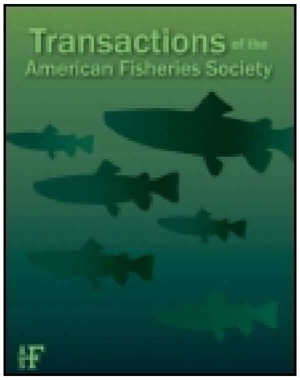

Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

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Version of record first published: 28 Jan 2013.

To cite this article: Sarah E. Friedl , Jeffrey A. Buckel , Joseph E. Hightower , Fred S. Scharf & Kenneth H. Pollock (2013): Telemetry-Based Mortality Estimates of Juvenile Spot in Two North Carolina Estuarine Creeks, Transactions of the American Fisheries Society, 142:2, 399-415

To link to this article: http://dx.doi.org/10.1080/00028487.2012.730108

Transactions of the American Fisheries Society 142:399–415, 2013

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.730108

ARTICLE

Telemetry-Based Mortality Estimates of Juvenile Spot in Two North Carolina Estuarine Creeks

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Abstract

We estimated natural mortality rates (M) of age-1 Spot *Leiostomus xanthurus* by using a sonic telemetry approach. Sonic transmitters were surgically implanted into a total of 123 age-1 Spot in two North Carolina estuarine creeks during spring 2009 and 2010, and the fish were monitored by using a stationary acoustic receiver array and manual tracking. Fates of telemetered Spot were inferred based on telemetry information from estimated locations and swimming speeds. Potential competitors of age-1 Spot were assessed through simultaneous otter trawl sampling, while potential predators of Spot were collected using gill nets and trammel nets. The number of inferred natural mortalities was zero in 2009 (based on 29 telemetered Spot at risk) and four in 2010 (based on 52 fish at risk), with fish being at risk for up to about 70 d each year. Catches of potential competitors or predators did not differ between years, and age-1 Spot were not found in analyzed stomach contents of potential predators. Our estimated 30-d M of 0.03 (95% credible interval = 0.01–0.07) was lower than that predicted from weight-based ($M = 0.07$) and life-history-based ($M = 0.06$–0.36) estimates. Our field-based estimate of M for age-1 Spot in this estuarine system can assist in the assessment and management of Spot by allowing a direct comparison with M-values predicted from fish size or life history characteristics. The field telemetry and statistical analysis techniques developed here provide guidance for future telemetry studies of relatively small fish in open, dynamic habitat systems, as they highlight strengths and weaknesses of using a telemetry approach to estimate M.

Natural mortality rate (M) is an important parameter in many stock assessment models, and incorrect values can have significant effects on harvest recommendations (Clark 1999). Natural mortality is often estimated from life history parameters, such as body weight (Lorenzen 1996) or maximum age (Hoenig 1983), and is typically modeled as a fixed annual rate for adults,

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Received November 23, 2011; accepted September 11, 2012

whereas mortality data for juvenile stages are fairly deficient (Heupel and Simpfendorfer 2002). It has been argued that these methods of determining *M* do not account for variability among ages or between years (Vetter 1988; Quinn and Deriso 1999; Hightower et al. 2001; Young and Isely 2004). Despite the importance of *M* for stock assessments, it is difficult to estimate because natural deaths are generally not observable and are confounded by the effects of harvest (Quinn and Deriso 1999).

The Spot *Leiostomus xanthurus* is an estuarine-dependent sciaenid fish that is found along the Atlantic coast from the Gulf of Maine to the Bay of Campeche, Mexico, mostly occurring from the Chesapeake Bay to South Carolina (Phillips et al. 1989; ASMFC 2010). Adult Spot spawn offshore in the Atlantic during late fall or early winter, and their larvae move across the continental shelf into estuarine nursery habitats, with peak abundance in December and January (Weinstein and Walters 1981; Flores-Coto and Warlen 1993; ASMFC 2010).

Spot often are among the most numerous fishes in estuarine environments and serve ecologically important roles by transferring benthic production to higher trophic levels (Currin et al. 1984; Phillips et al. 1989; Flores-Coto and Warlen 1993). Spot are also the target of economically important directed fisheries, consistently ranking among the top-10 recreational and commercial fisheries by both weight and numbers landed in the south Atlantic (NOAA 2011). Spot have supported the number-one recreational fishery in North Carolina (in terms of the number of fish landed) for several years (NCDMF 2010). Although the fishery continues to be of value, the number of Spot landed in the recreational fishery has recently declined, thus prompting the listing of Spot as a species of concern in the most recent North Carolina stock status report. However, a lack of biological and fisheries data has prevented the completion of a formal stock assessment. The Atlantic States Marine Fisheries Commission first adopted an interjurisdictional fishery management plan for Spot in 1987 (Mercer 1987) and has recently highlighted several research needs, such as merging data from individual states, evaluating mortality by age, determining size and age at maturity, and identifying stocks and coastal movements through tagging or genetic studies (ASMFC 2010).

Piner and Jones (2004) estimated fishing mortality (*F*) and *M* for Spot in the Chesapeake Bay. Their estimate of *M* (0.9 per year) for Spot of ages 1–4 was obtained using the observed maximum age and Hoenig's (1983) regression equation, which was derived from a meta-analysis of many studies and organisms. A more direct approach to estimate *M* is through the use of tagging. Sonic transmitters have been used with success to provide detailed spatial and temporal information about *F* and *M* for several species in a variety of aquatic systems (e.g., Hightower et al. 2001; Simpfendorfer et al. 2002; Thompson et al. 2007; Bacheler et al. 2009). Additionally, information obtained from sonic transmitters has the advantage of not being reliant on reporting by fishers.

Our primary objective for this project was to determine the magnitude and sources of natural mortality of age-1 Spot in estuarine habitats by using state-of-the-art fish tracking technologies and mark–resight models. We assessed possible covariates of age-1 Spot *M*, such as the composition and abundance of competitors and predators, and we tested several assumptions related to aquatic telemetry work with small fish, including the elimination of transmitters consumed by predators, stationary receiver error, and tag retention and survival of small fish that receive relatively large implanted tags.

METHODS

Study Site

The telemetry study occurred in Clubfoot and Hancock creeks, two southern tributaries of the Neuse River in eastern North Carolina (Figure 1). Each creek is approximately 7 km long, 100–500 m wide, and 1–3 m in depth on average. The creeks are minimally influenced by lunar tides, and changes in depth are mainly wind driven. Both commercial fishing and recreational fishing are permitted in Clubfoot Creek, whereas Hancock Creek is limited to recreational fishing. These tributaries were chosen because they are known nursery areas for Spot (North Carolina Division of Marine Fisheries, unpublished data) and because their size and hydrography enabled us to passively monitor fish movements with a fixed receiver array.

Testing of Assumptions

We performed several short-term experiments to test the assumptions of our longer-term field study. The short-term experiments included examining (1) the effects of telemetry tags on Spot, (2) predator elimination of consumed telemetry tags, and (3) the accuracy of stationary receivers. The third experiment is described in a later section (see *Telemetry Relocations*). Further details of these short-term experiments are provided by Friedl (2011).

Effects of the telemetry tags on age-1 Spot.—For our field study, a high tag weight relative to Spot body size was necessary to obtain suitable transmitter performance. We performed a laboratory study to test the hypothesis that Spot of approximately 70 g (∼165 mm FL) could survive implantation of a telemetry tag weighing up to 7.5% of the fish's body weight and could retain the tag for a relatively long period. VEMCO V9-6L dummy transmitters (9 × 21 mm, 2.9 g in air; VEMCO Ltd., Halifax, Nova Scotia) were implanted into eight age-1 Spot (mean FL ± SE = 156.9 ± 2.8 mm; mean weight ± SE = 61.3 ± 3.5 g), and the incisions were closed using a simple continuous suture pattern. The transmitter-implanted fish were held for 80 d, and eight control fish (mean FL ± SE = 163.8 ± 4.8 mm; mean weight ± SE = 69.0 ± 5.9 g) were also held during this same time period. The ratio of tag weight to fish weight ranged from 3.1% to 7.4%. Tanks were visually inspected during two daily feedings for mortality and transmitter loss. Fish length and weight measurements were taken on days 0, 23, 44, 64, and 81. We also performed a second laboratory experiment that was

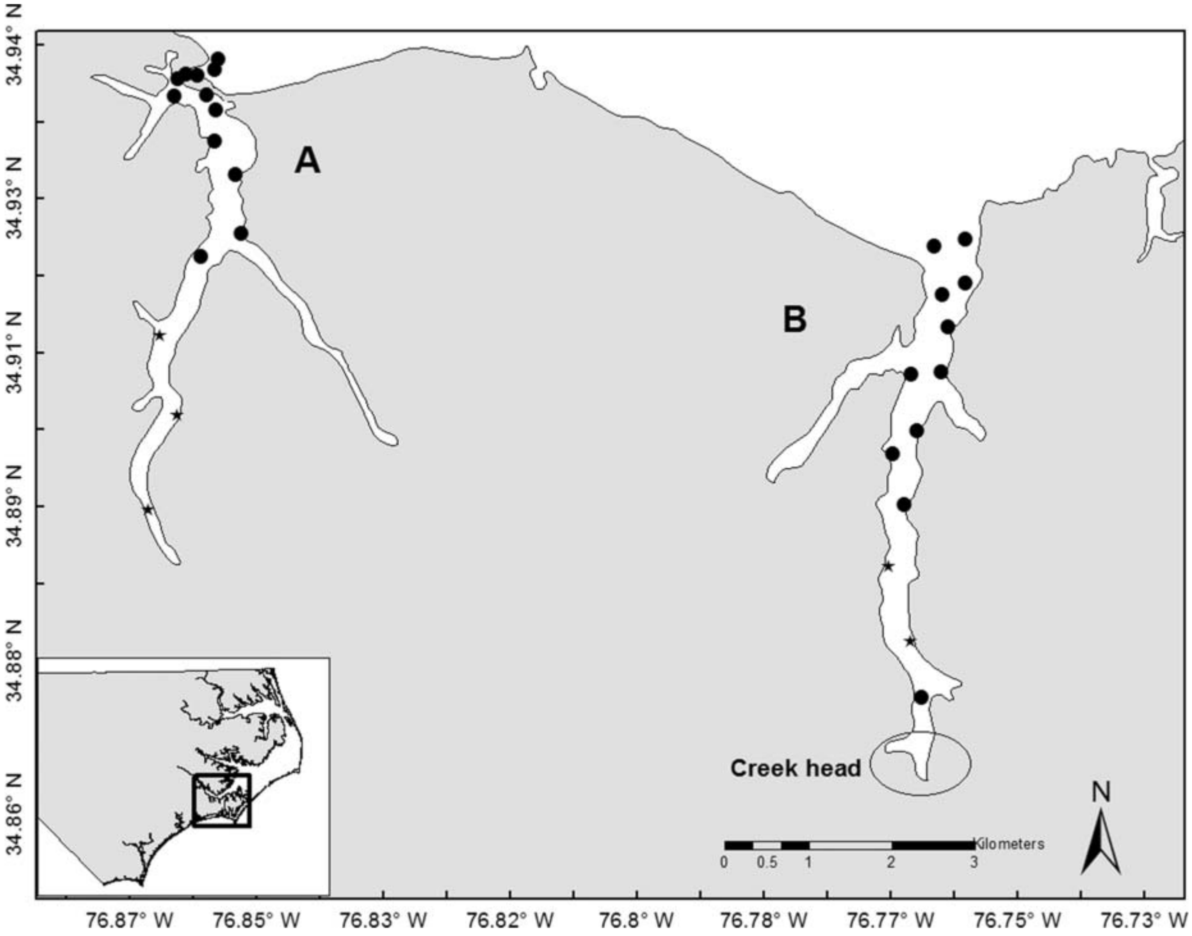

FIGURE 1. Study sites in North Carolina (A = Hancock Creek; B = Clubfoot Creek), where age-1 Spot were monitored with sonic telemetry. Shaded circles represent receivers that were used in both 2009 and 2010; stars represent additional receivers that were used in 2010.

similar to the first, with the exception that a simple interrupted suture pattern was used to close the incision after transmitter implantation.

Piscivore retention of transmitters.—One of the assumptions of the field telemetry approach is that if predators consume telemetry-tagged fish, those predators will eliminate the tags in the study area within a relatively short period of time. To test this hypothesis, 11 age-1 Spot (mean FL ± SE = 174.9 ± 3.0 mm) with V9-6L dummy transmitters were fed to 11 Striped Bass *Morone saxatilis* (mean FL ± SE = 654.5 ± 8.9 mm; mean weight ± SE = 3.9 ± 0.2 kg) that were held in ambient conditions (water temperature range = 19.7–23.9°C) at the Pamlico Aquaculture Field Laboratory, North Carolina State University, Aurora, during June 2009. After all Spot were visibly confirmed to have been eaten, the Striped Bass were moved to individual holding tanks, which were checked daily for transmitter elimination (regurgitation or defecation). The time to elimination was determined for each Striped Bass.

Transmitter Implantation

Spot were captured in Clubfoot and Hancock creeks during April and May 2009 by using an otter trawl (5.0-m headrope; 20.0-mm mesh; 3.2-mm tail bag liner) and a multipanel experimental gill net (six panels with stretched mesh sizes of 25.4, 50.8, 76.2, 101.6, 127.0, and 152.4 mm; each panel was 7.0 m long and 2.5 m deep). During April 2010, only a multipanel experimental gill net (three panels with stretched mesh sizes of 50.8, 63.5, and 76.2 mm; each panel was 15.2 m long and 2.5 m deep) was used to capture the fish. Age-1 Spot (2009: $n = 48$; 2010: $n = 75$; FL range = 142–225 mm; weight range = 46–174 g; Pacheco 1962; Dawson 1965) received surgically implanted VEMCO V9-6L ultrasonic transmitters (9 × 21 mm, 2.9 g in air; 69-kHz frequency; 60–90-s ping rate; 80- and 105-d active life). For surgeries, Spot were anesthetized with a 100-mg/L solution of MS-222 at the beginning of the procedure, and anesthesia was maintained throughout the surgery by continuously pumping MS-222 at 50 mg/L over the gills. Incisions (~10 mm in length) were made along the ventral midline and were closed with three to five simple interrupted sutures after the transmitter was inserted into the peritoneal cavity. After surgery, Spot were released into Clubfoot and Hancock creeks only after normal swimming behavior was observed (~2–5 min). Each transmitter was verified to be functioning properly before the tagged fish was released.

Telemetry Relocations

To detect Spot emigration and movement, an array of submersible receivers (VEMCO VR2 and VR2W; hereafter, "VR2/W") was stationed throughout each study tributary (2009, Clubfoot Creek: $n = 11$; 2009, Hancock Creek: $n = 12$; 2010, Clubfoot Creek: $n = 13$; 2010, Hancock Creek: $n = 15$). Within our study creeks, submersible receivers detected V9-6L tags at 300 m nearly 100% of the time; therefore, the receivers at each creek's mouth were stationed in fixed positions within 600 m of one another and within 300 m of shore (Figure 1). In this way, we ensured that 100% of emigrating fish were observed.

In addition to emigration, we used the fixed receivers to estimate the locations (latitude, longitude) of telemetered Spot. Spot locations were estimated from VR2/W detections by using the method of Simpfendorfer et al. (2002). This method uses detection data from multiple stationary receivers to generate estimates of fish position from the weighted mean receiver latitudes and longitudes, with weights being the number of detections for a unique fish at each receiver during a 60-min period. To test the accuracy of these location estimates, we deployed two test tags in Hancock Creek during May 2010 to estimate transmitter location and timing, which were based on VR2/W detections. The first test tag (identification number [ID] = 56197) was stationed at a fixed location for 26 d, and results indicated that our position estimates were within approximately 250 m of the actual transmitter location. The second test tag (ID = 53174) was placed at four different sites throughout Hancock Creek for 2 min each. Latitude, longitude, start time, and stop time were recorded at each site and compared with the stationary receiver detections. The second test tag was detected at three of the four sites; positions were within 0.001° latitude and longitude and times were within 1.5 min of those recorded in the field. Estimates of telemetered Spot locations from the receiver array also were similar to locations determined from manual tracking (see below). Thus, we are highly confident in our estimates of Spot locations and times as determined from the receiver array.

Locations of telemetered Spot were also determined through manual relocations at least every 7 d by using a VEMCO VR100 manual receiver and omnidirectional hydrophone; searches for telemetered fish were more frequent immediately after transmitter implantation. Manual searches continued for 80 d after the final transmitter implantation in 2009 and for 105 d in 2010; the length of time differed between years due to differences in tag battery life (2009 tag life = 80 d; 2010 tag life = 105 d). In each study creek, listening with a manual receiver and hydrophone occurred at 33 fixed stations that were separated by a distance of no more than 500 m; water temperature, salinity, and dissolved oxygen (DO) were recorded at each station. If a telemetered Spot was detected with the manual receiver at a fixed station, we continued to search for the fish until the signal strength of detection indicated that we were as close as possible to that individual. Signal strength and latitude–longitude coordinates were recorded each time a telemetered fish was detected, and the site with the greatest signal strength was used to assign daily fish locations. Any fish that was not detected during a manual search was still considered to be within the creek if (1) it was not detected as emigrating by the VR2/W array located at the creek mouth and (2) it was detected during the preceding and subsequent manual searches or by the VR2/W array.

Four possible fates were assigned to telemetered Spot based on their behavior after release: surgery-related mortality (SM), emigration (EM), end of battery life, or natural mortality (NM). To ensure that we did not misinterpret SMs as valid natural deaths or include fish that might have had unusual behaviors after surgery (e.g., higher emigration rates), we limited our analysis to fish that were confirmed to be present and alive for at least 7 d after transmitter implantation. Furthermore, fish that stayed and survived through the 7-d censorship period were only included in the numbers "at risk" after that period (Thompson et al. 2007). Therefore, if a telemetered Spot permanently stopped moving within 7 d of tag implantation, it was considered to be a SM and was excluded from the analysis. If a fish was alive and present for at least 7 d after implantation but was detected as leaving the study site (i.e., EM) or was alive and present for the entire battery life, the fish was included in the analysis on day 8 and was censored from the analysis on the day after the EM event or on the day when the transmitter ceased to function.

A telemetered Spot was assigned the fate of NM based on three criteria. The first criterion was that a fish permanently stopped moving after at least 7 d postimplantation. A nonmoving transmitter could occur due to a variety of factors, but the most likely explanation is predation (Lorenzen 1996). A stationary transmitter within the study area would suggest that a predator had consumed and subsequently eliminated the transmitter while the predator was still in the study creek. We assumed that the mortality event occurred 11 d before the transmitter became stationary (see Results); therefore, the predation mortality event was assigned a date 11 d prior to the date when transmitter movement ceased. If this "shifted" predation event occurred within the 7-d censorship period, the fish was excluded from the analysis; if the predation event occurred after the censorship period, the fish was classified as a NM.

The second criterion for assigning a fate of NM was that the estimated latitudinal changes, swimming speeds, or both (see below) were not within the "normal" ranges for age-1 Spot; this criterion relied on the assumption that we were able to differentiate between moving age-1 Spot and moving predators that had consumed a tagged fish. The third criterion was that the telemetered fish was not observed to emigrate from the creek, but its transmitter was no longer detected after at least 7 d postimplantation (having been relocated at least once manually or by the VR2/W array prior to the disappearance). This third circumstance was assumed to be a result of either bird predation or a natural mortality that caused the transmitter to be undetectable (e.g., because the fish washed up onto the shore or sank into the mud). Other possibilities included that the fish was harvested (i.e., *F*), the transmitter failed, or the fish emigrated but was undetected while doing so.

A series of steps was followed to assign fates to individual fish. First, daily detections from all receivers were summarized for each fish in order to determine broad daily movement patterns; this step allowed us to quickly identify dates of EM events and to exclude fish that were not present for at least the first 7 d after tagging. The second step was to calculate a 24-h variance in latitude for each fish, the maximum of which was compared with those of all other telemetered fish to determine whether outliers existed. Maximum latitudes were examined within each year since changes in VR2/W locations between years could have influenced our estimates of latitudinal location. Latitudinal position was adequate for our examination of variance in position (i.e., we did not need to use longitude values) because the two study creeks are oriented north to south.

The third step in fate assignment was to estimate average hourly swimming speeds for each fish that was considered at risk. Swimming speeds were calculated for each telemetered fish as distance traveled (m) between two hourly weighted mean latitude and longitude positions divided by 3,600 s; swimming speed calculations were performed for all hours for which positions could be estimated. There was minimal error in swimming speed estimates. Our fixed stationary tag had estimated swimming speeds slightly above zero (mean = 0.02 m/s); this error was similar to the swimming speed error (mean = 0.02 m/s) estimated for other stationary tags that were observed after Spot mortality events (see below). The maximum swimming speed for each fish was compared with previously estimated cruising and burst swimming speeds for age-1 Spot (Wyllie et al. 1976; Neumann et al. 1981; Moser 1987). Any fish that exhibited an estimated swimming speed of 0.7 m/s or greater was automatically considered to represent a predation event since Spot of this size cannot maintain such speeds for an hour. Telemetered fish with estimated swimming speeds of 0.7 m/s or greater were categorized as NMs attributable to predation on the day that the abnormally high swimming speed occurred. Additionally, we compared average observed emigration swimming speeds of telemetered age-1 Spot with the swimming speeds of known predators, such as Red Drum *Sciaenops ocellatus* and common bottlenose dolphins *Tursiops truncatus* (data from Bacheler et al. 2009).

For approximately 25 d in late April and early May 2010, three receivers in Clubfoot Creek did not function correctly for unknown reasons. Because these receivers did not record transmitter detections, the positions and swimming speeds estimated during this time period may not be as precise as those estimated with data from the full array.

Estimation of Mortality and Emigration

Instantaneous rates of *M* and emigration (*E*) of age-1 Spot were estimated by using an integrated Bayesian method in OpenBUGS software (Lunn et al. 2009). Our model included two independent likelihood components for the telemetry and trawl CPUE data (Appendix 1). The telemetry component was modified from a Bayesian analysis of tag return data (Link and Barker 2010). In our case, there were three possible fates for a telemetered fish that was at risk on day *i*: (1) survival (and remaining in the system), (2) NM, or (3) EM. Fates were determined from multiple relocations of telemetry-tagged age-1 Spot by manual tracking and stationary receivers as described above. Each day was considered a separate trial for the telemetry component, and a multinomial distribution was used to calculate likelihoods. Trawl CPUE of age-1 Spot was assumed to decline exponentially due to combined losses from *M* and *E*. Trawl catches are count data, so we modeled the expected catch on each date by using a Poisson distribution (McCarthy 2007). Predicted CPUE was assumed to decline exponentially at rate Z' (where $Z' = M + E$). Thus, the total loss rate Z' is shared between the two likelihood components used in the multinomial cell probabilities for telemetered fish and in the Poisson model for the annual trawl catches. Credible intervals (CIs) for *M* and *E* were the 2.5th and 97.5th percentiles of the posterior distribution. Our estimate of 30-d *M* was compared with estimates for Spot of this size based on weight (Lorenzen 1996) and von Bertalanffy growth parameters (Brody growth coefficient *k* and asymptotic length L_∞; Piner and Jones 2004; ASMFC 2010) using a length-based *M* formula developed by Gislason et al. (2010).

In addition to the telemetry data assumptions already listed, we assumed that (1) all marked fish that were alive in the study area at time *i* had the same survival rate to time $i + 1$; (2) marked and unmarked fish had the same survival rates; (3) the probability of a transmitter being shed or failing was negligible (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009); (4) movement patterns could be used to determine whether a tagged fish remained alive or had died due to NM (Jepsen et al. 1998; Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005; Thompson et al. 2007; Bacheler et al. 2009); and (5) emigrating fish could be detected and therefore censored from the analysis.

Competitor Sampling

Catch data for Spot and their potential competitors were collected in each study tributary by using an otter trawl (5.0-m headrope; 20.0-mm mesh; 3.2-mm tail bag liner) that was towed for 4.5 min at a speed of approximately 4.5 km/h. In total, 70 trawl samples were obtained in 2009 ($n = 30$) and 2010 ($n = 40$). Sampling in 2009 was conducted on three study days: day 4 (26 April; Hancock Creek sample 1) or day 9 (1 May;

Clubfoot Creek sample 1), day 30 (22 May; both creeks), and day 62 (23 June; both creeks). In 2010, all sampling dates were the same for both creeks: study days 11, 35, 57, and 82 (11 April, 5 May, 27 May, and 21 June, respectively). We used systematic random sampling techniques as described by Williams et al. (2002). Each study creek was divided lengthwise by a midline transect, with perpendicular widthwise transects dividing the creek into five strata of equal length. On a given sampling day, the initial starting distance along the midline transect was randomly selected from a pool of three potential distances, and that selected distance was then used as the starting point for each of the subsequent strata. Whether the sample occurred east of, west of, or directly on the midline transect was randomly selected for each individual stratum. This procedure was applied to each study creek for each competitor sampling event, and one tow was made per stratum.

Trawl samples were sorted by species, and individuals were measured (FL, TL, and SL); species that were represented by more than 30 individuals of the same size range were subsampled. Species were considered to be potential competitors of Spot based on abundance, size, and benthic habits. Age-classes (i.e., age 0 and age 1) of Spot and potential competitors were distinguished based on length frequency distributions and were analyzed separately for catch rate comparisons between years. Catch was log transformed and averaged over the 10 hauls taken on each sampling day. Competitor abundance was compared between years by using a two-tailed *t*-test, with all sample days as replicates for each year. Water temperature, salinity, and DO were measured at the start and end points of each trawl, and latitude–longitude coordinates were recorded.

Predator Sampling

Potential predators of age-1 Spot were sampled in each study creek by using trammel nets (183 × 2.1 m, with one 63.5-mm stretched mesh inner panel surrounded by two 356.0-mm stretched mesh outer panels) and gill nets (200.0 m long; 101.5-mm stretched mesh; 1.0 m deep). Predator sampling in 2009 was conducted on six dates per creek: study days 3, 12, 21, 35, 48, and 49 (25 April, 4 May, 13 May, 27 May, 9 June, and 10 June) in Clubfoot Creek; and study days 6, 14, 22, 35, 48, and 49 (28 April, 6 May, 14 May, 27 May, 9 June, and 10 June) in Hancock Creek. Predator sampling in 2010 occurred on the same five dates in both creeks: study days 13, 30, 44, 62, and 76 (13 April, 30 April, 14 May, 1 June, and 15 June, respectively). In 2009, 55 gill-net sets and 12 trammel-net sets were performed, capturing a total of 184 and 48 predators, respectively. In 2010, 55 gill-net sets and 30 trammel-net sets were conducted, in which a total of 120 and 125 predators, respectively, were caught. Systematic random sampling (see *Competitor Sampling* above) was used to determine specific sample sites throughout the study creeks, and relative abundances of individual predator species and total predators were calculated. Statistical analysis of the gill-net catch was limited to sample days when telemetered fish were at risk during each year; therefore, a two-tailed *t*-test was used to compare predator CPUEs from each of the five sample days in 2009 with predator CPUEs from only the first four sample days in 2010. Predator catches from trammel nets were not included in this comparison because trammel-netting was not consistently random with respect to strata.

Predators were measured (FL, TL, or both) and, when possible, stomach contents were retrieved by using gastric lavage techniques (Hartleb and Moring 1995), which allowed predators to be released alive. Stomach contents from predators caught in both types of gear were used for diet analysis; contents were stored on ice and frozen prior to analysis. All collected stomach contents were analyzed, but only 375-mm and larger piscivores were considered potential predators of Spot because this predator size is theoretically large enough to consume age-1 Spot (∼140–220 mm FL) based on a prey length : predator length ratio of approximately 40% (Scharf et al. 2000). Prey were identified based on external morphological features; diagnostic bones (e.g., otoliths, dentaries, or opercula) were used to identify recovered prey that were in advanced stages of digestion. Prey items were measured for TL or carapace width when direct measurements could be made, and the prey were identified based on external morphology and published references (Williams 1984; Hoese and Moore 1998; Carpenter 2002). Excess moisture was removed from prey items by blotting with a paper towel before wet weight (g) was measured. The composition (percent weight) of the diet consumed by potential Spot predator species was characterized.

RESULTS

Testing of Assumptions

Effects of the telemetry tag on age-1 Spot.—We observed no age-1 Spot mortalities due to transmitter implantation during the 80-d simple continuous suture experiment, and there were no mortalities among control fish. However, only a 75% tag retention rate was observed with the continuous suture treatment. Growth was not significantly different between control and experimental groups, as evidenced by nonsignificant interaction terms in repeated-measures ANOVAs (FL, treatment × day interaction: $F = 3.29$, df $= 4$, $P = 0.07$; weight, treatment × day interaction: $F = 2.90$, df $= 4$, $P = 0.09$). Survival and tag retention were both 100% in the simple interrupted suture experiment. Thus, we determined that the V9-6L sonic tag did not have an adverse effect on growth or mortality of age-1 Spot but did require a simple interrupted suture for 100% tag retention.

Piscivore retention of transmitters.—Seven Striped Bass consumed 11 age-1 Spot into which dummy transmitters were implanted; three Striped Bass consumed only one Spot each, and the remaining four Striped Bass consumed two Spot each. Ten tags were eliminated from the piscivores and recovered from the bottom of the tanks. The eleventh tag was never eliminated and was recovered from the predator's stomach upon necropsy on day 32. For the three Striped Bass that consumed only one tagged Spot each, tags were eliminated on days 6 and 7 or

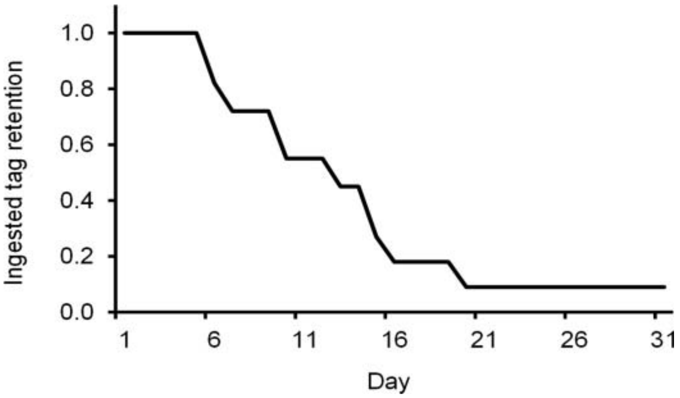

FIGURE 2. Proportion of transmitters retained over time in Striped Bass predators that ingested age-1 Spot tagged with VEMCO V9-6L dummy transmitters in the laboratory. Ten tags were eliminated (regurgitated or defecated) from the predators during the 31-d experiment; the remaining tag was recovered upon necropsy of a predator on day 32.

TABLE 1. Summary of assumed fates for telemetered age-1 Spot that were tracked in Hancock and Clubfoot creeks during 2009 and 2010. Number of individuals of each fate is followed by the proportion of the total number tagged (in parentheses) for that year.

Number tagged and subsequent fate	2009	2010
Number tagged	48	75
Surgery-related mortality	3 (0.06)	7 (0.09)
Transmitter failure	0	2 (0.03)
Emigration within 7 d	16 (0.33)	8 (0.11)
Predation mortality (surgery related)	0	6 (0.08)
Natural mortality (predation)	0	4 (0.05)
End of battery life	2 (0.04)	0
Emigration after 7 d	27 (0.56)	48 (0.64)
Average number of days at risk	17.86	18.98

obtained upon necropsy (day 32). Of the four Striped Bass that each consumed two Spot, two of the predators eliminated both tags on the same day (day 10 and day 15, respectively). The other two predators eliminated each tag individually (on days 6 and 13 and on days 16 and 20, respectively). Excluding the tag that was not eliminated, the average number of days to transmitter elimination after a predator ingested a tagged Spot was 11 d; however, tag elimination was observed as early as 6 d and as late as 20 d (Figure 2).

Telemetry

Ultrasonic transmitters were surgically implanted into 48 age-1 Spot (mean FL ± SE = 163 ± 1 mm; mean weight ± SE = 71 ± 2 g) in 2009 and 75 age-1 Spot (mean FL ± SE = 167 ± 2 mm; mean weight ± SE = 79 ± 3 g) in 2010. The condition (weight adjusted for differences in length) of telemetered fish at tagging was not different between the 2 years of the study (ANCOVA: $F = 1.01$; df = 1, 120; $P = 0.32$). In both years, all of the telemetry-tagged Spot were relocated by VR2/W receivers. In 2009, 26 of the 48 tagged Spot were manually relocated within the study creeks; in 2010, 73 of the 75 tagged fish were manually relocated.

We were unable to include all telemetered Spot in our analysis to estimate E and M. In 2009, 19 fish were excluded from the analysis due to either an inferred SM ($n = 3$ fish) or an EM event within 7 d postimplantation ($n = 16$ fish; Table 1). In 2010, 21 fish were excluded from the analysis due to an inferred SM ($n = 7$ fish), an inferred predation event that back-dated to the censorship period ($n = 6$ fish; see below), or an EM event within 7 d postimplantation ($n = 8$ fish; Table 1).

For fish at risk, telemetered age-1 Spot and those inferred to have been consumed by predators were differentiated based on swimming speeds and variation in position (latitude) that were considered "normal" for age-1 Spot. Latitudinal variance estimates ranged from 113,413 to 1,404,952 m^2 in 2009 and from 39,701 to 5,243,179 m^2 in 2010 (Figure 3). Maximum swimming speed estimates ranged from 0.10 to 0.50 m/s in 2009 and from 0.10 to 1.14 m/s in 2010 (Figure 3). There were no fish with estimated maximum swimming speeds over 0.70 m/s in 2009 (see Methods). However, in 2010, one fish had a maximum swimming speed exceeding 0.70 m/s (ID = 27794), and this was assumed to represent a predation event (see further description below).

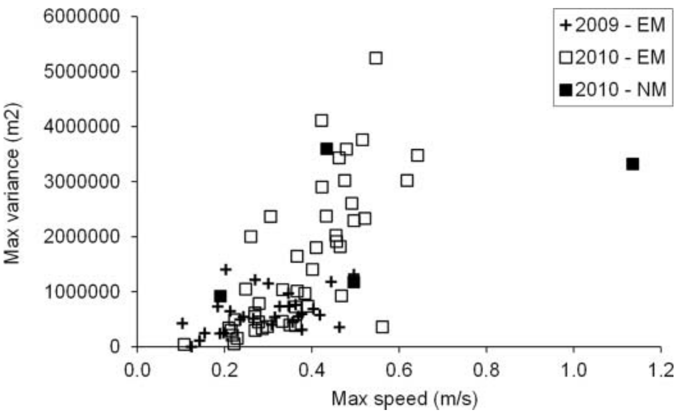

FIGURE 3. Maximum (Max) latitudinal variance (m^2) and maximum swimming speed (m/s) estimates for telemetered age-1 Spot in Hancock and Clubfoot creeks during 2009 and 2010. We inferred no mortalities in 2009 (plus symbols = emigration [EM]) but four in 2010 (open squares = EM; shaded squares = natural mortality [NM]). One NM was inferred from this graph (high maximum swimming speed; fish identification number = 27794). Of the three NMs that were not represented by outliers, two were inferred based on changes in fish behavior followed by a lack of movement, and one was inferred based on a sudden cessation of tag detections after the fish had been relocated multiple times.

Emigration swimming speeds of telemetered age-1 Spot averaged 0.005–0.230 m/s during the final 48 h of detections and

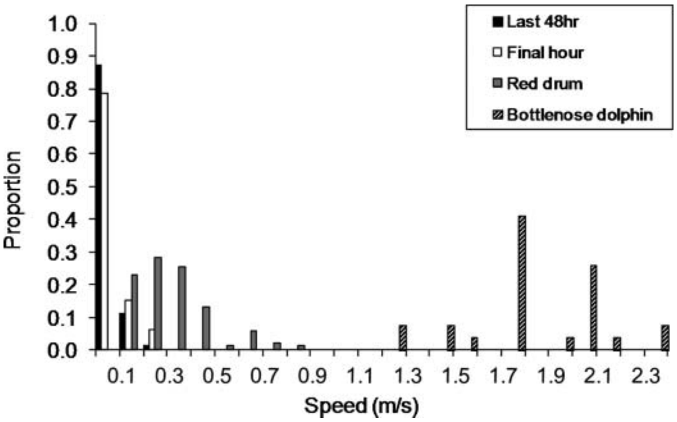

FIGURE 4. Estimated average emigration swimming speeds for telemetered age-1 Spot in Hancock and Clubfoot creeks, presented in comparison with estimates for Red Drum and common bottlenose dolphins (from the same or similar study creeks; Bacheler et al. 2009). Two different estimated average speeds for age-1 Spot are shown: the average for the final 48 h of detections (including emigration) and the average for the final hour of detection.

averaged 0.001–0.230 m/s during the final hour of detection (Figure 4). The final-hour estimates of age-1 Spot swimming speed were significantly different (median test: $\chi^2 = 57.81$, df = 1, $P < 0.0001$) from the estimated average speeds of Red Drum (range = 0.01–0.74 m/s), but there was some overlap. Final-hour swimming speed estimates for age-1 Spot were also found to be significantly different (median test: $\chi^2 = 35.89$, df = 1, $P < 0.0001$) from the estimated average speeds of common bottlenose dolphins (range = 1.10–2.20 m/s), and there was no overlap (Figure 4).

Four fish in 2009 and eight fish in 2010 temporarily emigrated ($\geq$24 h) from the study creek in which they were tagged but later returned for at least 36 h. Observations of swimming behavior and speed enabled us to infer that signals were being generated by age-1 Spot and not by a predator that had consumed a telemetered fish while it was out of detection range. In 2010, three fish emigrated from Hancock Creek into Clubfoot Creek for at least 36 h, allowing the same observations and assumptions as outlined above for emigration and return within a creek. In both scenarios, Spot were considered at risk during the time period in which they inhabited a study creek, but the fish were censored during the temporary emigration period.

Based on the above results, we assumed the following fates for Spot that were considered to be at risk. Of the 29 fish used in the analysis for 2009, 2 were alive and present until the end of transmitter battery life and 27 emigrated from the study system (after the 7-d censorship period), including one that emigrated through the head of Clubfoot Creek. There were no inferred NMs in 2009 (Table 1). During 2010, we assumed the occurrence of two tag failures because the transmitters were not detected either manually or by the VR2/W array immediately after release of the fish. There were 48 EM events after 7 d postimplantation, including two EMs through the head of Clubfoot Creek. We inferred a total of 10 predation mortality events; after events that took place during the probationary period were excluded, 4 of the 10 predation events were inferred to be NMs.

Of the four assumed NMs, two were based on a combination of changes in behavior followed by a lack of movement at least 18 d after tag implantation (IDs = 27732 and 27786; Figure 5). The third NM was a fish that was detected as emigrating from the creek, and its assumed fate was based solely on extreme changes in latitudinal location and swimming speed (ID = 27794; Figure 5). The fourth NM was a fish that was no longer detected in the creek after being present, active, and relocated multiple times after transmitter implantation (ID = 27748; Figure 5). Assumed NMs were distributed evenly across the size range of telemetered Spot during 2010, whereas most of the assumed SMs occurred in telemetered Spot that were smaller than 70 g (information on sizes and fates of individual fish is provided in Table A.1 of Appendix 2).

Although telemetered age-1 Spot were present in our study creeks for a total of 75 d in 2009 and 71 d in 2010, a large percentage of the fish emigrated from the study area (see Table 1) and did so in a short period of time. Beginning on day 8 postimplantation (i.e., the first day after the censorship period), individual telemetered Spot used in the analysis were at risk in the study creeks for an average of 17.9 d in 2009 (range = 1–75 d) and 19.0 d in 2010 (range = 1–60 d).

Mortality and Emigration

The total daily loss rate of age-1 Spot was high ($Z' = 0.025$), and the majority (96%) of this daily loss was due to emigration (mean daily $E = 0.024$; CI = 0.022–0.027). This result indicates that approximately 2.4% of age-1 Spot emigrated from these estuarine creeks each day during April and May. The mean daily M was 0.001 (CI = 3.073×10^{-4} to 0.002), and the four assumed NMs in 2010 were fairly evenly distributed throughout the study period. The daily instantaneous rates of E and M were used to calculate a 30-d E of 0.73 (CI = 0.65–0.81; Figure 6A) and a 30-d M of 0.03 (CI = 0.01–0.07; Figure 6B). Our field-based M estimate of 0.03 was lower than the Lorenzen weight-based estimate for a 70-g fish (30-d $M = 0.07$). Our estimate was also lower than the life-history-based estimates for 170-mm Spot (ASMFC 2010: Chesapeake Bay Multispecies Monitoring and Assessment Program [$L_\infty = 409$ mm, $k = 0.19$], 30-d $M = 0.06$; Virginia Marine Resources Commission [$L_\infty = 384$ mm, $k = 0.28$], 30-d $M = 0.08$; North Carolina Division of Marine Fisheries [$L_\infty = 299$ mm, $k = 0.65$], 30-d $M = 0.13$; Piner and Jones 2004 [$L_\infty = 233$ mm, $k = 2.60$], 30-d $M = 0.36$; Figure 6B).

Competitors

Three taxa (captured in addition to Spot) were considered potential competitors of age-1 Spot: Atlantic Croaker *Micropogonias undulatus*, Pinfish *Lagodon rhomboides*, and flounders *Paralichthys* spp. The catch of age-0 Spot and the catch of age-0 competitors were not significantly different between 2009 and 2010 (age-0 Spot: $t = 0.27$, df = 5, $P = 0.79$; age-0 competitors:

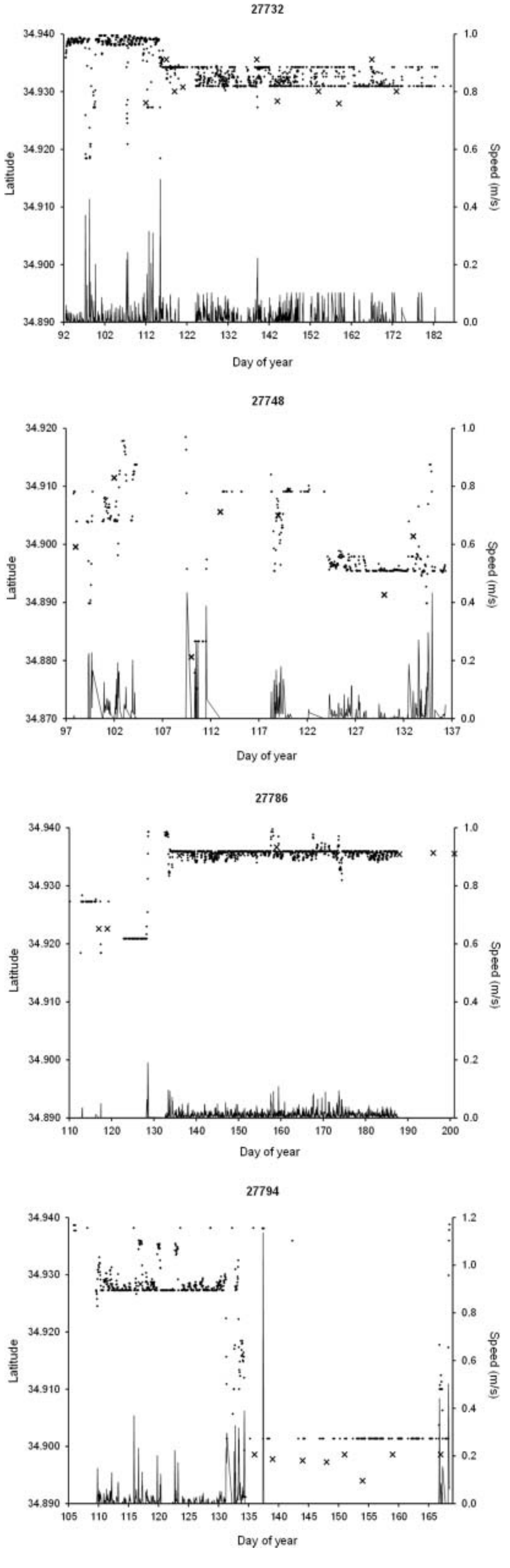

FIGURE 5. Estimated average hourly latitudinal positions (dots), manual tracking relocations (× symbols), and swimming speeds (m/s; solid lines) of the four telemetered age-1 Spot that were inferred natural mortalities in 2010.

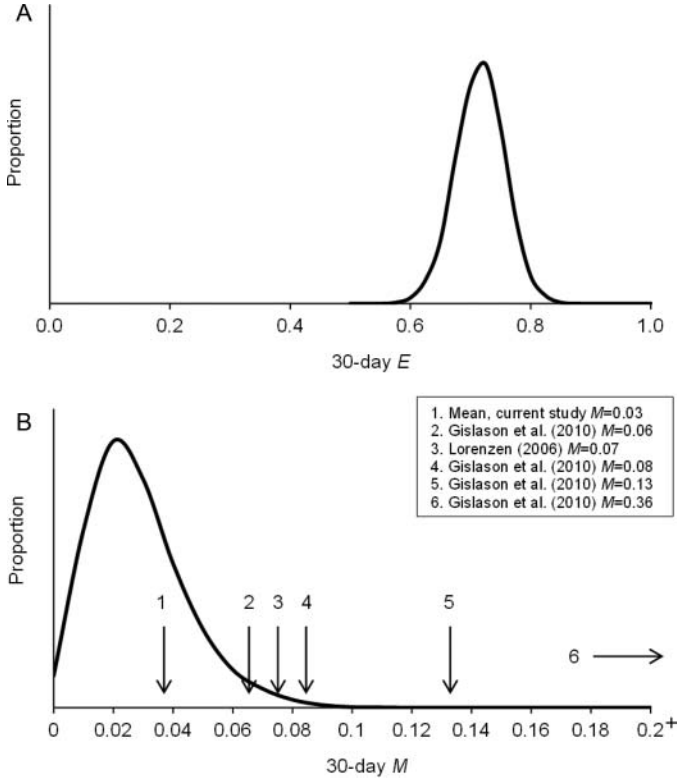

FIGURE 6. Posterior probability distributions for **(A)** the 30-d instantaneous emigration rate (E) and **(B)** the 30-d instantaneous natural mortality rate (M) of age-1 Spot based on Bayesian analysis of telemetry and trawl CPUE data. Panel B includes the mean estimate from this study ($M = 0.03$), compared with a Lorenzen (1996) weight-based estimate ($M = 0.07$) and Gislason et al. (2010) life-history-based estimates (ASMFC 2010: $M = 0.06$ from Chesapeake Bay Multispecies Monitoring and Assessment Program, $M = 0.08$ from Virginia Marine Resources Commission, $M = 0.13$ from North Carolina Division of Marine Fisheries; Piner and Jones 2004: $M = 0.36$).

$t = 0.68$, df = 5, $P = 0.53$). The catches of age-1 Spot and age-1 competitors also did not significantly differ between 2009 and 2010 (age-1 Spot: $t = 0.79$, df = 5, $P = 0.46$; age-1 competitors: $t = 0.66$, df = 5, $P = 0.54$). Temperature, salinity, and DO were within tolerance ranges for Spot in both years (Table 2).

Predators

The composition of predator species caught in gill nets and trammel nets was similar between years (Figure 7). Predator catches included Black Drum *Pogonias cromis*, Bluefish *Pomatomus saltatrix*, Red Drum, Spotted Seatrout *Cynoscion nebulosus*, Striped Bass, and White Catfish *Ameiurus catus*, but the catches were dominated by Longnose Gars *Lepisosteus osseus*. Gill-net catches of potential predators (all predator species combined) for sample days when telemetered Spot were at risk did not significantly differ between 2009 and 2010 ($t = 0.32$, df = 7, $P = 0.76$).

Stomach contents were analyzed from a total of 376 piscivores ($\geq$375 mm; $n = 188$ fish per year). Age-1 Spot were not detected in the stomach contents of any predator. In both years,

TABLE 2. Temperature, salinity, and dissolved oxygen (DO) means and ranges for Clubfoot and Hancock creeks during April–June 2009 and 2010. Values were measured during competitor trawl sampling and were within the tolerance ranges for Spot in both years.

		2009		2010	
Variable	Month	Range	Mean	Range	Mean
Temperature (°C)	Apr	22.8–25.95	24.09	22.95–26.40	24.80
	May	20.75–22.45	21.61	24.1–26.85	25.80
	Jun	27.8–29.30	28.46	29.40–32.10	31.16
Salinity (‰)	Apr	7.75–14.40	11.32	3.50–10.00	6.50
	May	6.40–14.10	10.85	5.10–9.50	7.42
	Jun	11.0–15.70	13.04	6.55–11.60	8.89
DO (mg/L)	Apr	4.77–7.95	6.09	6.61–8.55	7.26
	May	7.15–10.04	8.84	7.28–10.91	9.40
	Jun	5.99–9.21	7.43	5.97–8.14	7.12

diets of Longnose Gars (the most abundant predator) were dominated by Clupeidae (herrings). Additional fish prey that were recovered from the stomachs of Longnose Gars and other predators belonged to the families Sciaenidae (drums and croakers), Mugilidae (mullets), Ophichthidae (snake eels), and Syngnathidae (pipefishes). The size of finfish prey items ranged from 17 to 185 mm TL, thus overlapping the TL range of telemetered age-1 Spot (range = 150–243 mm TL; mean = 177.3 mm).

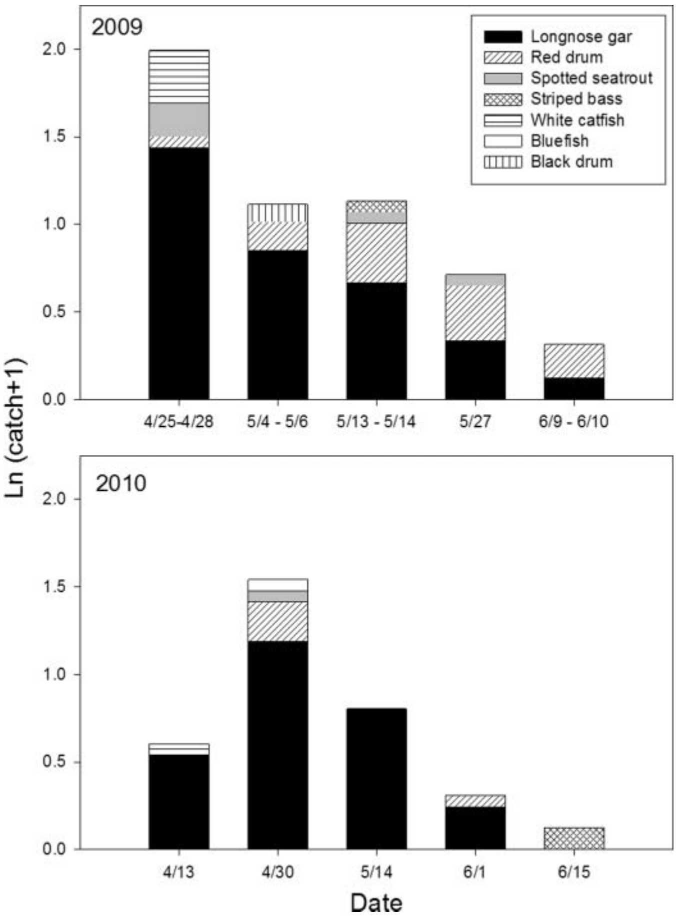

FIGURE 7. Daily gill-net catch per unit effort ($\log_e[x + 1]$ transformed) for 375-mm TL and larger predators in Hancock and Clubfoot creeks during 2009 and 2010.

DISCUSSION

Estimation of Spot Mortality

We provide the first field-based estimate of M (30-d M = 0.03) for age-1 Spot, a relatively small estuarine fish, by using a telemetry tag approach that was originally developed in a closed reservoir system (Hightower et al. 2001). Direct estimates of M in open, dynamic systems are difficult to obtain (Vetter 1988; Quinn and Deriso 1999), and we found this to be true for age-1 Spot due to their high daily E (0.024). Estimates of M for age-0 Spot have previously been reported (Weinstein and Walters 1981; Currin et al. 1984; Weinstein et al. 1984; Ross 2003), but those estimates were based on assumed periods of residency and were likely confounded with emigration. In the present study, EM events were identified and fates were assigned through the use of an acoustic receiver array and manual tracking; additionally, the decline in trawl CPUE for age-1 Spot also informed the estimate of Z', which included both M and E.

Hightower et al. (2001) and Bacheler et al. (2009) used this same telemetry approach on larger fish that had a relatively low risk of predation. The values of M estimated in those two studies were lower than values predicted from a model based on predation risk as a function of size ("natural" system model; Lorenzen 1996). Similar to those studies, our estimated M for age-1 Spot was lower than the Lorenzen weight-based estimate; the M estimated in our study was also lower than life-history-based estimates derived from various values of k and L_∞ (Piner and Jones 2004; ASMFC 2010). It is important to note that our estimates were based on a relatively short time frame (i.e., April–June) in estuarine creeks and that monthly estimates of M may be higher or lower for age-1 Spot at other times of year or in other locations. In contrast to the findings described above, Heupel and Simpfendorfer (2002) found that telemetry-based estimates of *M* for juvenile Blacktip Sharks *Carcharhinus limbatus* were higher than those predicted from life-history- and age-based methods.

Heupel and Simpfendorfer (2002) and Bacheler et al. (2009) also estimated mortality in estuarine systems by using stationary acoustic receivers to document emigration and determine fates. Bacheler et al. (2009) used a receiver array that was designed to detect EM events and speeds of telemetered Red Drum, while Simpfendorfer et al. (2002) estimated residency and movement behaviors of juvenile Blacktip Sharks by using an array that was distributed within an X–Y coordinate system throughout an estuary. Our receiver array was designed to promote coverage of as much of the study creeks as possible; despite the lack of complete coverage, we were able to estimate locations and swimming speeds of Spot to aid in the assignment of fates.

Two of the fish with a fate of NM were assigned that fate based on situations in which the tag stopped moving but was still detected; one NM was determined from abnormally high swimming speeds. Although no age-1 Spot were recovered during our analysis of piscivore stomach contents, predators were able to consume fish prey of sizes similar to those of Spot (Friedl 2011). In a follow-up study in North Carolina, predator diet analyses showed that age-1 Spot were present in Longnose Gar stomachs (S. Binion and J. Buckel, North Carolina State University, unpublished data); thus, we hypothesize that three of the four inferred NMs were a result of predation. For the fourth Spot that was assigned a fate of NM, tag detections ceased, but this individual exhibited normal movement behaviors prior to the loss of detections. The abrupt cessation of tag detections could have been due to transmitter failure, bird predation (i.e., NM), or fishing mortality. Spot recruit to the fishery by age 1 (Mercer 1987; Piner and Jones 2004), so it is possible that this fish was harvested. Predation by cormorants or ospreys *Pandion haliaetus* was also possible. Double-crested cormorants *Phalacrocorax auritus* were often observed preying on small fish during the at-risk period for telemetered Spot; ospreys are abundant fish predators in North Carolina, and age-1 Spot fall within their prey size range (Carss and Godfrey 1996).

We observed NMs in 2010 but not in 2009. However, the number of NMs in 2010 was low, and given the sample size of telemetered fish in 2009 there was a high likelihood of obtaining zero mortality in 2009. Thus, we used a pooled-years model to estimate a single *M* by using fates of telemetered fish and trawl loss rates in both years. The lack of a large difference in NM between years matches up with other between-year similarities: age-1 Spot size and condition; temperature, salinity, and DO; and competitor and total predator catches.

Testing the Assumptions of Fate Assignments

There are several assumptions associated with the telemetry approach for estimating mortality, some of which were more easily violated in our study given the relatively small size of Spot. Assumptions of the model were listed in Methods; assumptions regarding SM, tag expulsion by telemetered age-1 Spot, identification of predator-consumed transmitters, and predator elimination of consumed tags are discussed below.

The size range of Spot that could receive implanted transmitters was constrained by the size range of tags available. Attempts were made to use a smaller tag (VEMCO Model V7), but we found that it had a very poor detection range within our study system. The transmitters we implanted into Spot in the field represented 1.7–6.3% of the weight of tagged fish; these values were lower than or within the range of the tag weight : fish weight ratios (3.1–7.4%) that were used in our laboratory study, during which no adverse effects of either the surgery or the transmitter were observed. Our laboratory findings agree with a growing list of similar studies (e.g., Childs et al. 2011) demonstrating that small fish have high survival and tag retention when fitted with relatively large tags. Although we were confident in assuming that no tag expulsion occurred in the field (i.e., based on our laboratory findings for the use of simple interrupted sutures), Spot at the smaller end of the size range did appear to suffer SM when released into their natural environment. This source of mortality could be reduced in future field studies by working with larger Spot or by using a smaller tag. The possibility for surgical complications is greater when fish are tagged on-site (Wagner and Cooke 2005; Moser et al. 2007), and laboratory results should be considered a "best-case" scenario.

In telemetry studies, the probationary or censorship period that is implemented in order to account for SM is generally subjective and is intended to be extremely conservative; the length of the probationary period depends on the study system and on the species being tagged (Thorsteinsson 2002). Because telemetered Spot emigrated so quickly from the study creeks, our probationary period (7 d) was shorter than we would have liked. Based on the 100% survival rate observed in our laboratory study, we assumed that the implementation of a 7-d probationary period would not bias our results. Additionally, fish were not introduced into the analysis until after this 7-d period to prevent a possibly erroneous assumption of 100% survival during the first 7 d postimplantation.

We assumed that our fate assignments of telemetered age-1 Spot were correct. Spot locations and swimming speeds were a critical component of fate assignment. Acoustic receivers recorded the correct time and general vicinity of the two test tags that were deployed in 2010, and the estimated average hourly speeds had minimal error. However, one of the initial assumptions of our study was that EM of live telemetered fish would be distinguishable from the "emigration" of transmitters from Spot that had been consumed by predators. Although swimming speeds of common bottlenose dolphins were clearly different than presumed emigration speeds of age-1 Spot, there was some overlap between the swimming speeds of Spot and age-2 Red Drum (Bacheler et al. 2009). Consequently, this may have influenced our ability to distinguish between a live age-1 Spot and a predator swimming out of the creek with a tagged age-1 Spot in its stomach. Novel approaches to distinguishing live individuals of the study species from individuals that have been consumed by predators are needed to further refine the telemetry survival approach. For example, Thorstad et al. (2011) used telemetry tags with depth sensor capabilities to aid in distinguishing surface-oriented Atlantic Salmon *Salmo salar* smolts from their predators (Atlantic cod *Gadus morhua* or Pollock *Pollachius virens*), which sometimes occupied deeper water after consuming telemetry-tagged smolts. Kawabata et al. (2011) used diel movement patterns in telemetered Blackspot Tuskfish *Choerodon schoenleinii* to identify putative predation events.

Another potential confounding factor for proper fate assignment was transmitter elimination (regurgitation or defecation) by a predator. To our knowledge, ours is the first study to estimate time to elimination for an ingested transmitter in a piscivorous fish; the relatively long time period from consumption to tag elimination has implications for future telemetry studies. It has generally been assumed that mortality can be inferred from a stationary transmitter (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005; Thompson et al. 2007; Bacheler et al. 2009; Thorstad et al. 2011). Our results showed that the time between transmitter consumption and elimination may be considerable. Thus, NMs may have to be inferred based on detailed movement information, especially with telemetry studies involving smaller fish. For example, one fish (ID = 27794) was assigned a fate of NM based on high within-creek swimming speeds. Additionally, studies that use array detections as recaptures to estimate survival in open-population models (e.g., Kocik et al. 2009; Welch et al. 2009) should examine the possibility that those detections are from a predator that has consumed a tagged fish and retained the tag (e.g., Kawabata et al. 2011; Thorstad et al. 2011).

Conclusions

Recently, there has been a call for more marine telemetry studies (Cooke et al. 2011). Telemetry studies are easier to design and perform when they are focused on large fish in closed systems (Hightower et al. 2001; Young and Isely 2004; Thompson et al. 2007), but our results suggest that estimates of mortality can be obtained for smaller fish species in open systems as long as great care is taken during study design. Researchers need to be aware of and understand the assumptions of telemetry work (e.g., SM, transmitter expulsion, and predator retention of tags for long periods) when determining fates of telemetered fish. For bias related to predator retention of tags, fine temporal and spatial resolution of tag locations from continuous monitoring throughout the study area is required for the most accurate assignment of fates.

Our field-based estimate of *M* for age-1 Spot is valuable for several reasons. First, it allows for a direct comparison with *M* estimates that are predicted based on fish weight (Lorenzen 1996) or based on length and life history parameters (Gislason et al. 2010); these and similar models have been used to provide estimates of *M* for stock assessments. Second, the study design and modeling used here are novel, and we recommend that telemetry and other sources of data (e.g., CPUE, diet) be combined to improve the accuracy and precision of *M* estimates. Lastly, our estimate of *M* can be considered for use in the next stock assessment for Spot, a species that has economic and ecological significance in North Carolina and the southeastern USA. Estuaries provide an important habitat for Spot (Currin et al. 1984; Stokesbury and Ross 1997; ASMFC 2010); thus, direct estimates of important demographic rates in these dynamic systems will assist in the management of this species.

ACKNOWLEDGMENTS

We thank all of the field personnel who assisted with the data collection and analysis, especially Tyler Averett, Cheston Peterson, Paul Rudershausen, Joe Facendola, Jon Vanderfleet, Ben Kornegay, and Melissa Brewer. We are grateful to Craig Harms, Eric Anderson, and Betsy Stringer for Spot surgical guidance and advice and to Craig Sullivan, Andrew McGinty, and Mike Hopper (Pamlico Aquaculture Field Laboratory) for their assistance with and facility use for the Striped Bass experiment. We also thank Nate Bacheler and two anonymous reviewers for their thoughtful and critical reviews of this manuscript. Funding was provided by North Carolina Sea Grant (R/MRD-57 and R/10-HCE-1). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The North Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute.

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APPENDIX 1: MODEL OF SPOT LOSS RATES

Our model describes the decline over time of age-1 Spot within the study creeks based on two sources of information: (1) sonic-tagged fish that were monitored by using telemetry equipment and (2) untagged Spot that were monitored by trawling. For both groups, the total instantaneous rate of decline (Z'; loss rate for fish within the study creeks) is the sum of the rates for natural mortality (M) and emigration (E). We did not estimate M and E separately for the 2 years because of our limited sample size and the few inferred natural deaths. The rates M and E can be estimated separately with telemetry data, whereas only the combined total is estimable with trawl data. Based on movements of telemetered fish, we assumed that immigration of untagged Spot was negligible.

The number of telemetered Spot at risk in period i of year y ($R_{y,i}$) was equal to the number of newly released fish (those that had just completed the 7-d probationary period) plus a "virtual release" of fish at risk in period $i-1$ that survived to period i. Fish at risk during period $i-1$ had two other potential fates: death due to natural causes and emigration from the study area. The three potential fates for fish at risk were analyzed by using a multinomial distribution under the assumption that fate could be determined for all fish at risk. This is simpler than the model used by Hightower et al. (2001) because that study required the introduction of a detection probability since not all fish were detected on each occasion, thus resulting in unknown fates for some individuals.

The expected number of fish at risk at time $i-1$ that would be classified as alive at time i was

$$E[a_{y,i}] = R_{y,i-1}p_a,$$

where $p_a = \exp(-M - E)$. The expected number of fish that would be first relocated dead due to natural causes at time i was

$$E[m_{y,i}] = R_{y,i-1}p_m,$$

where $p_m = \frac{M}{(M+E)}[1 - \exp(-M - E)]$. The expected number of fish from release R_i that emigrated from the study creeks was

$$E[e_{y,i}] = R_{y,i-1}p_e,$$

where $p_e = \frac{E}{(M+E)}[1 - \exp(-M - E)]$. The likelihood for telemetry data (L_{tel}) was the product of multinomial distributions from the I releases (or virtual releases):

$$L_{tel} = \prod_{y=1}^{2}\prod_{i=2}^{I}\binom{R_{y,i-1}}{a_{y,i}, m_{y,i}, e_{y,i}} \times \left(p_a^{a_{y,i}}\, p_m^{m_{y,i}}\, p_e^{e_{y,i}}\right).$$

Trawl CPUE of age-1 Spot was assumed to decline exponentially due to combined losses from natural mortality and emigration. The catch in period i of year y was assumed to follow a Poisson distribution with expected value

$$\lambda_{y,i} = N_{0,y}\exp[-(M + E) \times i].$$

The likelihood (L_{CPUE}) is the product over the N_y observed CPUE values:

$$L_{CPUE} = \prod_{y=1}^{2}\prod_{i=1}^{N_y}\frac{e^{-\lambda_{y,i}}\lambda_{y,i}^{CPUE_{y,i}}}{CPUE_{y,i}!}.$$

The likelihoods estimated by using telemetry (L_{tel}) and CPUE (L_{CPUE}) data were assumed to be independent; therefore, model parameter estimates were obtained from the joint likelihood (product),

$$L = L_{tel}L_{CPUE}.$$

We used Bayesian methods and OpenBUGS software to estimate model parameters. An uninformative prior distribution for positive real values (gamma, mean = 1, variance = 100; McCarthy 2007) was used for E, M, and $N_{0,y}$, the intercepts (a nuisance parameter) for the exponential decay model. We excluded the first 1,000 samples (burn-in) to avoid any influence of the initial conditions; final estimates and posterior distributions were based on a minimum of 10,000 samples. The Gelman–Rubin statistic (R) was used to confirm convergence based on R-values less than 1.05 (McCarthy 2007; Lunn et al. 2009). The OpenBUGS code is available from the authors.

APPENDIX 2: FATES OF TAGGED SPOT

TABLE A.1. Assigned fates of age-1 Spot that received surgically implanted VEMCO V9-6L sonic transmitters (23 April–21 May 2009; 1–22 April 2010) and were released into Clubfoot and Hancock creeks. Fate assignments are emigration (EM), surgery-related mortality (SM), natural mortality (NM), end of battery life (BL), transmitter failure (TF), and predation. The first day at risk was 8 d postimplantation (i.e., immediately after the 7-d censorship period; see Methods). In all cases, the date of assigned fate occurred within the same year as fish release (i.e., 2009 or 2010). Gray shading indicates fish that were excluded from analyses due to SM, EM from the study site within 7 d postimplantation, predation-related mortality within 7 d postimplantation, or TF.

Transmitter number	Creek	First day at risk	Fate	Fate date	Number of days at risk	Weight (g)	FL (mm)
2009 releases and fates							
56185	Hancock	15 May	EM	17 May	3	76	163
56186	Clubfoot	N/A	SM	25 May	N/A	72	165
56187	Clubfoot	N/A	EM	24 May	N/A	88	173
56188	Hancock	30 Apr	EM	15 May	16	60	160
56189	Clubfoot	28 May	EM	2 Jun	6	89	177
56190	Clubfoot	28 May	EM	9 Jun	13	74	165
56191	Clubfoot	N/A	EM	23 May	N/A	74	167
56192	Clubfoot	N/A	EM	24 May	N/A	90	175
56193	Hancock	15 May	EM	23 May	9	64	154
56194	Clubfoot	28 May	EM	29 May	2	71	166
56195	Clubfoot	28 May	EM	31 May	4	55	150
56196	Hancock	N/A	EM	12 May	N/A	83	169
56198	Clubfoot	N/A	EM	27 May	N/A	70	160
56199	Hancock	N/A	EM	12 May	N/A	65	160
56200	Hancock	N/A	EM	14 May	N/A	74	164
56201	Hancock	15 May	EM	15 May	1	63	156
56202	Clubfoot	18 May	EM	23 May	6	79	163
56203	Hancock	15 May	EM	17 May	3	63	157
56204	Clubfoot	18 May	EM	30 May	13	60	155
56205	Hancock	N/A	EM	11 May	N/A	82	168
56206	Clubfoot	N/A	SM	6 May	N/A	57	155
56207	Hancock	N/A	EM	13 May	N/A	106	184
56208	Clubfoot	7 May	EM	15 Jun	40	59	157
56209	Clubfoot	N/A	EM	15 May	N/A	57	153
56210	Clubfoot	N/A	EM	15 May	N/A	68	160
56211	Clubfoot	19 May	EM	27 May	9	59	155
56212	Clubfoot	N/A	EM	24 May	N/A	96	177
56213	Clubfoot	8 May	EM	17 May	9	65	160
56214	Clubfoot	N/A	EM	4 May	N/A	51	151
56215	Hancock	3 May	EM	10 Jun	36	75	170
56216	Clubfoot	2 May	EM	3 May	2	53	150
56217	Hancock	30 Apr	EM	4 Jun	36	90	175
56218	Hancock	30 Apr	EM	17 May	18	74	168
56219	Clubfoot	18 May	EM	15 Jun	29	55	155
56220	Clubfoot	N/A	EM	3 May	N/A	58	153
56221	Hancock	15 May	EM	18 May	4	112	185
56222	Clubfoot	7 May	EM	13 May	7	74	171
56223	Hancock	30 Apr	EM	15 May	15	61	157
56224	Hancock	15 May	EM	11 Jun	28	65	160
56225	Hancock	30 Apr	EM	15 May	15	64	158
56226	Hancock	30 Apr	BL	13 Jul	75	46	146

(Continued on next page)

TABLE A.1. Continued.

Transmitter number	Creek	First day at risk	Fate	Fate date	Number of days at risk	Weight (g)	FL (mm)
56227	Hancock	30 Apr	EM	15 May	16	64	158
56228	Hancock	30 Apr	EM	10 May	11	61	160
56229	Hancock	15 May	EM	31 May	17	104	181
56230	Clubfoot	N/A	SM	2 May	N/A	53	150
56231	Hancock	N/A	EM	27 Apr	N/A	66	160
56232	Hancock	30 Apr	BL	13 Jul	75	64	162
56234	Hancock	N/A	EM	10 May	N/A	109	190
2010 releases and fates							
27725	Clubfoot	13 Apr	EM	29 Apr	17	56	156
27726	Hancock	N/A	SM	5 Apr	N/A	98	184
27727	Clubfoot	13 Apr	EM	1 May	19	63	159
27728	Clubfoot	14 Apr	EM	27 Apr	9	72	170
27729	Hancock	N/A	Predation	9 Apr	N/A	80	176
27730	Clubfoot	13 Apr	EM	24 Apr	12	62	163
27731	Hancock	12 Apr	EM	25 Apr	14	100	187
27732	Hancock	9 Apr	NM	15 Apr	7	56	155
27733	Hancock	12 Apr	EM	13 May	32	161	219
27734	Clubfoot	13 Apr	EM	16 May	34	68	161
27735	Clubfoot	14 Apr	EM	16 Apr	3	83	173
27736	Hancock	12 Apr	EM	26 Apr	15	174	225
27737	Clubfoot	N/A	EM	13 Apr	N/A	63	159
27738	Clubfoot	14 Apr	EM	23 May	40	112	193
27739	Hancock	19 Apr	EM	21 Apr	3	82	170
27740	Clubfoot	N/A	Predation	19 Apr	N/A	120	195
27741	Clubfoot	N/A	Predation	19 Apr	N/A	63	179
27742	Clubfoot	N/A	Predation	15 Apr	N/A	59	159
27743	Clubfoot	14 Apr	EM	25 Apr	12	83	175
27744	Clubfoot	14 Apr	EM	25 May	40	47	150
27745	Clubfoot	N/A	EM	12 Apr	N/A	86	174
27746	Clubfoot	14 Apr	EM	18 Apr	5	62	155
27747	Clubfoot	14 Apr	EM	14 Apr	1	70	164
27748	Clubfoot	14 Apr	NM	5 May	18	75	164
27749	Clubfoot	14 Apr	EM	7 May	24	59	156
27750	Clubfoot	N/A	Predation	17 Apr	N/A	115	197
27751	Clubfoot	14 Apr	EM	8 May	25	58	160
27752	Clubfoot	14 Apr	EM	16 May	33	58	152
27753	Clubfoot	14 Apr	EM	16 May	28	67	164
27754	Clubfoot	N/A	EM	13 Apr	N/A	58	153
27755	Clubfoot	N/A	SM	7 Apr	N/A	55	148
27756	Clubfoot	14 Apr	EM	21 Apr	8	123	198
27757	Clubfoot	N/A	TF	7 Apr	N/A	153	216
27758	Clubfoot	N/A	EM	12 Apr	N/A	70	161
27759	Clubfoot	14 Apr	EM	20 Apr	7	48	148
27760	Clubfoot	14 Apr	EM	6 May	23	63	155
27761	Clubfoot	14 Apr	EM	2 May	19	55	152
27762	Clubfoot	14 Apr	EM	23 May	39	72	166
27763	Clubfoot	N/A	SM	7 Apr	N/A	63	158
27764	Clubfoot	14 Apr	EM	17 May	34	82	175

TABLE A.1. Continued.

Transmitter number	Creek	First day at risk	Fate	Fate date	Number of days at risk	Weight (g)	FL (mm)
27765	Hancock	19 Apr	EM	4 May	16	56	154
27766	Hancock	N/A	EM	13 Apr	N/A	60	158
27767	Hancock	20 Apr	EM	18 Jun	60	53	149
27768	Clubfoot	21 Apr	EM	23 May	33	50	145
27769	Hancock	N/A	TF	15 Apr	N/A	59	150
27770	Hancock	26 Apr	EM	26 Apr	1	97	173
27771	Clubfoot	N/A	EM	17 Apr	N/A	66	162
27772	Clubfoot	21 Apr	EM	13 May	23	97	175
27773	Hancock	22 Apr	EM	26 Apr	5	82	167
27774	Hancock	N/A	Predation	27 Apr	N/A	47	145
27775	Clubfoot	21 Apr	EM	22 Apr	2	56	152
27776	Clubfoot	21 Apr	EM	1 May	11	103	183
27777	Hancock	23 Apr	EM	46 Apr	4	62	155
27778	Hancock	26 Apr	EM	27 May	32	74	165
27779	Hancock	22 Apr	EM	22 May	31	127	193
27780	Hancock	N/A	SM	19 Apr	N/A	53	148
27781	Hancock	22 Apr	EM	5 May	14	116	190
27782	Hancock	N/A	SM	15 Apr	N/A	56	150
27783	Hancock	N/A	SM	15 Apr	N/A	52	145
27784	Hancock	26 Apr	EM	26 Apr	1	111	185
27785	Hancock	29 Apr	EM	30 Apr	2	102	178
27786	Hancock	29 Apr	NM	11 Jun	41	74	163
27787	Hancock	26 Apr	EM	8 May	13	101	178
27788	Hancock	26 Apr	EM	1 Jun	37	109	187
27789	Hancock	27 Apr	EM	7 May	11	85	163
27790	Hancock	29 Apr	EM	8 May	10	83	169
27791	Hancock	N/A	EM	25 Apr	N/A	123	192
27792	Hancock	26 Apr	EM	8 May	13	60	150
27793	Hancock	N/A	SM	19 Apr	N/A	48	142
27794	Hancock	26 Apr	NM	3 May	8	99	172
27795	Hancock	N/A	EM	25 Apr	N/A	101	181
27796	Hancock	29 Apr	EM	28 May	30	83	166
27797	Hancock	26 Apr	EM	20 May	25	107	180
27798	Hancock	29 Apr	EM	12 May	14	70	159
27799	Hancock	29 Apr	EM	16 May	18	48	143