to be an important component of the species' life history, future studies of population dynamics and winter movements will be needed to obtain a better understanding of the potentially complex structure of Atlantic Tripletail stocks.

The Atlantic Tripletail *Lobotes surinamensis* is a medium-sized, deep-bodied fish inhabiting tropical and subtropical seas (Gudger 1931; Fischer 1978). The Atlantic Tripletail is one of only two members of the perciform family Lobotidae. In the western Atlantic Ocean, the species is distributed from Massachusetts southward to Argentina and throughout the Gulf of Mexico and Caribbean Sea (Hoese and Moore 1998). Although one adult Atlantic Tripletail was recorded as far north

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as Nova Scotia, Canada (Gilhen and McAllister 1985), greater abundances are observed south of Virginia (Hildebrand and Schroeder 1927; Gudger 1931). Juveniles and adults are found in a variety of habitats, from shallow nearshore waters (Gudger 1931; Baughman 1941) to pelagic waters more than 160 km offshore (Caldwell 1955). Regardless of location, Atlantic Tripletails frequently are observed in close association with shaded structures, including pilings, wrecks, flotsam, buoys, and *Sargassum* algae (Kelly 1923; Gudger 1931; Hughes 1937; Baughman 1941; Dooley 1972).

The Atlantic Tripletail is a highly prized food fish, supporting popular recreational and limited commercial fisheries (Gudger 1931; Baughman 1941). Marine Recreational Fisheries Statistics Survey data suggest that most of the recreational harvest along the U.S. Atlantic coast occurs in Florida and Georgia; however, the low number of angler intercepts precludes reliable estimation of annual harvests (NMFS 2010). Commercial harvest along the Atlantic coast has averaged less than 3 metric tons annually since 2000, with approximately 90% of these landings originating from the east coast of Florida (NMFS 2010). The greatest harvest of Atlantic Tripletail occurs during the summer months (NMFS 2010) coinciding with the spawning season, which can last from May through September (Gudger 1931; Baughman 1941; Ditty and Shaw 1994; Brown-Peterson and Franks 2001; Cooper 2002; Strelcheck et al. 2004). Spawning is thought to occur in offshore waters (Ditty and Shaw 1994). Several previous studies have focused on life history parameters of Atlantic Tripletail populations in the Gulf of Mexico (Baughman 1941; Ditty and Shaw 1994; Franks et al. 1997, 2001, 2003; Brown-Peterson and Franks 2001; Strelcheck et al. 2004). However, few studies have investigated Atlantic stocks of this species (Merriner and Foster 1974; Armstrong et al. 1996; Cooper 2002; Parr 2011), leaving significant knowledge gaps regarding estuarine residence, seasonal habitat use, movements, exploitation rates, and reproductive ecology in the region.

In recent years, the number of recreational anglers targeting and harvesting Atlantic Tripletails in Georgia has increased (GADNR 2007). Increases in recreational fishing pressure on Georgia's Atlantic Tripletail population, especially during the spawning season, suggest that effective management of this population is needed to prevent localized overfishing. Unfortunately, basic information on Atlantic Tripletail life history is generally lacking or incomplete. Consequently, formal stock assessments, which are critical for quantifying the status and sustainability of the resource, have been hindered by the current uncertainty surrounding Atlantic Tripletail life history and population dynamics.

An understanding of the movement patterns of a fish species is critical for identifying the spatial and temporal scales at which that species should be managed, the factors influencing those movements, and information regarding stock structure (Begg and Waldman 1999). Movement is a key process that allows fish to meet their energy demands in spatially and temporally dynamic environments (Schlosser and Angermeier 1995) while also allowing selection of habitats that help to maximize growth and survival (Gowan and Fausch 2002; Heupel and Simpfendorfer 2008). Examination of processes that directly influence habitat use, such as individual movement, can also aid in identifying environmental factors that are important for the species (White and Garrott 1990; Rogers and White 2007).

Atlantic Tripletails are observed seasonally in the bays, sounds, and estuaries of the northern Gulf of Mexico and the U.S. Atlantic coast from Florida to Virginia, with the greatest concentrations occurring during the summer months (Gudger 1931; Baughman 1941; Merriner and Foster 1974). However, apart from accounts of the species' seasonal occurrence, the extent to which Atlantic Tripletails use estuaries is unknown (Ditty and Shaw 1994). In Georgia, angler reports suggest that the species is present in local estuaries during April–October, but to date the seasonal residence, movements, and habitat use of Atlantic Tripletails anywhere within the South Atlantic Bight have not been examined. Therefore, the goal of this study was to identify the seasonal residence and movement patterns of large juvenile and adult Atlantic Tripletails (>40.0 cm TL; size at 50% maturity = 45.9 cm; Parr 2011) within a Georgia estuary. Our specific objective was to describe residence, movement, and estuarine habitat use over seasonal, diel, tidal, and hourly scales to improve the current knowledge of Atlantic Tripletail life history and ecology. These data will provide insight into the value of estuarine habitats and aspects of reproductive ecology as well as information on stock structure—all of which may be critical to successful management of Atlantic Tripletail populations along the southeastern U.S. Atlantic coast.

STUDY SITE

The Ossabaw Sound Estuary (OSE) is located approximately 20 km south of Savannah, Georgia (Figure 1). Estuarine exchange with the Atlantic Ocean occurs through Ossabaw Sound, a 5.25-km-wide opening between Wassaw Island to the north and Ossabaw Island to the south. Within Ossabaw Sound, Raccoon Key separates the mouths of the Ogeechee and Little Ogeechee rivers into the South Channel and North Channel, respectively. The Ogeechee River is the major source of freshwater input to Ossabaw Sound, providing a mean annual discharge of 115 m^3/s through the South Channel (Meyer et al. 1997).

Like other Georgia estuaries, the OSE is characterized by sand and mud substrates, large expanses of smooth cordgrass *Spartina alterniflora*, and a large tidal range averaging 2.1 m (Johnson et al. 1974). Tidal currents usually range from 50 to 75 cm/s, with stronger currents observed during ebb tides than during flood tides (Dörjes and Howard 1975).

METHODS

Fish Tagging

During June–July in 2010 and 2011, hook-and-line sampling was used to capture large juvenile and adult Atlantic Tripletails

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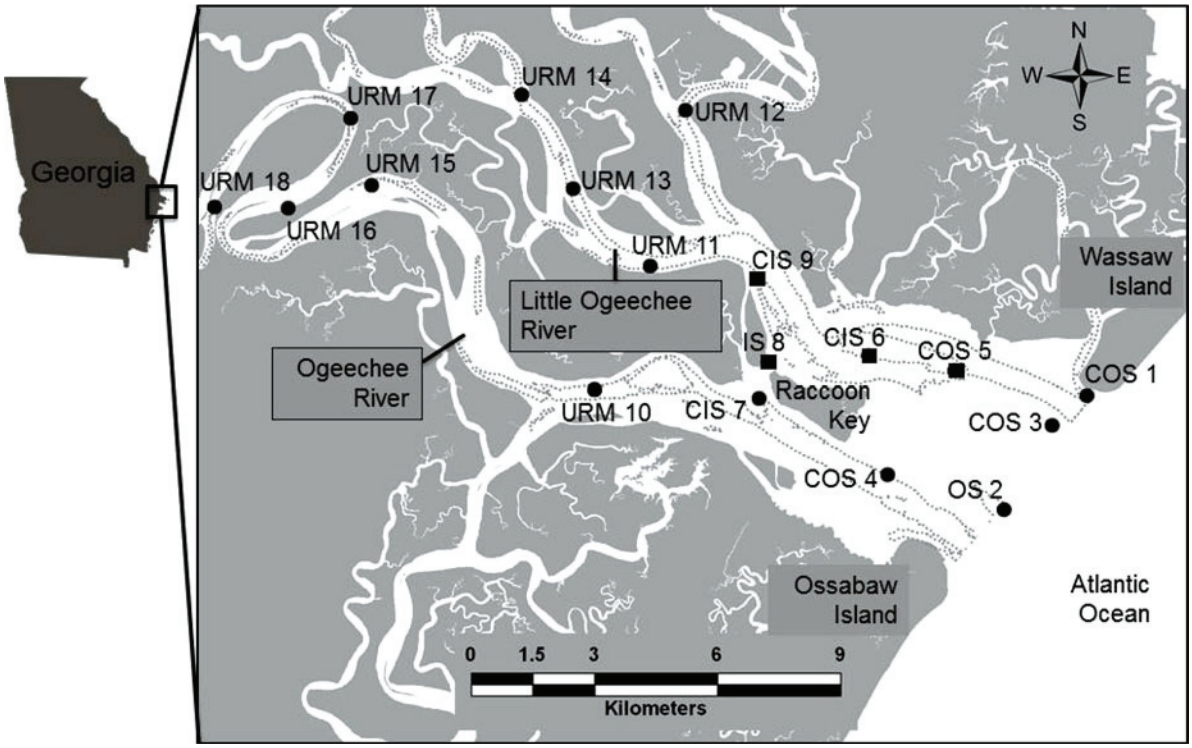

FIGURE 1. Map of the Ossabaw Sound Estuary, Georgia. Individual receiver locations are indicated by the black squares (receivers deployed in both 2010 and 2011) or circles (receivers deployed in 2011 only). Receivers are labeled with habitat codes (COS = channel outer sound; OS = outer sound; CIS = channel inner sound; IS = inner sound; URM = upriver marsh). The dotted line represents the 6-m depth contour.

(>40.0 cm) around fixed structures within the estuary during periods of low tidal current. Tackle consisted of 18.1- or 22.7-kg-test braided line rigged with a slip-float, an 18.1-kg fluorocarbon leader, and an octopus hook baited with live white shrimp *Litopenaeus setiferus* or Atlantic Menhaden *Brevoortia tyrannus*. Captured individuals were transported in an aerated live well to the nearby Marine Extension Service at the University of Georgia, where they were measured (cm TL) and weighed (kg) and received a coded acoustic transmitter (Vemco V16–4H; Amirix Systems, Inc.) via surgical implantation. To implant a transmitter, we placed the fish ventral side up in a padded, V-shaped cradle with only the ventral surface of the fish above water to ensure that the gills remained submerged in the holding tank during the operation. A sterile scalpel was used to make a 3–4-cm incision between the pelvic fins and anus, with the incision being slightly offset from the ventral midline. The sterilized transmitter was lightly coated with triple antibiotic ointment (Neosporin; Johnson and Johnson Consumer Companies, Inc.) and then was inserted into the peritoneal cavity. The incision was closed with three to four absorbable Vicryl sutures (2–0 needle; Ethicon, Inc.) using a simple interrupted pattern. Each transmitter had an expected battery life of 858 d and was coded with a random signal repeat interval of 30–90 s to minimize continuous signal overlap. The fish was then externally tagged with a T-bar anchor tag (Hallprint Pty. Ltd.) that had researcher contact information printed on it in case of recapture by local anglers. After tagging, Atlantic Tripletails were held in a 2,271-L recirculating tank for 1–2 d to ensure that the fish had completely recovered from the surgery before their release. If no surgical complications were observed during this period, the fish were returned to their original capture site and released. To increase the probability that recaptured Atlantic Tripletails would be reported by local anglers, contact information was also printed on the transmitters, and information about the study was presented to anglers at local meetings and printed in the state fishing regulations.

Acoustic Monitoring

Both passive and active telemetry methods were used to detect tagged Atlantic Tripletails within the OSE. A stationary array of Vemco VR2W receivers was deployed to continuously monitor and record the presence of tagged individuals. Each receiver was equipped with an omnidirectional hydrophone and recorded the date, time, and unique transmitter identification code each time a tagged fish swam within range of the receiver. Where possible, receivers were fixed directly to pilings by using a custom-made stainless-steel bracket that was bolted to the piling approximately 1 m below the mean low water mark. In areas of the OSE where pilings were not available, a cinder block, a polypropylene rope (1.27 cm), and a subsurface float

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were used to suspend receivers on their vertical axis, approximately 1 m above the seafloor. In most locations, the cinder block was anchored either to a piling or to the shoreline to facilitate receiver recovery. Range testing at several receivers revealed an average tag detection radius of approximately 400 m (range = 200–800 m); however, range is known to vary depending on water depth, sea state, bottom substrates, and the degree of receiver biofouling (Heupel et al. 2008). Similar detection ranges were observed for receivers deployed with either method. All receivers were spaced approximately 1–3 km apart, which eliminated the potential for simultaneous detections at multiple receivers.

At the beginning of the study in May 2010, the acoustic array consisted of four VR2W receivers. Receivers were positioned in a linear fashion along the North Channel to discern patterns of ingress, egress, and residency exhibited by tagged Atlantic Tripletails within the monitoring area. During May 2011, seven additional receivers were deployed to expand the spatial coverage of the array within the study area. Detections of Atlantic Tripletails on the two upriver-most receivers prompted deployment of six additional receivers farther up the Little Ogeechee River and the Ogeechee River during July and September 2011 (two were deployed in July; four were deployed in September). One additional receiver was deployed in the outer sound during July. Once a receiver was deployed, data were downloaded from the receiver at 3–6-week intervals until the conclusion of the study in May 2012.

Data describing detections of tagged individuals by the stationary array were supplemented with active tracking of individuals by using a portable receiver (Vemco VR100), an omnidirectional hydrophone (VH165), and a directional hydrophone (VH110). Two methods of active tracking were used between 15 June and 19 September 2011. The first method, conducted two to three times per week, involved systematically searching the study area using a search interval of 300–400 m. At each stop, the omnidirectional hydrophone was lowered into the water. If a tagged fish was detected, the directional hydrophone was lowered into the water, and triangulation and homing were used until a reading of 95 dB or above was detected at a gain of 12 or less (~4 m from the fish). A GPS unit was used to determine the location, which was recorded along with the date, time, and relevant environmental variables. The second method of active tracking employed continuous tracking of either stationary or actively moving fish for 4–6-h periods or until contact was lost. Continuous tracking was conducted approximately once per week and opportunistically (i.e., when actively moving fish were detected by the first method). Active telemetry of tagged Atlantic Tripletails was normally conducted during daylight hours, but a few continuous tracking events were also attempted at night.

Data Analysis

Estuarine residence.—Residence of tagged Atlantic Tripletails was assessed daily; a fish was considered resident in the OSE when two or more detections per day were recorded for that individual. Daily residence histories for each tagged Atlantic Tripletail were plotted to permit visual assessment of the temporal patterns of residency within the study area. Individual residence (IR) of each fish was calculated by dividing the number of days the individual was detected (days of detection [DD]) by the total fish-days (TFD; number of days between the first and last detections for that individual). Pearson's product-moment correlation coefficient was used to analyze the relationships between residence measures (DD, TFD, and IR) and fish size. To determine patterns in residency for the entire monitored population, the proportion of tagged individuals that were present per day (i.e., daily residence index) was plotted against environmental variables, including water temperature, photoperiod, and lunar phase. Pearson's product-moment correlation coefficient was used to assess the relationship between the daily residence index and the environmental variables. Water temperature data were obtained from the National Oceanic and Atmospheric Administration (Tides and Currents, station 8670870). Daily sunrise and sunset and lunar phase data were obtained from the U.S. Naval Observatory (Astronomical Applications Department; aa.usno.navy.mil/). Photoperiod was derived from the daily sunrise and sunset times.

Movement patterns.—Potential diel and tidal activity patterns were examined for all tagged Atlantic Tripletails that were detected for at least 4 d after their release. Initially, scatter plots of individual fish detections at each receiver were examined visually to identify any obvious patterns in diel activity at specific locations. To avoid potential biases either from stationary individuals or from tidal effects on receiver detection efficiency, raw detection data were standardized by the time of day such that only one hourly detection per receiver was used to identify individual fish locations throughout a day (i.e., many detections at a receiver were reduced to one detection for that hour). To determine potential effects of the tidal cycle on fish activity, the standardized detection frequency of each receiver was binned in 20-cm increments corresponding to tide height. A *G*-test (Sokal and Rohlf 1995) was used to determine whether the frequency of standardized detections by tide height differed from the expected frequency of tide heights that were observed during the monitoring period for that receiver. The proportion of all observed movements occurring with or against the tidal current was also assessed to evaluate patterns of active and passive swimming. To minimize the possibility of misclassifying a movement (i.e., with or against tidal currents), only movements that occurred between adjacent receivers within a 3-h interval were included in this analysis. Movements of actively tracked individuals were described in relation to tide stage and other environmental variables.

Possible periodicity in the short-term movement patterns of Atlantic Tripletails as related to diel or tidal cycles was examined by using Lomb–Scargle periodograms (Lomb 1976; Scargle 1982). The Lomb–Scargle method is a type of spectral analysis that enables one to estimate the power of periodic components of time-series data at all possible frequencies. To compute the

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Lomb–Scargle periodograms, detection data for each fish were analyzed with the program PAST (Hammer et al. 2001).

Spatial habitat use.—Variation in habitat use within the OSE was first examined visually by using scatter plots of individual fish detections at each receiver. This approach facilitated the identification of broad-scale trends in spatial habitat use (e.g., possible shift from inner to outer receivers). To account for varying durations of receiver deployment, all detection data were also standardized by receiver-days (i.e., number of days for which the receiver was active). The number of standardized detections at each receiver per receiver-day and the number of individual fish visiting each receiver were calculated and compared by using percentiles to determine high-use areas in the OSE. The monthly standardized detections per fish-day at each receiver were also calculated for each fish and were analyzed using a two-way ANOVA to quantitatively assess the relationship between spatial habitat use and season. The interaction of receiver and month—both considered fixed effects—was also included in the model to identify any potential trends in use of the OSE through time. Model residuals were evaluated for normality with the Shapiro–Wilk statistic and for homogeneity of variances with Levene's test. When necessary, data were normalized with a $\log_e(x + 0.01)$ transformation to minimize heteroscedasticity. Significant differences among means were evaluated using Tukey's honestly significant difference test. The sequential addition of receivers throughout 2011 precluded any valid statistical analyses of combined receiver data. Therefore, to maintain data interpretability, changes in monthly standardized detections per fish-day were examined only for receivers that were deployed during the same time period. All statistical analyses of spatial habitat use were performed with the Statistical Analysis System version 9.3 (SAS Institute, Cary, North Carolina), and all tests of significance were conducted at an α level of 0.05.

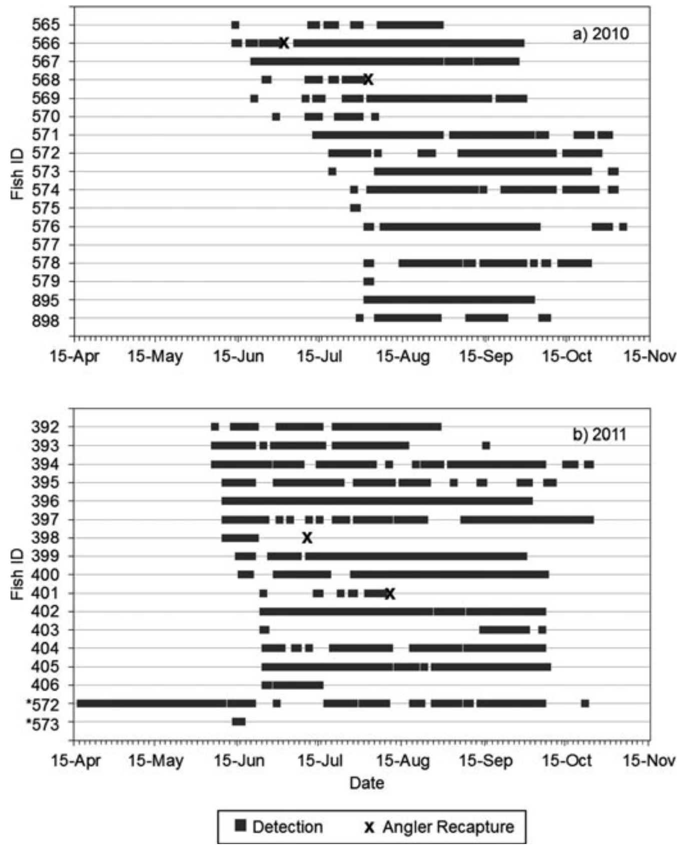

FIGURE 2. Abacus plots depicting daily residence (gray shading; only data from Vemco VR2W receivers are shown) and angler recaptures (x) of individual Atlantic tripletails within the Ossabaw Sound Estuary, Georgia, during **(a)** 2010 and **(b)** 2011. Asterisks denote fish that were tagged in 2010 and that returned in 2011.

RESULTS

Estuarine Residence

Over the 2 years of the study, 32 individual Atlantic Tripletails received acoustic transmitters and were released into the OSE; 29 of these fish were included in the data analyses (Table 1). More Atlantic Tripletails were captured in the North Channel than in the South Channel (25 and 7 fish, respectively). Tagged Atlantic Tripletails ranged in size from 42.1 to 71.0 cm TL (median = 59.4 cm TL) in 2010 and from 42.7 to 67.8 cm TL (median = 57.3 cm TL) in 2011. After release, most fish (∼75%) remained in the OSE throughout most of the summer and early fall, with only brief periods (usually < 3 d) of absence from the receiver array (Figure 2). Only one fish was never detected after its release; two fish were only detected for 1 d after their release. Subsequent searches for these individuals via active tracking methods suggested that the fish had either died or shed their transmitters. Three other tagged fish were harvested by recreational anglers (1 fish in 2010; 2 fish in 2011). All other tagged fish were monitored intermittently for periods ranging from 3 to 189 d (median TFD = 100; Table 1), yielding a median IR of 67% (range = 17–100%). Residence time within the OSE was not significantly correlated with TL of individual Atlantic Tripletails (DD: $r = -0.13$, $P = 0.50$; TFD: $r = -0.23$, $P = 0.23$; IR: $r = -0.17$, $P = 0.37$).

Seasonal occurrence of Atlantic Tripletails within the OSE appeared to be influenced by water temperature. The residence index was positively correlated with increasing mean daily water temperature in the OSE ($r = 0.63$, $P < 0.001$). Over the duration of the study, water temperatures ranged from 8.5°C to 33°C, but Atlantic Tripletails were only detected at temperatures exceeding 20°C (Figure 3). The start of estuarine residence was difficult to estimate because many fish were already present before tagging began. However, two of the fish that were tagged in 2010 (fish 572 and 573) returned to the OSE as early as 17 April 2011; furthermore, one individual that was tagged in 2010 (fish 572) and two fish that were tagged in 2011 (fish 402 and 396) returned to the OSE between 21 and 26 March 2012. Water temperatures during these periods in both 2011 and 2012 were approximately 21°C.

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TABLE 1. Summary information for all 32 Atlantic Tripletails monitored within the Ossabaw Sound Estuary, Georgia, between June 2010 and May 2012 (ID = identification number; DD = days of detection; DD_a = days of detection, including active telemetry; TFD = total fish-days; IR = individual residence; IR_a = individual residence, including active telemetry; * = fish in its second year of residence; ** = fish in its third year of residence). The three shaded rows indicate fish that were excluded from analyses.

Fish ID	TL (cm)	Weight (kg)	Release date	DD (d)	DD_a (d)	TFD (d)	IR (%)	IR_a (%)	Standardized detections
565	68.0	6.8	14 Jun 2010	34		77	44		264
566	71.0	9.1	14 Jun 2010	97		107	91		853
567	61.1	5.4	21 Jun 2010	88		98	90		507
569	60.2	5.0	21 Jun 2010	63		100	63		373
568	68.7	7.7	25 Jun 2010	13		37	35		58
570	62.4	5.4	29 Jun 2010	16		38	42		96
571	46.6	1.8	14 Jul 2010	85		110	77		541
572	42.1	1.8	20 Jul 2010	63		100	63		269
573	61.6	5.4	20 Jul 2010	79		106	75		543
574	52.2	3.2	28 Jul 2010	66		98	67		404
575	59.0	5.0	28 Jul 2010	2		2	100		5
898	48.6	3.2	30 Jul 2010	41		71	58		233
895	42.1	1.8	2 Aug 2010	61		62	98		240
576	48.8	3.2	2 Aug 2010	64		96	67		550
577	44.0	2.0	2 Aug 2010	0		0	0		0
578	52.9	3.6	2 Aug 2010	51		83	61		303
579	60.0	6.0	2 Aug 2010	2		2	100		10
572*	≥42.1	≥1.8	17 Apr 2011	99	109	189	52	58	589
392	62.7	6.8	6 Jun 2011	60		84	71		192
393	63.0	6.8	6 Jun 2011	59		102	58		276
394	42.7	1.8	6 Jun 2011	89		141	63		250
395	54.2	4.3	10 Jun 2011	64		122	52		197
396	57.3	4.6	10 Jun 2011	106	108	114	93	95	400
397	46.0	2.3	10 Jun 2011	89	90	137	65	66	704
398	45.6	2.3	10 Jun 2011	11		12	92		73
573*	≥61.6	≥5.4	14 Jun 2011	3		3	100		153
399	56.4	5.4	15 Jun 2011	82	85	107	77	79	390
400	58.4	6.4	16 Jun 2011	88		114	77		353
401	67.8	7.7	24 Jun 2011	6	11	42	14	26	10
402	59.4	5.4	24 Jun 2011	97		105	92		496
403	46.7	2.7	24 Jun 2011	18		105	17		99
404	58.6	4.5	25 Jun 2011	50	62	104	48	60	196
405	57.1	3.6	25 Jun 2011	83	92	106	78	87	379
406	60.6	5.4	25 Jun 2011	18		21	86		98
572**	≥42.1	≥1.8	21 Mar 2012						115
402*	≥59.4	≥5.4	22 Mar 2012						17
396*	≥57.3	≥4.6	26 Mar 2012						46
Median	57.9	4.6		63	63	100	67	67	

Most of the tagged individuals left the estuary during early October in both years. Median date of departure was 8 October in 2010 (range = 8 August–5 November) and 6 October in 2011 (range = 16 June–24 October); water temperature at the median date of departure during both years was 24°C. In each year, the final detection in the OSE was recorded when water temperatures had dropped to approximately 21°C. Decreases in daily residence also seemed to correspond with declines in mean daily water temperature (Figure 3). Trends in daily residence did not appear to be correlated with changes in photoperiod or lunar phase.

Movement Patterns

Scatter plots of individual fish detections did not indicate any obvious patterns in diel activity for the entire population;

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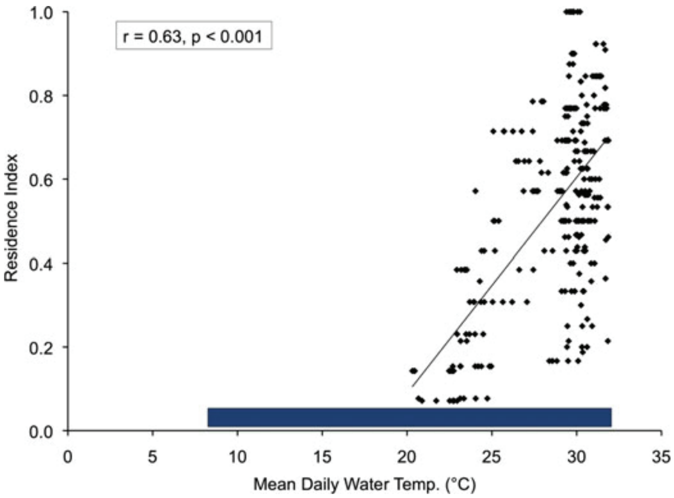

FIGURE 3. Scatter plot showing the significant positive correlation between the daily residence index for Atlantic Tripletails and mean daily water temperature in the Ossabaw Sound Estuary, Georgia. The blue bar represents the range of water temperatures that were observed in the estuary during the study. Atlantic Tripletails were not detected at temperatures below 20°C.

however, some individuals did appear to move in a predictable manner. For example, two fish displayed a diel pattern of regularly moving upriver at night, but this behavior was not typical of the entire group of tagged fish. The scatter plots did reveal detection patterns that were likely related to the tidal cycle. Analysis of standardized detection frequency by tide height frequency at individual receivers indicated that Atlantic Tripletail detections differed depending on tide height and receiver location (*G*-tests: df $= 16$, $P < 0.001$). For example, the upriver marsh receivers (e.g., URM 12, 13, and 14) had low detection frequencies at low tide heights but higher detection frequencies at higher tide heights.

Analyses of telemetry data from both passive and active tracking methods revealed a strong relationship between Atlantic Tripletail movement and the tidal cycle. Lomb–Scargle periodograms supported the assertion that Atlantic Tripletail movements were tidally influenced, as dominant peaks were observed at 12.4 h for almost all fish (Table 2). In fact, both active and passive tracking showed that the fish always moved with the tidal current regardless of direction. In most instances, the fish reversed its direction of movement when the current changed on each subsequent tidal cycle. This often-repeated pattern of tidal movement enabled some individuals to travel as far as 12 km during a single flood tide or ebb tide, facilitating regular access to the open waters near the mouth of Ossabaw Sound as well as to protected riverine waters. Interestingly, tagged fish were rarely stationary at any receiver for more than 2 h.

Active telemetry tracking yielded a total of 295 location estimates for 76% (13/17) of available fish, including 22 continuous tracks (for 11 different individuals) that averaged 277 min (range = 73–699 min). Mean surface dissolved oxygen at these locations was 5.20 mg/L (range = 3.20–6.21 mg/L), and the mean salinity level was 33.1‰ (range = 30.7–35.2‰). Of the 22 continuous tracks, 8 represented the movements of monitored fish as they changed locations. Movement rates (mean = 1.96 km/h) of these individuals showed that the fish were passively drifting with the current during most of the tidal cycle, which allowed them to remain at a relatively constant salinity throughout the active tracking period (Figure 4). Continuous tracking of stationary individuals showed that some fish often held positions on fixed structures (e.g., usually navigational buoys outside the mouth of Ossabaw Sound) for several hours at a time (maximum

TABLE 2. Results of Lomb–Scargle periodogram analyses performed on hourly detection data from Atlantic Tripletails that were monitored within the Ossabaw Sound Estuary, Georgia, between June 2010 and October 2011. The primary peak represents the dominant periodicity (h) in movement pattern; the secondary peak represents any subordinate patterns that were detected. An asterisk indicates a fish in its second year of residence.

Fish ID	Hours of data	Analyzed	Primary peak (h)	Secondary peak (h)
565	1,826	Y	12.1	
566	2,558	Y	12.4	24.0
567	2,331	Y	24.0	12.4
568	857			
569	2,390	Y	12.4	6.2
570	895			
571	2,603	Y	12.4	
572	2,376	Y	12.4	6.2
573	2,530	Y	12.4	
574	2,324	Y	12.4	
575	15			
576	2,276	Y	24.1	12.3
577	0			
578	1,974	Y	12.4	
579	17			
895	1,466	Y	12.4	6.2
898	1,666	Y	12.4	
392	1,999	Y	12.5	6.2
393	2,434	Y	12.4	6.2
394	3,351	Y	12.4	6.2
395	2,915	Y	12.4	
396	2,721	Y	12.4	6.2
397	3,260	Y	12.4	
398	264			
399	2,543	Y	12.4	
400	2,705	Y	12.4	6.2
401	974			
402	2,492	Y	12.4	
403	2,491	Y	12.5	
404	2,462	Y	12.4	
405	2,514	Y	25.0	12.3
406	469			
572*	4,497	Y	12.4	24.0
573*	43			

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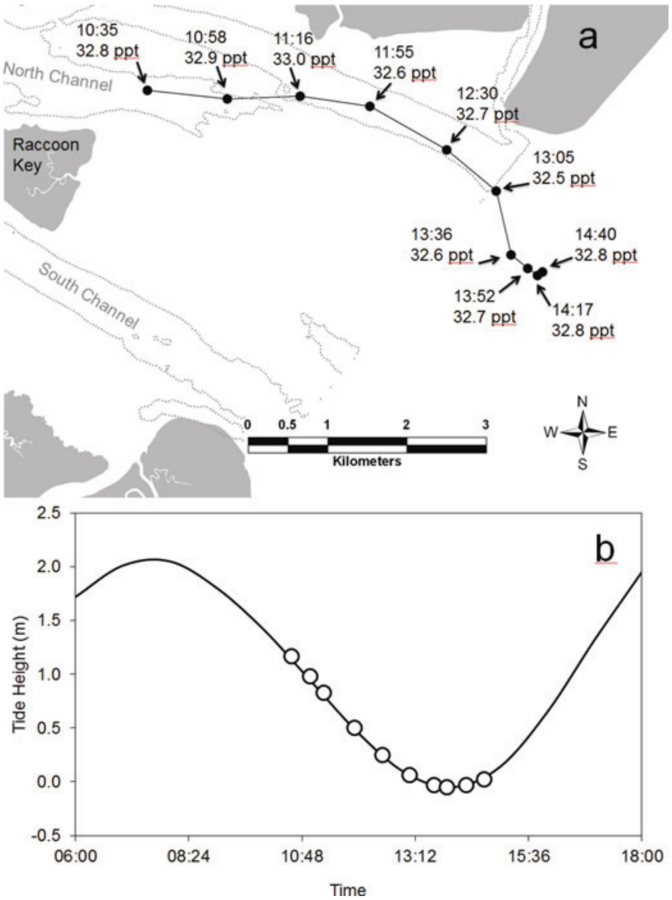

FIGURE 4. (**a**) Continuous track of fish 405, displaying tidal movement typical of all Atlantic Tripletails that were monitored within the Ossabaw Sound Estuary, Georgia (sequential fish locations [black circles] and corresponding time and salinity [ppt = ‰] are indicated); and (**b**) tide height (white circles) associated with each of the fish locations depicted in panel (a).

observed time at a structure was 11 h, 39 min; however, fish still resided at the structure at the termination of the continuous tracking event). Changes in salinity recorded at the locations of stationary individuals varied from 1.2‰ to 3.0‰ within a single tidal cycle. Continuous tracking conducted at night (n = 3 tracks) indicated similar patterns of tidally influenced movements.

Spatial Habitat Use

The spatial distribution of detections recorded over the 2 years of the study revealed that most of the habitat use was focused within the OSE's North Channel from the mouth of Ossabaw Sound to approximately 8.5 km upriver. Four (67%) of the six receivers within this area were above the 75th percentile in standardized detections per receiver-day (2.71), and five (83%) of the six receivers were above the 75th percentile in number of fish detected (11; Table 3). Although all receivers detected Atlantic Tripletails, only one of the three receivers located in the South Channel and only one of the nine receivers at upriver locations detected more than 10 individual fish.

Standardized detections per fish-day were significantly related to month and station in 2010 and only to station in 2011; there was no significant interaction between month and station in either year (Table 4). During 2010, significantly fewer standardized detections were recorded in June and July than in November; the lowest standardized detections in 2011 also occurred in July. During both years, fish spent more time in habitats close to the channel than in habitats away from the channel. Standardized detection data also suggested that the fish spent more time in North Channel habitats than in South Channel or upriver marsh habitats.

Scatter plots of individual fish detections showed a variable pattern of spatial habitat use within the OSE. Several individuals (fish 397, 404, and 572) exhibited brief periods of absence from Ossabaw Sound during July and August, followed by a return to the inner sound or upriver habitats during late August and September. For example, in 2011, fish 572 was frequently detected in the inner sound during April and May, but by late June this individual had moved out past the mouth of Ossabaw Sound. Fish 572 did not return until late August, when it was again detected at receivers in both the inner and outer sound. Interestingly, some individuals frequently used upriver habitats throughout their period of OSE residence (fish 392, 393, and 400), while others (fish 395 and 397) only used these areas seasonally, gradually moving from Ossabaw Sound upriver through the South Channel in the early fall—a total distance of approximately 33 km.

Active tracking revealed that 44% of the tagged fish exhibited strong fidelity to specific structures at some point during their estuarine residence within the OSE. Of the seven individuals that exhibited this behavior, five were commonly located just outside the mouth of Ossabaw Sound under a single navigational buoy in either the North Channel or the South Channel. These fish were located outside the range of the receiver array and were only detected by the stationary receivers when they moved into Ossabaw Sound on the flood tide. Likewise, the remaining fish (n = 2) were found beneath a large channel marker within the estuary on an almost daily basis. Active tracking, however, showed that these fish would regularly leave the structure on either an ebb tide or a flood tide, only to return again at the end of the tidal cycle. Four (57%) of the seven fish that exhibited site fidelity to specific structures were frequently detected at the same structure where they were initially captured. Furthermore, two of the fish that returned in 2012 (one tagged in 2010; the other in 2011) were detected at the same structure where they resided in 2011. When fish were not observed at fixed structures, they were typically observed to move with the current in open water along the edge of the river channel, but occasionally they were also detected over shallow sandbars, near flooded marsh, and even within small tidal creeks.

DISCUSSION

The results of this study provide new information regarding the behavior, seasonal movements, and estuarine habitat use of

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TABLE 3. Summary of receiver data describing detections of tagged Atlantic Tripletails in the Ossabaw Sound Estuary between June 2010 and May 2012 (RKM = river kilometer of the receiver location). Receiver habitats are channel outer sound (COS), outer sound (OS), channel inner sound (CIS), inner sound (IS), and upriver marsh (URM). The number after the habitat code is the receiver rank from closest to the mouth of the sound (1) to the farthest upriver (18). Receiver-days are the number of days within the monitoring period. The number of fish detected during 2010–2012 is shown.

Receiver	RKM	Monitoring period	Receiver-days	Standardized detections	Standardized detections/ receiver-day	Fish detected		
						2010	2011	2012
COS 1	0.0	20 May 2011–29 Jun 2011	41	6	0.15		2	
OS 2	0.0	20 May 2011–20 Jul 2011	62	20	0.32		5	
COS 3	0.0	18 Jul 2011–1 May 2012	289	784	2.71		11	3
COS 4	2.9	24 May 2011–1 May 2012	344	252	0.73		10	0
COS 5	2.9	6 Jun 2010–8 Jul 2011	398	2,261	5.68	15	10	
CIS 6	5.0	6 Jun 2010–1 May 2012	696	2,599	3.73	16	16	3
CIS 7	7.0	24 May 2011–1 May 2012	344	122	0.35		7	0
IS 8	7.0	6 Jun 2010–1 May 2012	696	424	0.61	15	15	3
CIS 9	8.5	6 Jun 2010–14 Jul 2011	404	2,241	5.55	16	17	
URM 10	10.5	24 May 2011–9 Aug 2011	78	2	0.03		2	
URM 11	11.8	31 May 2011–1 May 2012	337	440	1.31		15	0
URM 12	13.0	24 May 2011–1 May 2012	344	65	0.19		8	0
URM 13	14.5	17 Jul 2011–9 Aug 2011	24	136	5.67		5	
URM 14	17.2	17 Jul 2011–1 May 2012	290	114	0.39		5	0
URM 15	18.9	13 Sep 2011–1 May 2012	232	7	0.03		2	0
URM 16	25.1	13 Sep 2011–1 May 2012	232	119	0.51		1	0
URM 17	28.0	13 Sep 2011–1 May 2012	232	152	0.66		1	0
URM 18	33.0	13 Sep 2011–1 May 2012	232	142	0.61		1	0

Atlantic Tripletails in coastal Georgia. The high degree of residence observed for Atlantic Tripletails within the OSE indicates that estuarine habitats are essential for this seasonally abundant and popular sport fish. Sustained summer residence was typical for most individuals; although most fish went undetected at some point during the study, the gaps in detection usually spanned only 1–3 d. Detection gaps could have resulted from environmental fluctuations that affected the detection range of our receivers, but a more probable explanation is that the fish simply left the monitoring area or the sound intermittently. This inference was supported by data from active tracking, which documented movements of fish as they either (1) left Ossabaw Sound and took up new positions at fixed structures located just outside of the sound or (2) remained within the sound but out of range of the receiver array. Furthermore, flooding and the loss of core receivers (e.g., COS 5 [channel outer sound] and CIS 9 [channel inner sound]) in 2011 may have allowed fish to go undetected for longer periods. Consequently, we suspect that the actual estuarine residence time of the monitored Atlantic Tripletails may have been higher than what we observed. Although seasonal patterns of estuarine residence were consistent regardless of fish size, most of the fish in our study were probably mature adults, as their median TL was 57.9 cm, which is approximately equal to the size at which 100% of Atlantic Tripletails are mature (Parr 2011). Like most other migratory fishes, Atlantic Tripletails likely exhibit a life history that comprises several ontogenetic shifts in habitat use. Because demographic rates—and ultimately population productivity—are almost certainly affected by growth and survival at each of these different life stages, future studies should focus on the specific habitat needs of each discrete life stage.

TABLE 4. Results of two-way ANOVAs testing for the effect of month and station on standardized detections of Atlantic Tripletails per fish-day within the Ossabaw Sound Estuary during 2010 and 2011. Variables that significantly ($P \leq 0.05$) affected the standardized detections per fish-day are shown in bold italics.

Year	Source	df	*F*	*P*
2010	***Month***	5	3.19	***0.009***
	Station	3	8.83	***<0.001***
	Month × station	14	1.35	0.185
	Error	148		
2011	Month	4	1.42	0.232
	Station	5	9.79	***<0.001***
	Month × station	18	0.71	0.794
	Error	132		

The seasonal occurrence of Atlantic Tripletails within the OSE confirms the migratory nature of the species, as was previously reported (Merriner and Foster 1974). For most of the

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tagged Atlantic Tripletails in our study, the timing of tagging precluded us from estimating when estuarine residence was initiated; however, two individuals that were tagged in 2010 and three individuals that were tagged in 2010 and 2011 did return to the OSE in subsequent years. Eighty percent of these arrivals occurred in late March or early April, when water temperatures reached 21°C. Likewise, most fish left the estuary during fall as water temperature dropped to 21°C; this finding indicates that water temperature is an important proximate cue influencing both the timing and duration of estuarine residence. Although not previously reported for Atlantic Tripletails, similar migratory patterns have been documented for several other fishes, including the Striped Bass *Morone saxatilis* (Able and Grothues 2007), Tautog *Tautoga onitis* (Cooper 1966), and Chinook Salmon *Oncorhynchus tshawytscha* (Keefer et al. 2008).

Scatter plots of fish detections were useful in identifying potential diel and tidal activity patterns; however, inferences from these data should be viewed cautiously because diel variation in receiver detection has also been shown to follow a similar pattern (Heupel et al. 2008; Payne et al. 2010). Nonetheless, telemetry data from active tracking showed that Atlantic Tripletails were especially active at night. An increase in detections at higher tidal stages and a reduction in detections at lower tidal heights also suggested that some of the tagged fish tended to visit certain areas at specific tidal stages. These results were further corroborated by the Lomb–Scargle periodograms, which indicated a dominant 12.4-h periodicity (the precise duration of the normal tidal cycle) in the daily movements of most tagged fish. Because diel and tidal activity patterns have not been previously reported for Atlantic Tripletails, we suggest that future studies employ the use of sentinel tags (Payne et al. 2010) to account for any potential diel or tidal variation in receiver detection ranges.

Previous research has shown that the fine-scale movements and habitat use of many other marine fishes are largely influenced by tidal stage. Young-of-the-year Summer Flounder *Paralichthys dentatus*, for example, used tidal currents to move into and out of small tidal creeks to feed and potentially conserve energy (Rountree and Able 1992; Szedlmayer and Able 1993). Sandbar Sharks *Carcharhinus plumbeus* within a summer nursery area in Virginia also moved into the estuary with the incoming tide and left the estuary with the outgoing tide (Conrath and Music 2010). In our study, data from active tracking revealed that tagged Atlantic Tripletails frequently drifted with the moving tide, sometimes covering up to 12 km in a single tidal cycle. In addition to the obvious energetic benefits of drifting behavior, this pattern of passive movement also allowed the fish to maintain themselves within a relatively narrow range of salinities throughout the tidal cycle. Because osmoregulation in fishes may consume 10–50% of the total energy budget (Boeuf and Payan 2001), the passive movements of Atlantic Tripletails observed in our study may have helped the fish forage over large areas of the estuary while making minimal energetic expenditures. Although corroborative studies are needed, such energy-conserving behavior may help to explain the rapid growth rates of Atlantic Tripletails, as previously documented by other researchers (Merriner and Foster 1974; Franks et al. 2001; Parr 2011). Other estuarine species (e.g., Red Drum *Sciaenops ocellatus*) have also been documented to move up rivers and into marsh habitats to forage during the flooding tide (Collins et al. 2002). In contrast, some of the tagged fish in our study did not always move with tidal currents but instead remained under fixed structures throughout the tidal cycle. The range of salinities observed in Ossabaw Sound was relatively narrow (30.7–35.2‰), which may help to explain this different behavioral pattern, although other environmental or biological factors may also have been important in determining how and when the fish moved within the estuary. Future studies of Atlantic Tripletail foraging ecology may provide new insights regarding the purpose of the intra-estuarine movements observed in our study.

Despite the aforementioned variations in array configuration and receiver detection, our results suggested that in 2010 and 2011, Atlantic Tripletails spent most of their time within the 8.5-km stretch of the North Channel just inshore of the mouth of Ossabaw Sound. Although daily movements of the fish were more extensive than expected, our data suggest that fish spent less time in the South Channel or upriver sites, where salinities are typically lower and more variable (Wenner et al. 2005). However, these data could be inflated because most of the tagged fish were captured in the North Channel, and data demonstrated that some individuals exhibited strong site fidelity. Movements to and from these structures occurred almost daily; therefore, this pattern of movement from a "home structure" may be a typical behavior pattern for at least some individuals within the population. Even so, there was great variation in spatial habitat use among individuals, as several patterns were observed, and some fish did regularly move between the North Channel and the South Channel.

Although our data do not provide any direct evidence of spawning movements, several of the larger tagged Atlantic Tripletails left Ossabaw Sound for prolonged periods during their period of estuarine residence. Active tracking was successful in locating these individuals and revealed that they established residence beneath channel markers just outside the mouth of the sound (fish 572 and 403 in July 2011: see Figure 2). Because these movements occurred in summer—the known spawning period for the species (Ditty and Shaw 1994)—we suspect that these fish probably spawned somewhere in the nearshore (within 10 km) marine habitat. Interestingly, previous studies of Atlantic Tripletail reproductive biology have reported low incidences of reproductively active fish within inshore habitats (Brown-Peterson and Franks 2001; Cooper 2002; Parr 2011). Because the authors of these prior studies also used angling to obtain their samples, they hypothesized that spawning fish may not actively feed. Nevertheless, the extensive use of estuarine habitats during the summer months could make spawning adults particularly vulnerable to anglers. The spawning of Atlantic Tripletails within or near Ossabaw Sound

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should be confirmed by using a more expansive acoustic array in combination with a regimented ichthyoplankton sampling protocol in both areas during the late-summer months.

An understanding of Atlantic Tripletail stock structure dynamics has other important implications for fisheries management. For example, if fidelity to specific regions or estuaries is higher than previously thought, overexploitation could result—at least in some localized areas. In our study, only four (14%) of the tagged fish were confirmed to have been harvested by anglers during their period of residence in OSE. Although this exploitation rate is low in comparison with the 21–63% reported for other regional sport fish species (Jenkins et al. 2000; Denson et al. 2002), another five of the tagged fish in our study disappeared from the OSE in early summer. If we assume that these fish were also harvested by anglers, then our estimate of fishing mortality increases to 31%. Although future studies are needed to specifically evaluate annual exploitation of Atlantic Tripletails in south Atlantic estuaries, our estimate of 14–31% suggests that current levels of fishing mortality are similar to those for other recreationally harvested species. Total annual mortality is still unknown for Atlantic Tripletails in the OSE and for most other populations, in part because of the migratory nature of the species. Our results suggest that Atlantic Tripletails exhibit a high degree of estuarine fidelity, with little mixing of populations, from April to October; however, population dynamics and winter movements remain poorly understood. Future studies will be necessary to obtain a better understanding of the species' potentially complex stock structure and to provide quantitative data on population dynamics, thus ensuring effective management of the increasingly popular recreational fisheries for Atlantic Tripletails within the South Atlantic Bight.

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