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Authors: Callihan, Jody L., and Cowan, James H

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ARTICLE

## Sex Differences in Residency of Adult Spotted Seatrout in a Louisiana Estuary

Jody L. Callihan\*<sup>1</sup> and James H. Cowan Jr.

Department of Oceanography and Coastal Sciences, Louisiana State University,  
2251 Energy Coast and Environment Building, Baton Rouge, Louisiana 70803, USA

Michael D. Harbison

Louisiana Department of Wildlife and Fisheries, 1213 North Lakeshore Drive, Lake Charles,  
Louisiana 70601, USA

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### Abstract

Spotted Seatrout *Cynoscion nebulosus* is the most highly sought after recreational species along the U.S. Gulf coast. However, movement information for this economically and ecologically important species is currently limited to data from mark–recapture studies. We used remote acoustic telemetry, a high-resolution, fisheries-independent technique, to examine the residency of adult Spotted Seatrout ( $n = 172$ ) in a Louisiana estuary, Calcasieu Lake ( $\sim 300 \text{ km}^2$ ). An estuarine-wide array of 60 receivers was deployed for a 2.5-year period (May 2007–October 2009) to detect and quantify how long fish were present in the estuary and determine the proportion of fish that emigrated from the system. We then determined how these metrics (detection period and emigration) were related to fish size, sex, and season of release. Emigration was highly seasonal and occurred exclusively during late spring and summer when water temperatures exceeded  $24^\circ \text{C}$ . Surprisingly, male Spotted Seatrout, regardless of their size, were more likely than females to “permanently” emigrate from the estuary (i.e., not return within the 1-year battery life of transmitters) as evidenced by their shorter mean detection periods (males = 134 d, females = 177 d) and higher incidence of emigration (29–42% of males, but only 14–16% of females emigrated). Assessment and management strategies for this species may be improved by explicitly considering this behavioral difference between sexes. Namely, conducting stock assessments at a finer spatial scale (i.e., estuarine-specific versus state-wide) appears warranted given the high estuarine fidelity of females ( $\sim 85\%$ ), which exacerbates their potential for localized depletions due to anthropogenic stressors (e.g., fishing pressure, habitat alteration, or pollution).

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Many adult fishes have a high capacity for dispersal given their mobility and longevity. Still, there is considerable variation in movement ranges and patterns across species, even those that have similar morphology and are found in similar habitats (Palumbi 2004). In addition, movements are known to vary within species, whereby some individuals are more exploratory

(migratory) and move greater distances than their retentive (residential) counterparts, which may or may not be related to factors such as fish size, sex, or age (Quinn and Brodeur 1991; Secor 1999; Fraser et al. 2001). Movements affect interactions with conspecifics and other species as well as exposure to anthropogenic stressors (e.g., fishing pressure, habitat alteration, and

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Subject editor: Donald Noakes, Thompson Rivers University, British Columbia, Canada

\*Corresponding author: jllcallih@ncsu.edu

<sup>1</sup>Present address: Department of Biology, North Carolina State University, 210 David Clark Labs, Campus Box 7617, Raleigh, North Carolina 27695, USA.

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pollution). As such, understanding movement patterns and life histories are crucial for effective management of important fishery resources.

Spotted Seatrout *Cynoscion nebulosus* are one of the most highly sought after and intensively managed recreational species in U.S. coastal waters. This popular sport fish occurs in estuaries and nearshore waters along both the U.S. Atlantic coast (south of Cape Cod) and Gulf of Mexico (hereafter GOM) (Robins and Ray 1986). However, the majority of the recreational catch (80–85% annually) is taken in the northern GOM (Florida to Texas), where this species is most abundant (National Marine Fisheries Service, Fisheries Statistics Division, personal communication). Spotted Seatrout found in the GOM are generally believed to be nonmigratory and remain in the same (natal) estuary throughout their lives (maximum observed age = 12 years: Maceina et al. 1987) (Tabb 1966; Bortone 2003). Consequently, each estuarine system along the GOM is thought to contain a discrete stock of Spotted Seatrout whose dynamics are largely governed by local processes and are thus independent of adjacent estuarine stocks due to low connectivity (movement) among systems. Recent management actions have been based on this assumed spatial structure as estuarine-specific regulations were implemented for this species in Louisiana (Calcasieu Lake in 2006) and Texas (Lower Laguna Madre in 2007).

Inferences regarding estuarine fidelity of Spotted Seatrout are primarily based upon mark–recapture data, which to date are the only source of direct movement information for this species in the Gulf region. These historical tagging studies suggest that Spotted Seatrout have limited movement ranges as the overwhelming majority of tag returns (>95%) occurred within 50 km of the tagging site and in the same system in which fish were released (Moffett 1961; Adkins 1979; Rogillio 1980, 1985; Baker et al. 1986; Arnoldi 1987; Baker and Matlock 1993; Hendon et al. 2002). Nevertheless, occasional recaptures at much greater distances (160–500 km) and in other estuarine systems (Moffett 1961; Arnoldi 1987) highlight the potential for dispersal in this species.

The caveats of inferring movement patterns of fish from mark–recapture data are well known. Mark–recapture data are cross-sectional and, as such, provide no information on movements during the period between tagging and recapture. Thus, there is potential for underestimating the extent of movement. For instance, fish recaptured near their tagging site may have undergone substantial (unrecognized) movement while at liberty (Klimley 1998; Bolle et al. 2005). Moreover, in studies where the bulk of tag returns are provided by fishers, as is the case with Spotted Seatrout, recapture locations are likely biased toward areas with higher fishing effort, higher reporting rates, or both. Without accurate data on these parameters, which are often difficult to obtain in diffuse recreational fisheries, it is not possible to appropriately correct tag–return data. This limits the ability of mark–recapture data to provide quantitative movement information (e.g., mixing rates among areas) (Hilborn 1990; Gillanders et al. 2001; Parsons et al. 2011).

One evolving tool used to study fish movements is remote acoustic telemetry (Voegeli et al. 2001; Heupel and Webber 2012). In addition to being fisheries-independent, a major advantage of this approach over mark–recapture techniques is that it provides high-resolution (quasi-longitudinal) data. An array of strategically deployed receivers can continuously monitor the presence of acoustically tagged individuals in a given area for extended periods of time (months to years) (Able and Grothues 2007; Kerwath et al. 2009; Sagarese and Frisk 2011; Wingate et al. 2011). Accordingly, this technique allows precise quantification of the temporal dynamics of the location in space of tagged individuals. This includes the amount of time spent within a study area (residency), as well as the magnitude and timing of emigration from (and possible re-entry to) the monitored region.

We conducted a large-scale (estuarine-wide) and long-term (2.5 years) acoustic telemetry study to investigate the residency of adult Spotted Seatrout in a Louisiana estuary, Calcasieu Lake. Specifically, we quantified how long fish were detected in the estuary and the proportion of fish that emigrated from the system, and determined if these metrics (detection period and emigration) were related to fish size, sex, and season of release. We were particularly interested in sex effects as there have been no studies to date on sex-specific movements of Spotted Seatrout. We expected that, commensurate with mark–recapture data, the majority of fish would remain within the confines of the estuary and that any excursions outside our estuarine array would be brief and temporary in nature. Our results provide insight into the stock structure and also inform spatial management options for this recreationally and economically important species.

## METHODS

**Study area.**—Calcasieu Lake is a shallow (<2.5 m) estuary located in southwestern Louisiana (Figure 1), has a predominantly mud bottom with scattered low-relief oyster reefs, and is fringed by salt marshes. A dredged ship channel (15 m deep) connects the estuary to the nearshore GOM and to the Port of Lake Charles 60 km inland.

Due to its morphology, Calcasieu Lake is well suited for telemetry studies on fish. First, the system is relatively small (~300 km<sup>2</sup>). Therefore, it was possible to achieve acoustic coverage of most of the system using a moderate number of receivers deployed in an array that was capable of intermittently detecting tagged fish to verify their presence within the estuary. Second, and most importantly, there are only two exit points from the system: (1) the lower ship channel and (2) the Gulf Intracoastal Waterway (GIWW). Both of these exit points are narrow waterways (GIWW, <100 m wide; ship channel, ~400 m wide) amenable to acoustic monitoring. To leave Calcasieu Lake, fish would have to pass through one of these exit points.

**Receiver array.**—During the first week of May 2007, we deployed an array of 49 acoustic receivers (Vemco VR2s and VR2Ws) throughout Calcasieu Lake (Figure 1). The array was

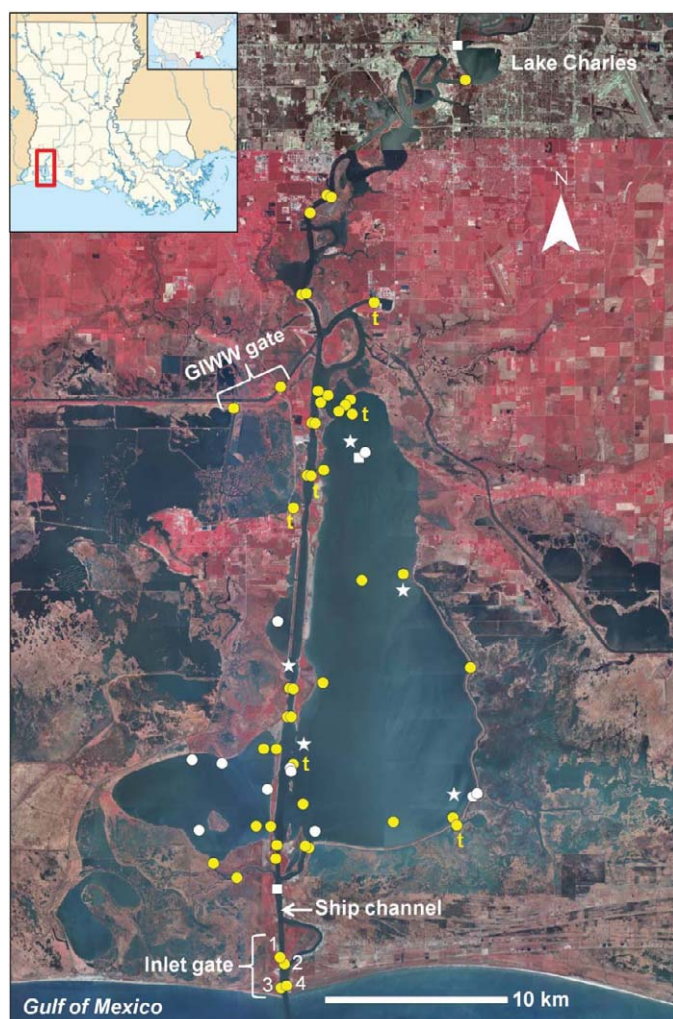


FIGURE 1. Calcasieu Lake estuary study area and receiver array. Circles represent locations of acoustic telemetry receivers. Yellow circles represent the initial array ( $n = 49$  receivers) and white circles represent receivers ( $n = 11$ ) added in year 2. The two acoustic gates at the inlet and in the Gulf Intracoastal Waterway (GIWW) that were used to monitor fish emigration are labeled on the map. Receiver stations identified with a "t" were equipped with a temperature logger (HOBO Pro version 2); white squares indicate locations of U.S. Geological Survey stations that recorded water temperature (<http://waterdata.usgs.gov/nwis/rt>). Stars denote locations where tagged Spotted Seatrout were released.

later expanded to 60 total receivers in spring 2008 (Figure 1). At the two exit points, receivers were deployed in a gate configuration (Grothues et al. 2005; Heupel et al. 2006) to monitor emigration and immigration of fish. Specifically, two receiver lines (with two receivers in each line) were deployed in the lower ship channel (hereafter referred to as the "inlet gate") and two single receivers were deployed in the western portion of the GIWW (hereafter referred to as the "GIWW gate") (Figure 1). The eastern portion of the GIWW was not monitored because a navigation lock restricted fish access to this region. Within the interior portion of the estuary, receivers were deployed in an irregular grid, with many locations representing presumed

hotspots (based on discussions with local management agencies and fishers) in an attempt to maximize the frequency of detections of fish that remained in the system. Receivers located in open-water habitats were attached to moored buoys, and those in channel habitats were attached to pilings. Extensive range testing revealed that receiver detection ranges were highly variable and sensitive to changing environmental conditions, but typically exceeded 200 m.

We serviced and downloaded data from the receiver array at approximately 6-week intervals. During servicing trips, we also replaced any missing receivers. Thirty receivers were lost during the course of this 2.5-year study (May 2, 2007, to October 28, 2009), mainly due to boat strikes, but also from human tampering and gear failure. Nevertheless, there were at least 37 operational receivers in the array at all times during the first year of the study and 53 thereafter (following expansion of the array). The inlet gate was fully operational (i.e., with four active receivers) throughout most of the study (86% of days). However, there were some periods during which a single receiver was inoperable and only three receivers were actively monitoring fish passage at the inlet gate. Specifically, station 1 of the inlet gate was inoperable from May 30 to June 20, 2007, and station 3 was inoperable from July 21 to September 19, 2007, and from April 22 to May 29, 2008. Both receivers comprising the GIWW gate were inoperable from September 19 to December 6, 2007. Finally, to prevent gear loss during Hurricanes Gustav and Ike, all receivers were removed from the estuary on August 28, 2008, and the array was redeployed on October 2, 2008.

**Fish tagging.**—All study fish were provided by volunteer anglers who captured Spotted Seatrout (target size,  $>300$  mm TL) throughout the estuary by hook and line and transported fish to an anchored tagging vessel (8 m in length). Fish were held onboard the tagging vessel in a flow-through, 600-L, live-well system, and those in good condition were selected for tagging. Spotted Seatrout were surgically implanted with an individually coded acoustic transmitter (Vemco V9-2H or V13TP-1H). After anesthetization in a 60-mg/L solution of tricaine methanesulfonate, fish were measured (TL to the nearest millimeter), weighed (to the nearest gram), and externally marked with a plastic-tipped dart tag (Hallprint) containing a 10-cm streamer specifying a reward would be offered if recaptured fish were released and reported. To ensure that transmitters did not exceed 2% of body weight (Winter 1983), larger Spotted Seatrout ( $>650$  g) were implanted with V13TP-1H transmitters ( $13 \times 45$  mm, 12 g in air, power output of 158 dB re 1  $\mu$ Pa) and smaller fish (250–650 g) were equipped with V9-2H transmitters ( $9 \times 29$  mm, 5 g in air, power output of 147 dB re 1  $\mu$ Pa). Transmitters were inserted into the peritoneal cavity through a 20–30-mm incision offset and parallel to the linea alba between the pelvic and anal fins. The incision was closed using non-absorbable sutures (3-0 Prolene, Ethicon) applied in a simple interrupted pattern containing three to four stitches. A triple antibiotic ointment was topically applied to the incision to help

prevent infection, and fish were transferred to the onboard live well to recover from surgery. Fish were released into the estuary (see Figure 1 for locations) once they regained equilibrium and proper swimming orientation, typically ~10 min postsurgery.

During the tagging process, we also determined the sex of fish. Only male Spotted Seatrout are soniferous (Gilmore 2003). Therefore, if fish audibly grunted while being handled, they were classified as males. Otherwise, a catheter was inserted through their vent to obtain a gonad biopsy prior to surgery. If oocytes were present in the biopsy sample (based on later examination under a dissecting microscope), the individual was classified as a female. It was also possible to determine the sex of some individuals based on visual inspection of the gonads during surgeries.

Fish were released during four main tagging events, in the spring and fall of both 2007 and 2008. Multiple release events were necessary to ensure that tagged fish were available for detection throughout the entire study period (2.5 years) because the expected battery life of transmitters was only 1 year (10–15 months across transmitters). It would have been possible to achieve longer battery lives that more closely matched the study duration by increasing transmitter delays (the time between successive tag transmissions). However, this may have reduced our ability to detect fish that rapidly emigrated from the system. Delay periods were 150–300 s for all V9-2H transmitters (expected battery life, 300–350 d) and 60–180 s for most V13TP-1H transmitters (expected battery life, 340–390 d). Eighteen fish in the spring 2008 release group were implanted with V13TP-1H transmitters with a slightly longer delay (75–225 s) and expected battery life (460 d).

A 2-month laboratory holding experiment ( $n = 35$  tagged fish) confirmed that Spotted Seatrout responded favorably to the acoustic tagging process. Both survival (97%) and transmitter retention (100%) were excellent. Furthermore, tagged fish exhibited normal behavior, as they schooled with their untagged conspecifics and typically began feeding within 24 h postsurgery. The presence of acoustic transmitters did not appear to cause gonad regression (a potential stress response) as gonadosomatic indices ( $[\text{gonad weight} / \text{whole body weight}] \times 100$ ), measured at the end of the experiment were similarly high between tagged and untagged fish. This experiment also verified that our sex determination method (described above) was 100% accurate based on postmortem (ground-truthed) identification of gonads. Finally, this experiment revealed the retention of external dart tags was poor as ~40% of fish lost their tags and those tags still present at the end of the study were loose and barely intact.

*Processing of telemetry data.*—Prior to analysis, raw receiver data were screened for false detections and stationary transmitters, and were time-corrected for receiver clock drift. We used criteria established by Vemco (Pincock 2012) to identify and remove false detections. Specifically, an isolated detection (i.e., a single detection of a given transmitter at a particular receiver within a 24-h period) was deemed false if (1) there were no accompanying detections of the same transmitter at nearby

(<1 km) receivers and (2) there was at least one other transmitter detected within 1 h of the suspect detection (to cause a potential collision). Based on these criteria, 0.04% of all detections were considered false and removed from the data set. Four transmitters were continuously detected (approximately hourly) at the same receiver location for at least 4 months, with no detections elsewhere in the array. Detections from these presumably dead fish were removed from the data set, beginning with the first day of constant detections. Lastly, detection times were corrected for receiver clock drift using the linear drift correction provided in Vemco software (VUE, version 1.8.1).

*Data analysis.*—We only included in the data analyses those fish that appeared to survive the tagging process and were detected at multiple receiver stations (indicating fish movement) more than 1 week after being released. The intent of our emigration analyses was to estimate the proportion of these survivors that left the estuary for an extended period of time (e.g., long enough to potentially move to another estuary). Some fish left the system for only a brief period as they returned to the estuary less than 12 h after being detected at an acoustic gate. However, all other fish, upon being initially detected at an acoustic gate, were either (1) never again detected (despite the fact their transmitters had 3–12 months of remaining battery life) or (2) not again detected for at least 14 consecutive days. Therefore, for the purpose of our analyses, we assumed individuals exhibiting either of these detection patterns “emigrated” from the estuary.

We used multiple logistic regression to test for effects of fish size, sex, and release group on emigration. If a fish emigrated from the estuary (as defined above), it was scored as 1, otherwise, it received a score of 0. To determine which explanatory variables (and possible interactions) were significant, we used a backward-elimination model selection procedure. This technique sequentially removes the most nonsignificant effects (beginning with the highest order interactions) and reiterates the model until only significant effects remain (Agresti 1996).

We also calculated the detection periods of tagged fish as the number of days elapsed from release to final detection by the receiver array, similar to Pecl et al. (2006), Meyer et al. (2007), Kawabata et al. (2010), and Semmens et al. (2010). A two-way ANOVA was used to test for differences in detection periods among release groups and sexes. Fish length was not included as an explanatory variable in the ANOVA because an initial ANCOVA indicated that detection periods were not significantly related to fish length, thereby obviating the need for a covariate (fish length) and reducing the analysis to a two-way ANOVA. Fish implanted with longer-life transmitters had longer potential detection periods. Therefore, to ensure fair comparisons in these analyses, detection periods were capped at 300 d because all transmitters were expected to operate at least that long. For example, an observed detection period of 330 d would be assigned a value of 300. The assumptions of homogeneity of group variances and normality of residuals were satisfied for the ANOVA, and the significance of pairwise mean comparisons were

assessed using Bonferroni-adjusted  $P$ -values. All statistical analyses were performed in SAS (version 9.1.3) using  $\alpha = 0.05$ .

**Detection efficiency.**—To aid the interpretation of our results, we evaluated the detection efficiency of the inlet gate using ancillary data. Several tagged fish were known to be in the nearshore GOM based on (1) angler recaptures, (2) detections during mobile telemetry surveys using a Vemco VR28 system, and (3) detections at a pair of receivers temporarily deployed 2.5 km south of the inlet gate. These fish (transmitters) must have passed through the inlet gate to reach the GOM, which provided an opportunity to estimate detection efficiency (no such data were available for the GIWW gate). Detection efficiencies were calculated separately for each transmitter size (V9s versus V13s) as the percent of known migration events through a given receiver line that were successfully recorded, similar to Melnychuk et al. (2007) and Welch et al. (2009). As an example, if a fish was detected during mobile telemetry surveys in the nearshore GOM then returned to (and was detected in) the interior portion of the estuary, it would have undergone two *known* migration events (emigration, immigration) past both receiver lines of the inlet gate.

This analysis indicated the northern receiver line of the inlet gate successfully recorded 14 of 19 known migration events (74%) of fish ( $n = 11$ ) equipped with V13 transmitters, but only 4 of 10 migration events (40%) of fish ( $n = 10$ ) equipped with V9 transmitters. The southern receiver line successfully recorded all nine migration events involving V13-equipped fish ( $n = 6$ ), but only one of three migration events of V9-equipped fish ( $n = 3$ ). With two exceptions, both of which involved V9-equipped individuals, all known migration events occurred when respective receiver lines were fully operational (with two active receivers per line). Based on these detection efficiencies, the probability of a tagged fish passing through both receiver lines of the inlet gate undetected would be virtually nil for V13 transmitters (<1%) but 40% for V9 transmitters.

## RESULTS

### Tagging and Detection Summary

A total of 172 adult Spotted Seatrout (300–725 mm TL) were tagged and released across the four tagging events (Table 1). We were able to determine the sex of 150 tagged fish, of which 101 (67%) were females and 49 (23%) were males. Males were considerably smaller than females as only one male (but 34 females) exceeded 500 mm TL. Accordingly, most males (73%) were implanted with the smaller V9 transmitters, whereas the majority of females (66%) received the larger V13 transmitters. Most Spotted Seatrout appeared to survive the tagging process as 145 fish (84%) were detected more than 1 week after release and at multiple receiver stations. The receiver array logged 659,838 valid detections from these 145 fish, which comprised 80 females (317–675 mm TL), 45 males (300–559 mm TL), and 20 fish of unknown sex (325–609 mm TL).

Detection periods of Spotted Seatrout were highly dependent on release season. Most fish (63%) released in the fall were detected for at least 6 months. Meanwhile, fish released in the spring generally disappeared within 3 to 4 months, although some individuals (24%) were detected in the estuary for considerably longer periods ( $\geq 10$  months). Based on the ANOVA, the mean detection period for the fall 2007 release group (215 d) was significantly higher than both the spring 2007 ( $P = 0.05$ ) and spring 2008 ( $P = 0.006$ ) release groups, the detection periods (129 and 117 d) did not significantly differ from one another ( $P = 1.0$ ). Although the mean detection period for the fall 2008 release group (161 d) was higher than both spring release groups, these differences were not significant ( $P$ -values > 0.6). Detection periods did not differ significantly between the fall 2008 and fall 2007 release groups ( $P = 0.68$ ).

Detection periods also differed between sexes and were significantly higher ( $P = 0.04$ ) for females (177 d) than for males (134 d). This sex effect was consistent across release groups

TABLE 1. Attributes of tagged Spotted Seatrout. Numbers of fish tagged and released, and sex-specific TL ranges (mm) reported (in parentheses [with means]) for each release group. “Unknown” indicates fish whose sex was unable to be determined.

Release group	Release dates	Females	Males	Unknown
Spring 2007	May 9–12, 2007	33 (358–725 [540])	11 (302–470 [380])	7 (327–609 [496])
Fall 2007	Oct 9–11, 2007	12 (317–604 [438])	8 (328–452 [403])	4 (420–496 [441])
Spring 2008	Apr 14–20, 2008	26 (375–658 [475])	23 (300–559 [397])	6 (325–448 [400])
	May 31, 2008	5 (450–640 [502])		
Fall 2008	Oct 13–15, 2008	25 (317–545 [409])	6 (303–451 [364])	3 (333–466 [414])
	Dec 12, 2008		1 (433)	2 (429–591)



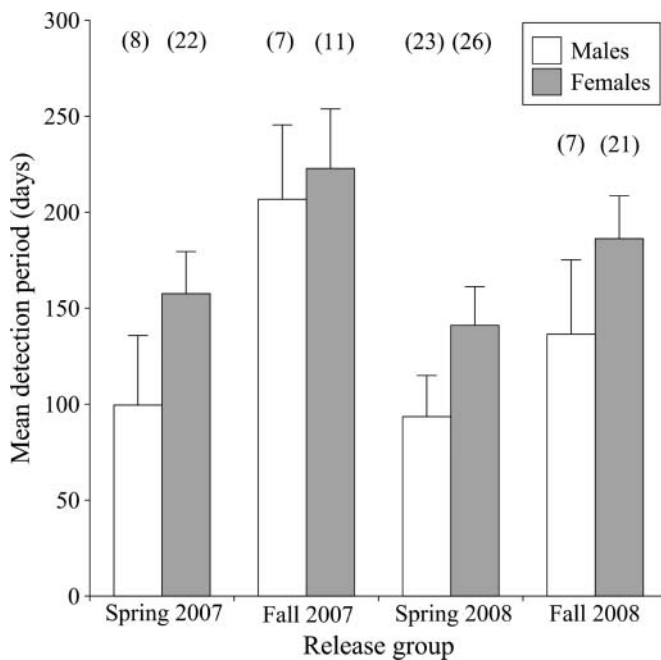


FIGURE 2. Detection periods (days elapsed until final detection) of tagged Spotted Seatrout. Mean ( $\pm$ SE) detection periods are shown for each sex–release group combination (white bars = males, gray bars = females). Sample sizes for each combination are given parenthetically above their respective bars. To ensure fair comparisons among release groups and sexes, detection periods were capped at 300 d as all transmitters were expected to operate at least that long (see text).

as evidenced by the nonsignificant interaction between sex and release group ( $P = 0.93$ ) (Figure 2).

### Emigration

Thirty fish (21% of known survivors) were detected at an acoustic gate during the course of this study. Two of these individuals returned to the estuary shortly after ( $<12$  h) they were detected at the inlet gate. However, the other 28 fish were either (1) never again detected or (2) not detected again until at least 15 d later (Figures 3–6). Accordingly, we assumed these individuals emigrated from the estuary.

There were several strong trends in emigration. First, fish only exited the system through the inlet gate (there were no detections at the GIWW gate during the study). Secondly, emigration was highly seasonal and occurred only during late spring and summer (late April to mid-September) when water temperatures exceeded  $24^{\circ}\text{C}$  (Figure 7). Finally, and most interesting, the proportion of males that emigrated from the estuary (29%, 13 of 45 fish) was twice that of females (14%, 11 of 80 fish).

The logistic regression analysis confirmed that sex had a strong effect on fish emigration. Sex was the only significant variable in the final model ( $P = 0.04$ ) as the main effects of both release group ( $P = 0.46$ ) and fish length ( $P = 0.12$ ) were nonsignificant, as were all interactions ( $P$ -values  $> 0.55$ ). The lack of an interaction between sex and release group ( $P = 0.71$ ) verified the sex effect was consistent across the four release

groups. Based on the odds ratio of 2.6, the odds of emigrating were a remarkable 13 times higher for male (versus female) Spotted Seatrout.

Most fish (82%) that emigrated from the estuary were never again detected despite the fact their transmitters had 3–12 months of remaining battery life (Figures 3–6). Of the few fish ( $n = 5$ ) that were detected again, two females (51 and 55) returned to the estuary 15 d later (Figure 5), while the other three individuals remained outside the array for longer periods. Female 56 and male 38 returned to the estuary 3 months later (in the early fall of 2008), but re-emigrated the following summer (Figure 5). Another fish (unsexed 5) was detected at the southern receiver line of the inlet gate 5 months after emigrating, but did not re-enter the interior portion of the estuary (Figure 3).

### DISCUSSION

Our study revealed a strong difference in the degree of estuarine residency between male and female Spotted Seatrout. Males were detected in the estuary for shorter periods of time than females and were much more likely to “permanently” leave the system as nearly one-third of tagged males (but only 10% of females) emigrated from and did not return to the estuary within the remaining battery lives of their transmitters. This estimate of male emigration was surprisingly high, given that mark–recapture studies (although not sex-specific) suggest that long-range movements (e.g., among estuaries) are rare ( $<5\%$ ). Although the fate of emigrants and where they moved to is unknown, our results suggest that adult connectivity among estuarine systems, while perhaps only low to moderate in magnitude, is predominantly male-mediated in GOM Spotted Seatrout. The tendency of females to remain in a given estuarine system ( $>85\%$  fidelity), as demonstrated in this study, has important implications for the assessment and management of this valuable fishery species.

Detection periods of tagged fish differed among release groups and also between sexes. Males were detected in the estuary for shorter periods than females primarily because they were more likely to emigrate from (and not return to) the system. Emigration also explained, in part, the strong difference in detection periods among release groups, whereby fish released in the spring were detected for shorter periods than fall-released fish. Due to the strong seasonality of emigration (summer only), spring-released fish began leaving the estuary soon ( $\sim 1$  month) after their release and therefore had shorter detection periods than did emigrants from fall releases, which did not leave the estuary until the following summer ( $>6$  months after release). Still, emigration did not entirely explain the shorter detection periods for spring-released fish because this difference persisted when emigrants were removed from the analysis. For example, in contrast to fall-released fish (especially fall 2007), many spring-released females equipped with V13 transmitters disappeared from the estuary within 4 months of their release. Given the high detection efficiency of V13 transmitters, it is

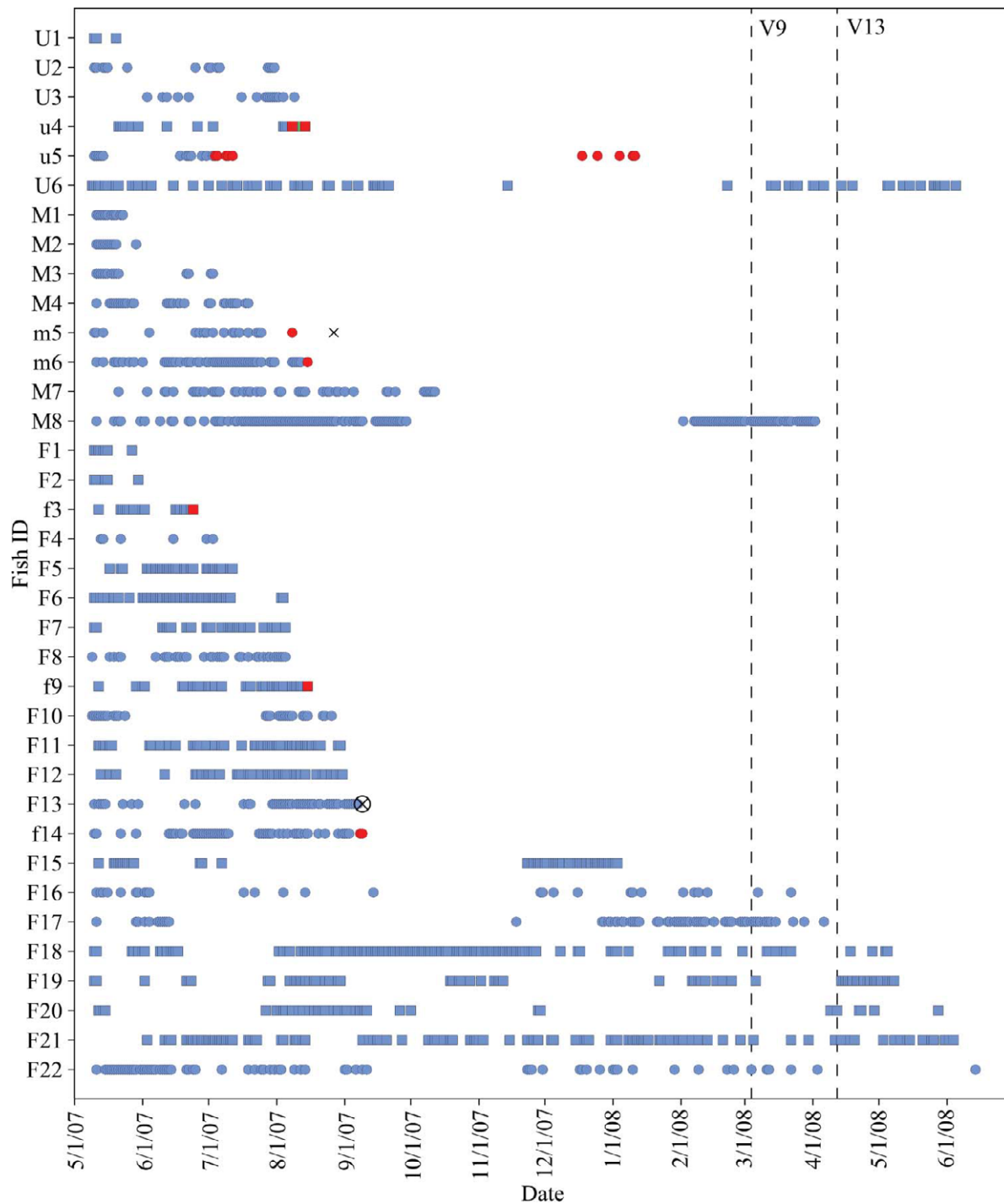


FIGURE 3. Detection histories of individual Spotted Seatrout released during spring 2007. Blue symbols indicate days on which fish were detected at any receiver in the interior portion of the estuary, red symbols indicate days that fish were detected at the inlet gate, and green symbols indicate days that fish were detected at both the inlet gate and interior receivers. Symbol shapes denote transmitter type (circles = V9-2H transmitters, squares = V13TP-1H transmitters with a 120-s average delay). Vertical dotted lines represent dates on which transmitter batteries were expected to expire based on manufacturer estimates. Encircled  $\times$  symbols denote presumed fish mortalities and noncircled  $\times$  symbols denote reported dates of angler removals of tagged fish. Fish with identification (ID) labels beginning in lowercase letters were assumed to emigrate from the estuary; U = sex unknown, M = males, F = females. Date on x-axis is month/day/year.



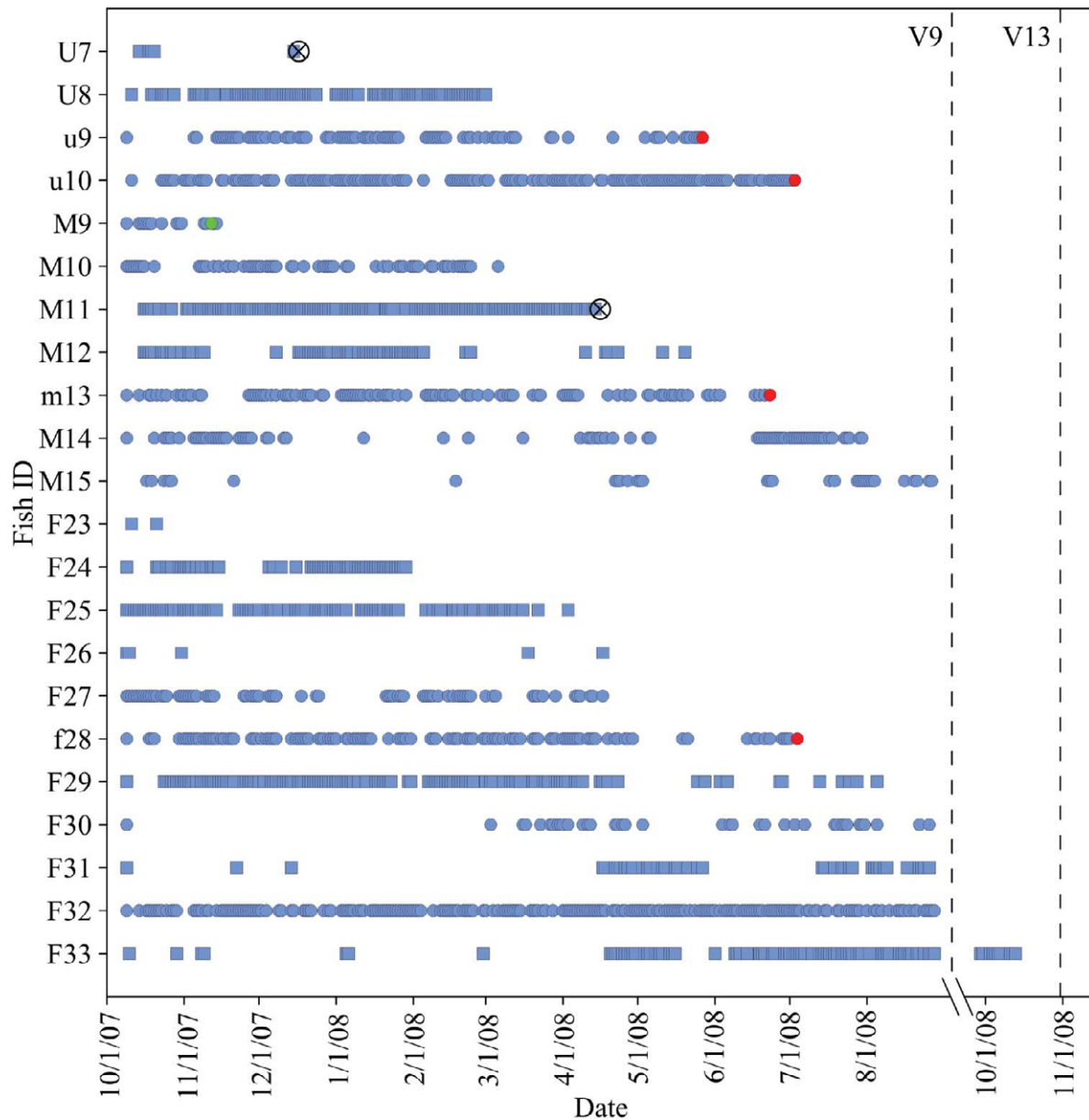


FIGURE 4. Detection histories of individual Spotted Seatrout released during fall 2007. Blue symbols indicate days on which fish were detected at any receiver in the interior portion of the estuary, red symbols indicate days that fish were detected at the inlet gate, and green symbols indicate days that fish were detected at both the inlet gate and interior receivers. Symbol shapes denote transmitter type (circles = V9-2H transmitters, squares = V13TP-1H transmitters with a 120-s average delay). Vertical dotted lines represent dates on which transmitter batteries were expected to expire based on manufacturer estimates. Encircled  $\times$  symbols denote presumed fish mortalities. Fish with identification (ID) labels beginning in lowercase letters were assumed to emigrate from the estuary; U = sex unknown, M = males, F = females. Date on x-axis is month/day/year. The break in the x-axis corresponds to the period when the receiver array was inactive due to Hurricanes Gustav and Ike.

unlikely these fish left the system undetected. It is possible these fish remained (alive) in the estuary and were occupying areas without receiver coverage and therefore were not detected during the remainder of their battery lives (a period of at least seven consecutive months). However, a more probable scenario is that many of these individuals succumbed to mortality within the estuary. Tagged fish were probably most active in the warmer

spring and summer months and therefore more susceptible to both fishing and natural mortality during this time. Accordingly, seasonal differences in mortality (higher in the spring–summer) also likely contributed to the shorter detection periods of fish released in the spring. Although all tagged fish were of legal size ( $>300$  mm TL), we did not expect high angler reporting of recaptured fish because the external dart tags marking fish

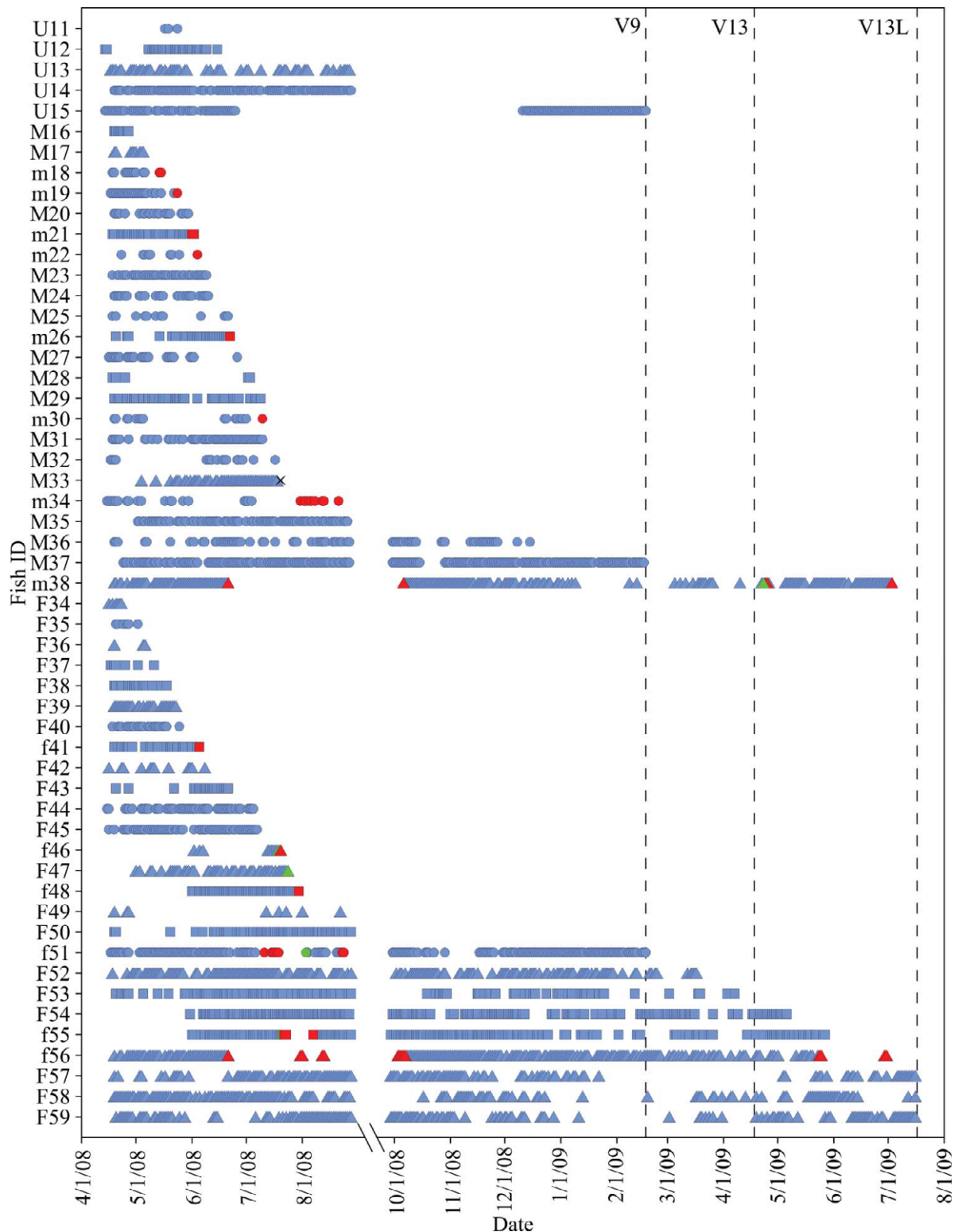


FIGURE 5. Detection histories of individual Spotted Seatrout released during spring 2008. Blue symbols indicate days on which fish were detected at any receiver in the interior portion of the estuary, red symbols indicate days that fish were detected at the inlet gate, and green symbols indicate days that fish were detected at both the inlet gate and interior receivers. Symbol shapes denote transmitter type (circles = V9-2H transmitters, squares = V13TP-1H transmitters with a 120-s average delay (V13), triangles = V13TP-1H transmitters with a 150-s average delay (V13L)). Vertical dotted lines represent dates on which transmitter batteries were expected to expire based on manufacturer estimates. The  $\times$  symbols denote reported dates of angler removals of tagged fish. Fish with identification (ID) labels beginning in lowercase letters were assumed to emigrate from the estuary; U = sex unknown, M = males, F = females. Date on x-axis is month/day/year. The break in the x-axis corresponds to the period when the receiver array was inactive due to Hurricanes Gustav and Ike.

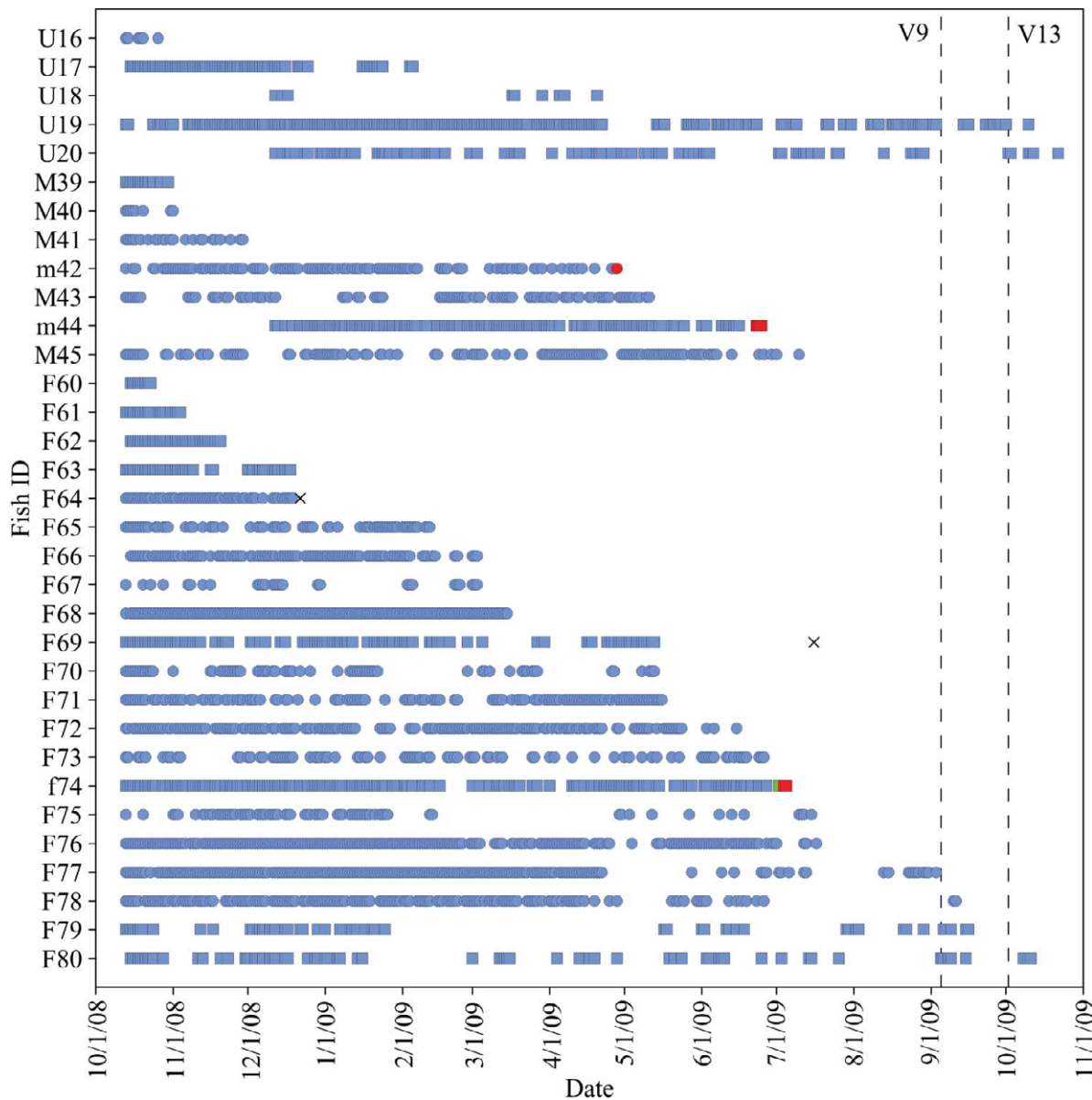


FIGURE 6. Detection histories of individual Spotted Seatrout released during fall 2008. Blue symbols indicate days on which fish were detected at any receiver in the interior portion of the estuary, red symbols indicate days that fish were detected at the inlet gate, and green symbols indicate days that fish were detected at both the inlet gate and interior receivers. Symbol shapes denote transmitter type (circles = V9-2H transmitters, squares = V13TP-1H transmitters with a 120-s average delay). Vertical dotted lines represent dates on which transmitter batteries were expected to expire based on manufacturer estimates. The  $\times$  symbols denote reported dates of angler removals of tagged fish. Fish with identification (ID) labels beginning in lowercase letters were assumed to emigrate from the estuary; U = sex unknown, M = males, F = females. Date on x-axis is month/day/year.

as study subjects had poor retention as revealed by our holding experiment (see above). Therefore, due to tag loss, many angler recaptures probably went unrecognized, which could explain the dearth of recaptures reported in this study ( $n = 6$  fish, of which four were retained by anglers).

A major assumption in this study was that all tagged fish that left the estuary were detected by one of our acoustic gates. Otherwise, emigration would be underestimated. Detection efficiency estimates for the inlet gate indicated this assumption

was met for V13, but not V9 transmitters as there was a 40% probability of the latter passing through the gate undetected. The fact that V9 transmitters were less likely to be detected was not surprising given their lower power output and longer time interval between transmissions. Because the majority of males (73%), but only 34% of females, were equipped with the weaker V9 transmitters, emigration of males was probably underestimated to a greater extent than for females. Therefore, correcting emigration estimates for the detection efficiency of V9

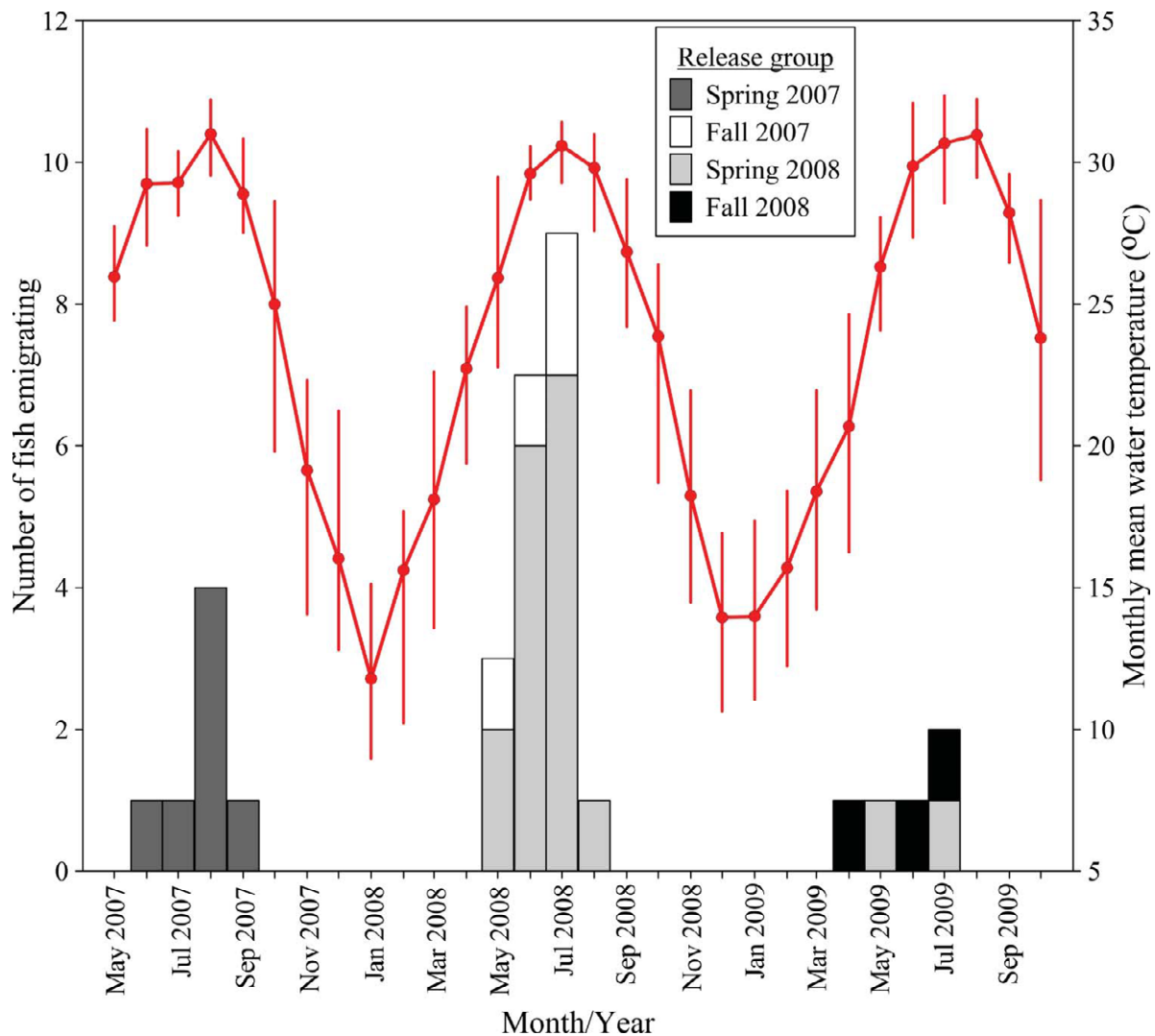


FIGURE 7. Emigration seasonality. Bars depict the number of Spotted Seatrout (by release group) that emigrated during each month of the 2.5-year study. A fish was assumed to emigrate from the estuary if it was detected at an acoustic gate (inlet or GIWW, see Figure 1) and not detected thereafter for at least 14 consecutive days. The red line with dots represents monthly mean water temperature in the estuary, and vertical red bars at each point denote the range of daily temperatures within each month (see Figure 1 for locations of temperature loggers). Note the receiver array was inactive during September 2008 due to Hurricanes Gustav and Ike.

transmitters would only strengthen the sex-specific difference in emigration we observed. Specifically, up to 42% of males, but only 16% of females, may have permanently emigrated from the system. Detection efficiency estimates were not available for the GIWW gate. However, this waterway does not appear to constitute an important migration corridor for Spotted Seatrout as they avoided (i.e., were not detected in) this area during the 789 d the gate was operational.

Although there are no other studies on sex-specific movements in Spotted Seatrout to compare our results with, our findings are consistent with genetic data from the GOM. In samples collected across the Texas coast, significant genetic divergence was found, in the form of isolation by distance, in mitochondrial DNA (Gold and Richardson 1998; Anderson and

Karel 2009) but not microsatellites (Gold et al. 2003; Ward et al. 2007). While microsatellites are inherited from both parents, mitochondrial DNA is maternally inherited and therefore only tracks female gene flow (Wirgin and Waldman 2005). Accordingly, one plausible explanation for the lower geographic diversity in microsatellites relative to mitochondrial DNA is that gene flow (migration) in Spotted Seatrout is male-biased (Gold et al. 2001, 2003; Anderson and Karel 2009). That is, males are more likely than females to leave their natal estuary and successfully spawn in another system. Although the natal origin of fish in our study was unknown (as is typically the case in adult tagging studies), our results agree with the notion of male-biased dispersal implied by genetic data as tagged males were three times more likely than females to leave the

estuary and potentially move long distances to another estuarine system.

While the underlying reasons for this sex difference in estuarine fidelity can only be speculated upon with the data in hand (e.g., males may leave during the summer spawning season to search for mates if drumming attempts to attract females become unsuccessful), our results still have important implications for the assessment and management of this valuable fishery species. Although the topic has received surprisingly little attention, the interpopulation movement (mixing) rate at which the dynamics of subpopulations start to become correlated (or coupled) is thought to be around 10% (Hastings 1993; Waples and Naish 2009). In our study, 14–16% of females emigrated from the estuary. Because of the unknown fate of emigrants, our emigration values should be viewed as a conservatively high estimate of movement to other systems. For example, “emigrants” may have remained just outside our array in the nearshore GOM or possibly have died in route to another estuarine system. Thus, given the apparently low interestuarine movement rates of female Spotted Seatrout (<10%), the dynamics (e.g., abundance trends) of estuarine subpopulations of females are probably controlled by local factors and are largely independent of one another (i.e., are asynchronous). As such, females may be particularly susceptible to localized depletions due to their high estuarine fidelity. For instance, female abundance could be declining in estuaries experiencing increased fishing pressure, habitat alteration, or both. However, such trends may only be recognized if assessment occurs at the appropriate (local) scale. Current stock assessment methods in Louisiana pool data across the entire state (i.e., assume a single statewide stock). With this method, localized depletions could be masked and, if left unabated, impair recruitment. Therefore, the most prudent approach may be to conduct assessments at smaller spatial scales, either locally (for more isolated estuaries) or perhaps regionally (for geographically proximate systems). In the case that symptoms of overfishing (e.g., truncation of the female age or size structure or a persistent decline in spawner abundance) manifest with a finer-scale approach, spatial management tools such as estuarine-specific bag and size limits or seasonal closures should be effective management options to reduce fishing mortality and promote sustainability.

Despite the wealth of data obtained, our study had several limitations. First, we focused on a single estuary. It is possible that movement and residency patterns may differ in other systems due to differences in the density of conspecifics, salinity regimes, prey availability, predator fields, or other environmental factors. To address this question, research is currently being planned to investigate residency dynamics of Spotted Seatrout in Lake Pontchartrain, Louisiana, a system that, while much larger than Calcasieu Lake, is nevertheless suitable for acoustic telemetry due to its limited number of entry and exit points. Another limitation of our study was that we only examined movements during a single life stage (adults). In most fishes, movement and dispersal occur at all life stages. While difficult

to obtain, information on transport and movement of early life history stages (eggs, larvae, and juveniles) is imperative for a synoptic understanding of stock structure (Hare 2005; Hueter et al. 2005). Our results suggest that egg-bearing females exhibit limited coastwide movement and thus are unlikely to contribute a substantial number of recruits (via adult movement) to adjacent systems. However, it is entirely possible that, due to larval transport, many recruits in a given estuary could have originated from spawning in distant systems. The extent and mechanisms of larval transport in Spotted Seatrout are poorly understood and warrant examination to provide insight into this species' recruitment dynamics. Such information could be obtained through a better understanding of spawning locations coupled with hydrodynamic models.

In conclusion, our study revealed that the movement patterns of an estuarine sciaenid differed greatly between sexes. Generally speaking, sex-specific movements in coastal fishes are understudied, and for those species able to be sexed, a great deal may be learned if sex is explicitly taken into account in studies of movement and behavior. For instance, as Hanson et al. (2008) noted, part of the variation in movements and behavior typically ascribed to differences among individuals or considered “noise” might be related to sex. As demonstrated in this study, consideration of sex-specific movements can lead to unexpected results and enhance our understanding of the basic ecology of coastal fishes and improve the management of important fishery resources.

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