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Using Acoustic Telemetry to Estimate Weakfish Survival Rates along the U.S. East Coast

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Abstract
The Weakfish *Cynoscion regalis*, an economically important species, has declined over the last 30 years, corresponding with an increase in total mortality according to the most recent stock assessment. We estimated estuarine-specific and coastwide apparent survival of Weakfish by using a Cormack–Jolly–Seber model to provide insights into the spatiotemporal component of mortality. Telemetered Weakfish ($n = 342$) were released across five estuaries ranging from North Carolina to New Jersey between 2006 and 2016. In estuaries from Delaware Bay and northward, egress peaked around the third week of September; in North Carolina, egress peaked by the first week of November. For three estuaries with adequate sample sizes, apparent survival estimates were similar and a joint model including all telemetered Weakfish estimated an extremely low annual apparent survival rate of 0.001 (95% credible interval [CrI] = 0.002–0.0003) or annual apparent instantaneous total mortality of 7.25 (95% CrI = 6.28–8.05). At a minimum, 61% of telemetered Weakfish emigrated in the fall, but only 2 of 149 fish with long-lived transmitters were detected as returning to estuaries the following year. This is a small proportion for a fish that exhibits spawning site fidelity. We conclude that the disappearance of telemetered Weakfish represents mortality that occurs between emigration and the spring spawning period, potentially during overwinter periods on the continental shelf. Our study provides insights into the magnitude, timing, and location of Weakfish loss and facilitates an improved understanding of Weakfish population dynamics for use in stock rebuilding.

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The utilization of acoustic telemetry has proliferated, with most applications investigating fish behavior, physiology, movement, and habitat selection (Hussey et al. 2015). A lesser-utilized application of acoustic telemetry is the estimation of fish mortality (Hightower and Harris 2017). Traditional stock assessments often require estimates or assumptions about mortality rates to approximate stock size and biological reference points (Cadrin and Dickey-Collas 2015; Punt et al. 2015). Hence, comparing stock assessment model mortality input (i.e., natural mortality [M]) and outputs (i.e., fishing mortality and total mortality [Z]) with estimates from acoustic telemetry allows for an independent comparison of mortality rates. In addition, acoustic telemetry offers insights into the location and timing of mortality, since telemetry mortality can be on any time scale and matched with seasonal stock locations, whereas most traditional stock assessments lack the enhanced spatiotemporal resolution.

Telemetry mortality estimates have been generated across multiple fish species by using passive arrays in lakes, rivers, estuaries, and artificial reefs (e.g., Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Welch et al. 2009; Stich et al. 2015; Williams-Grove and Szedlmayer 2016). With advances in technology and the advent of cooperative telemetry networks, such as the Ocean Tracking Network and the Atlantic Cooperative Telemetry Network, estimates of survival can now be expanded to include an entire fish stock over broad geographic ranges (Lindley et al. 2008; Rudd et al. 2014; Hightower et al. 2015). For instance, Hightower et al. (2015) estimated survival of the Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, an anadromous fish, from four riverine substocks by using detections from riverine and marine acoustic arrays across the U.S. East Coast. Those authors used a Cormack–Jolly–Seber (CJS) model, which is an open capture–recapture model that estimates detection probability and apparent survival. The multiple arrays in cooperative telemetry networks from Florida to Maine allowed the study to encompass the entire range of the Atlantic Sturgeon substocks, where emigrations into areas without receivers were temporary, and apparent survival estimates approximated true survival. In the present study, we applied CJS modeling to telemetry detections for the Weakfish *Cynoscion regalis*, a migratory marine fish that spawns in estuaries along the U.S. East Coast.

Historically, Weakfish supported a vibrant commercial and recreational fishery at the height of its spawning stock biomass in the 1980s (ASMFC 2016). The spawning stock biomass has since declined to record lows in 2008, with no appreciable recovery thereafter despite management efforts through continually reduced harvest, culminating in the 2010 regulation of a recreational one-fish (>305 mm) daily bag limit and a commercial 45-kg bycatch trip limit. The lack of stock recovery was somewhat surprising since the stock has the capacity to rebuild quickly: Weakfish can be sexually mature at age 0 or fully mature by about 230 mm TL (Merriner 1976; Shepherd and Grimes 1984; Nye et al. 2008). Females spawn multiple times per season, and batch fecundity ranges from 45,000 eggs for age-0 females to 1,726,000 eggs at age 4 (Merriner 1976; Nye et al. 2008). The reduced harvest combined with the lack of rebuilding prompted management to hypothesize that M has increased in recent years (NEFSC 2009). In the latest stock assessment time series from 1982 to 2014, the Bayesian statistical catch-at-age model estimated a time-varying M that increased through the time series to a high of 0.95 in 2008, with Z matching the increasing trends to a record high of 3.46 in 2007 (ASMFC 2016). However, these mortality estimates, especially M, contain uncertainty since they are not based on directed field studies (ASMFC 2016). Therefore, reliable estimates of survival, along with their spatial and temporal variability, are important for understanding the lack of rebuilding in the Weakfish stock.

The bulk of the Weakfish population ranges from New York to North Carolina (Mercer 1989). Weakfish of all ages (longevity is 17 years; Lowerre-Barbieri et al. 1995) migrate southward and/or offshore to overwinter on the continental shelf and then return northward and/or to estuaries and the nearshore areas around inlets to spawn the following spring (Nesbit 1954; Bigelow et al. 2002; Mann and Grothues 2009). A large percentage of fish show natal homing (Nesbit 1954; Thorrold et al. 2001). After spawning, Weakfish may move out of estuaries, possibly to the inner continental shelf, or they reside in estuaries until their fall emigration (Shepherd and Grimes 1984; Turnure et al. 2015a, 2015b). Robust estimates of long-term survival from telemetry-tagged Weakfish should be possible given their annual spawning migration into U.S. East Coast estuaries, many of which have receiver arrays.

Here, we estimate estuarine-specific and coastwide apparent survival of Weakfish by using telemetry data from prior studies in two New Jersey estuaries (Manderson et al. 2014; Turnure et al. 2015a, 2015b) and more recent telemetry data collected from North Carolina and Delaware Bay by North Carolina State University (NCSU). Combined, these studies cover the bulk of the distributional range of Weakfish and the time period (2004–2016) during Weakfish population decline. In addition, many predators of Weakfish, such as the common bottlenose dolphin *Tursiops truncatus* and Striped Bass *Morone saxatilis*, have increased in population during the Weakfish decline and spatiotemporally overlap with Weakfish on their overwintering grounds (Krause 2019). We hypothesize that apparent survival will be low given the current age structure (predominately ages 0–4) from the most recent Weakfish stock assessment (ASMFC

2016) and will be seasonally lowest in winter given the likely impact of predation (Krause 2019).

METHODS

Telemetered Weakfish were released in five estuaries from New Jersey to North Carolina (Figure 1). For detailed methods, refer to Manderson et al. (2014) for the Navesink River, New Jersey, and Turnure et al. (2015a, 2015b) for Great Bay, New Jersey. Array placement and estuarine site descriptions for Delaware Bay are provided by Kilfoil et al. (2017), those for the New River of North Carolina are provided by Scheffel et al. (2020), and those across multiple receiver arrays deployed from Florida to Maine are provided by research groups participating in the Atlantic Cooperative Telemetry Network Web site based at Delaware State University (www.theactnetwork.com). Our methods are primarily focused on NCSU-telemetered Weakfish in Delaware Bay, the New River, and Bogue Sound, and any major methodological differences between NCSU efforts and the Navesink River and Great Bay studies are highlighted (Table 1).

Telemetry study site.— Bogue Sound Weakfish were passively tracked in the waters surrounding Beaufort Inlet, North Carolina (Figure 2). Depths were generally less than 3 m in the lagoonal Bogue Sound and Back Sound and the partially mixed estuary of the Newport River. Depth increased to 4–7 m in navigable channels and up to 12–16 m in the dredged shipping channel leading from Beaufort Inlet to the Morehead City port. The study area was dominated by tidal inflow polyhaline conditions given its proximity to Beaufort Inlet (Logan et al. 2000). Commercial fishing is prohibited in the vicinity of the port and therefore was primarily conducted on the ocean side of the barrier islands. The recreational fishery frequented the port and surrounding structure, such as bridges.

The waters surrounding Beaufort Inlet were selected for this study because they offered excellent accessibility to

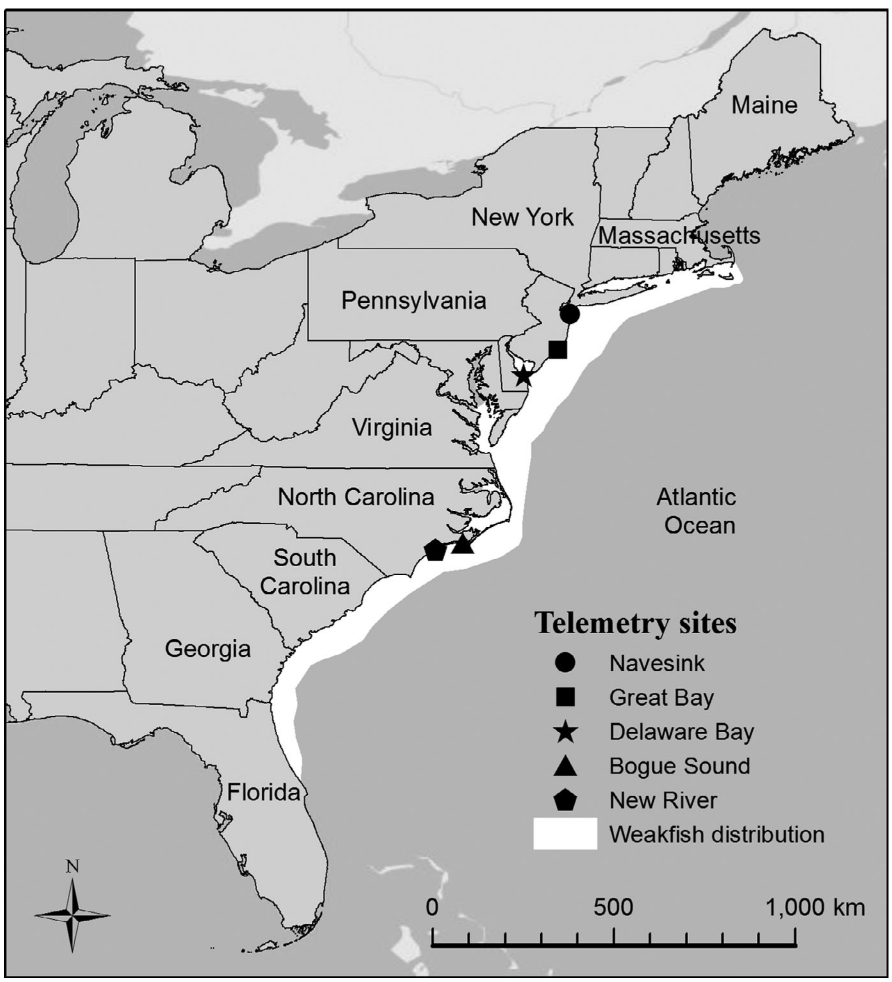

FIGURE 1. Telemetry release locations for Weakfish ($n = 342$) from three studies across the years 2006–2018. The Weakfish distribution ranges from Cape Canaveral, Florida, to Cape Cod, Massachusetts.

TABLE 1. Summary of telemetry study results for Weakfish, including the estuary (the Navesink River and Great Bay, New Jersey; Delaware Bay, New Jersey–Delaware; and the New River and Bogue Sound, North Carolina), year, sample size, first and last dates of release, minimum battery life of tags, median TL (with range in parentheses), median raw detections per telemetered fish (with range), total raw detections, false detections, and median number of detection days (with range). Blank cells indicate that the data were not ascertainable.

Location	Year	Sample size	Release date	Battery life (d)	Median TL (mm; range)	Median detections (range)	Total detections[a]	False detections[b]	Median days (range)[c]
Navesink River	2006	15	Jul 13–Aug 16	110	337 (224–535)	4,040 (41–16,568)	76,056		33 (4–64)
	2007	26	Jun 29–Oct 9	110	389 (304–500)	1,708 (31–11,391)	143,657		47 (6–88)
Great Bay	2007	26	Apr 30–Aug 31	229; 327; 627; 719	431 (292–864)[d]	242 (0–49,892)	71,986[e]		9 (0–101)
	2008	33	Jun 11–Sep 11	229; 438; 719	401 (273–591)[d]	142 (0–38,283)	98,681[f]		27 (0–364)
New River	2014	13	Jun 2–Oct 28	184	342 (314–417)	2,066 (50–126,950)	182,846	6	5 (1–39)
Delaware Bay	2015	18	Aug 24–Sep 17	513	318 (301–345)	36 (0–319)	1,065		14 (2–37)
Bogue Sound	2015	92	Sep 28–Oct 26	169; 184; 513	361 (312–436)	1,996 (2–51,035)	589,162	115	47 (1–192)
	2016	60	Mar 30–Apr 22	513	370 (315–485)	1,337 (8–22,072)	136,929	82	22 (1–269)
	2016	59	Sep 22–28	513	350 (317–474)	5,089 (122–140,268)	857,844	114	38 (0–136)
Total	2006–2016	342	Mar 30–Oct 26	110–719	361 (224–864)	1,996 (0–140,268)	1,987,559	317	33 (0–269)

[a]Includes false detections and the detections of fish deemed as deaths but does not include the control tag (released in fall 2016).
[b]Based on the False Detection Analyzer default setting in VEMCO VUE software.
[c]Number of days detected after altering capture histories for dead fish.
[d]Mean does not include censored fish in the "death within 7 d" category (3 fish in 2007 and 4 fish in 2008; see Table 2).
[e]Total includes 25 active detections.
[f]Total includes 118 active detections.

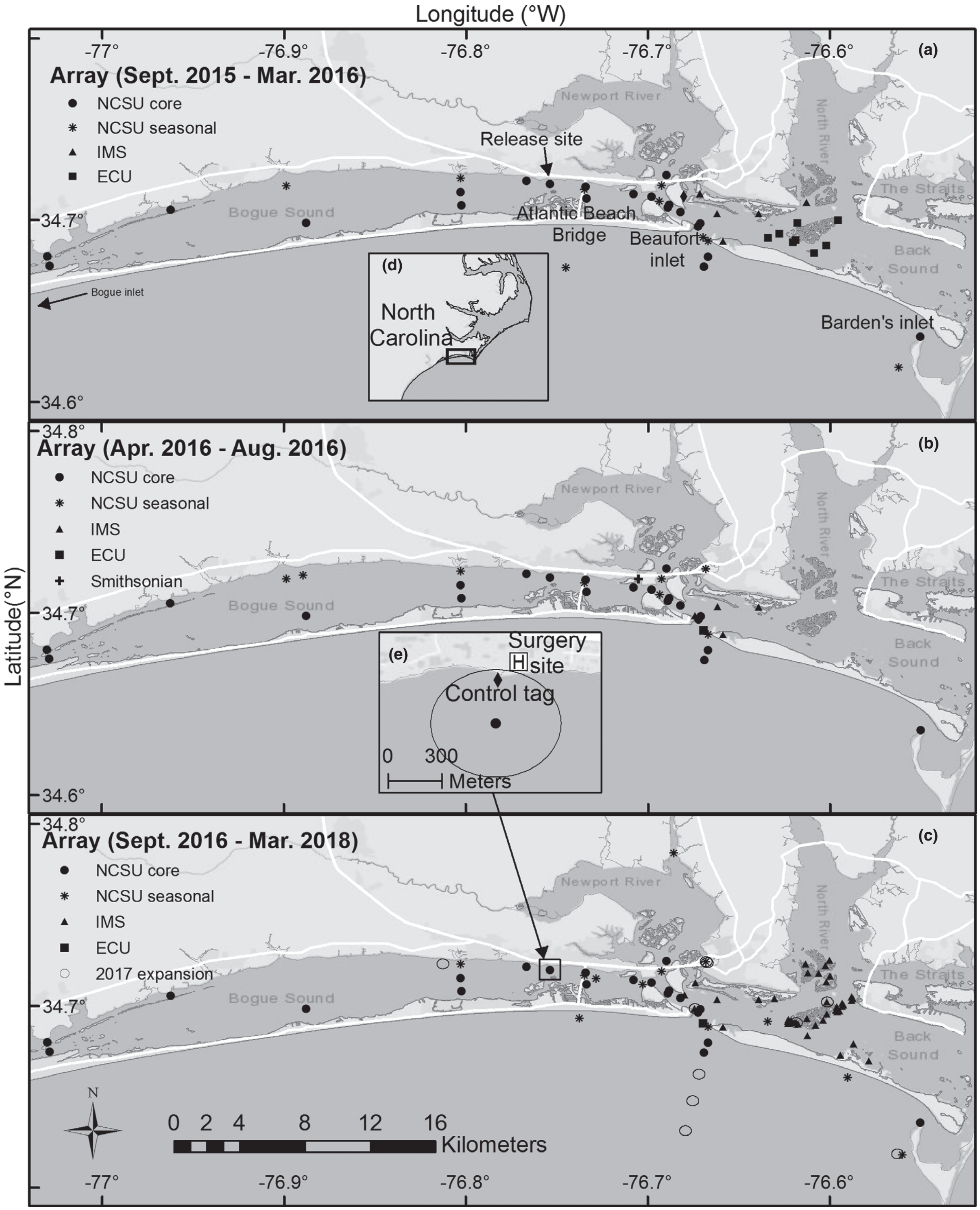

FIGURE 2. Bogue Sound array from September 2015 to March 2018, consisting of a variable receiver array deployed by North Carolina State University (NCSU), the University of North Carolina–Chapel Hill's Institute of Marine Sciences (IMS), East Carolina University (ECU), and the Smithsonian Environmental Research Center. The NCSU core locations were present from the first release of telemetered Weakfish until the last transmitter expired. Telemetered Weakfish were detected in **(A)** a 43-receiver array from September 2015 to March 2016, **(B)** a 35-receiver array from April to August 2016, and **(C)** a 76-receiver array during fall 2016 that expanded to 87 receivers in 2017 (the 2017 additions are represented with open circles drawn to scale with a 300-m radius; an average detection distance for all receivers). **(D)** Boxed inset depicts the location of Bogue Sound on the North Carolina coast. **(E)** Inset shows the surgery site and the control tag location within the 300-m range of a receiver.

migrating Weakfish, allowing for a series of collaborative acoustic arrays to provide extensive spatial coverage (Figure 2). In total, 22 core receivers were in place from the release of the first transmitters in September 2015 to the battery expiration of the last transmitters in late February 2018 (Figure 2). Additional receivers varied spatially and temporally, with the initial receiver array consisting of 43 receivers in fall 2015 (Figure 2A), of which eight were maintained by East Carolina University and retrieved in mid-November 2015 for a congruent study (Bangley 2016). In spring 2016, the array decreased to 36 receivers, of which a single receiver was briefly maintained by a citizen science project supervised by the Smithsonian Environmental Research Center and provided Weakfish detections during a 2-d period (Figure 2B). During fall 2016, a collaboration with researchers at the Institute of Marine Sciences (IMS), University of North Carolina–Chapel Hill, expanded the array to 76 receivers (Figure 2C). The number of receivers reached a maximum of 87 in mid-2017 and then fell to and remained at 37 until the last transmitter expired on February 25, 2018, after IMS researchers retrieved their receivers in fall 2017 (Figure 2C). Overall, 12 receivers were lost (2 in fall 2015; 2 in spring 2016; 1 in fall 2016; 7 in 2017), and an additional receiver was broken. Receivers were retrieved for approximately 1 week each summer for maintenance. The variable detection range of receivers in highly dynamic locations (e.g., current, tide, boat traffic, and wave-prone areas) rendered the testing of receiver range impractical and was not a requirement of our model assumptions. At the transmitter fish release site (Figure 2C), a control tag was placed within detection range of a receiver to provide additional information on possible transmitter expulsions, surgery-related mortalities, and seasonal detection patterns.

Transmitter implantation.— In Bogue Sound, Weakfish were captured by using hook and line within 1.61 km (1 mile) of the Atlantic Beach Bridge during fall 2015, spring 2016, and fall 2016 (Figure 2A). Healthy individuals larger than 305 mm were transported in a 378-L container to circular, flow-through, 1,500-L holding tanks inside the IMS. In total, 211 uniquely coded ultrasonic transmitters (VEMCO Model V13-1H; 13 × 36 mm, ~10.5 g in air, 69-kHz frequency; VEMCO, Bedford, Nova Scotia) were deployed in Bogue Sound; 80 of the 211 transmitters had 30–90-s random transmission rates and a typical battery life of approximately 184 d, and 131 of the transmitters had 50–130-s random transmission rates with a battery life of about 513 d. The surgical methodology followed the guidelines outlined by Wagner et al. (2011) but were tailored specifically for Weakfish with the assistance of staff from the NCSU College of Veterinary Medicine (e.g., Harms and Lewbart 2011). Individual Weakfish were anesthetized in a 40-mg/L solution of Aqui-S in seawater (active ingredient proportion = 50% isoeugenol; Aqui-S New Zealand, Ltd., Lower Hutt, New Zealand) until unresponsive to the touch while still gilling (~2 min). Each fish was measured (TL, mm) and weighed (wet weight, g), and a transmitter was implanted in the abdominal cavity. During the surgery, a continuous flow of Aqui-S at 20 mg/L was pumped over the gills to maintain sedation. The incision was closed with two to four simple interrupted sutures (PDS II synthetic absorbable suture in 3-0 thread size, with FS-1 reverse cutting needle; Ethicon Endo-Surgery, Inc., Cincinnati, Ohio), and the fish was allowed to recover (i.e., re-establish equilibrium and exhibit normal swimming behavior) before release.

All New River Weakfish had transmitters with the 30–90-s random transmission rate, whereas all Delaware Bay Weakfish had transmitters with the 50–130-s random transmission rate. New River Weakfish were captured by using hook and line or a strike-net method—an approach outlined by Bacheler et al. (2009), with the singular difference being the use of a 183-m gill net with 76-mm stretch mesh. Delaware Bay fish were captured using hook and line or beach seining (27- × 1.8-m seine with 25-mm mesh). New River Weakfish were tracked with a 76-receiver array in 2014 (Scheffel et al. 2020), and Delaware Bay Weakfish were tracked with an approximately 54-receiver array (Kilfoil et al. 2017). Of all NCSU-released fish, only 12 New River Weakfish were tagged with a single, 63.5-mm-long, wire-core internal anchor tag (FM-95W; Floy Tag and Manufacturing, Inc., Seattle). The anchor tags were red in color and stated "CUT TAG $100 REWARD"; each tag bore a unique tag number preceded by "NC" and a toll-free phone number. All NCSU fish were subjected to the aforementioned surgery protocol and had an average anesthetization time of 1 min, 59 s (SD = 48 s); surgery time of 7 min, 31 s (SD = 2 min, 17 s); and recovery time of 4 min, 43 s (SD = 2 min, 12 s). Lastly, all Weakfish were released within 24 h from the time of capture and within 2 km of their original capture site.

Age-1 and older Navesink River Weakfish (>224 TL mm) were captured by using hook and line and were transported to the James J. Howard Marine Sciences Laboratory (Highlands, New Jersey) for surgery. Each Weakfish was anesthetized with Aqui-S (Aqui-S New Zealand) at a concentration of 54 mg/L; a uniquely coded ultrasonic transmitter (VEMCO Model V9-6L; 9 × 20 mm, ~2 g in water, 69-kHz frequency, 40–120-s random transmission rate) was implanted in each fish, and a unique anchor tag was inserted in the dorsal musculature. Fish were released at randomly selected Navesink River locations within 8 d of their initial capture and were tracked with 27 receivers in 2006 and 33 receivers in 2007.

Reproductively mature Great Bay Weakfish (>230 mm TL) were captured by using hook and line; the exception was one individual that was caught in a stationary multimesh gill net (Turnure et al. 2015b). Weakfish were anesthetized with tricaine methanesulfonate (MS-222) in ambient seawater at 0.05 g/L and were implanted with single-frequency Lotek acoustic transmitters (CAFT and MS series; 8.4–39.3 g, 5-s burst rate, maximum battery life = 229–719 d; Lotek Wireless, Inc., St. John's, Newfoundland, Canada); the transmitters could only be detected with Lotek proprietary equipment. Fish were tracked with a gated array of six to nine wireless hydrophones (WHS-1100; Lotek) as well as manually. Each fish was released within 100 m of its original capture location and within 0–6 d of initial capture. A high-visibility external T-bar tag (Floy) was inserted between the first and second pterygiophores of the spiny dorsal fin to visually identify acoustically tagged fish.

Fates.— Two independent readers analyzed Weakfish movement patterns and then assigned death and temporary emigration fates via consensus by analyzing average hourly movements within the estuary, speeds of transmitter movement, and detection patterns at receivers for each fish (Table 2). Although the CJS model is not a fates-based analysis, it does require information on known-live fish and consequently the fates of detected dead fish. The emigration fate provided insight into the temporal variation in survival estimates. In most cases, the fate of "death" was assigned if Weakfish had continuous detections at the same receiver for multiple months; such fish were subcategorized as "cause unknown" deaths, which included natural mortality, catch-and-release mortality, transmitter expulsion, or surgery mortality. For some, a "predation" death was assigned if the fish exhibited erratic behavior, bypassed multiple receiver lines, and often registered maximum speeds greater than 4 km/h during these periods. Weakfish are important prey for common bottlenose dolphins (Gannon and Waples 2004), whose speeds are greater than 4 km/h (Bacheler et al. 2009), making probable the assumption of death by predation. Lastly, a "harvested" death was assigned to Weakfish that were harvested and reported by anglers. A death date was assigned to a Weakfish for the day previous to its activity cessation, the day of observed predation behavior, or the day of harvest. In the Navesink River, Weakfish that were detected alive at the dates of array retrieval on October 3, 2006, and October 31, 2007, were characterized as "alive in system." A proportion of fish were released and "never detected," and these individuals were censored from further analyses. For others, we felt confident in assigning them as a temporary "emigration" with an estuarine egress date, as their movements were detected within the estuary and were last detected at an estuarine inlet or ocean receiver. For fish that were last detected alive in the middle of the estuarine array, their classification under "disappeared in array" included unreported harvests, undetected emigrations, or undetected deaths.

Cormack–Jolly–Seber model.— We analyzed data separately for each estuary to detect spatial variation in survival, and we produced a pooled survival estimate for sexually mature Weakfish (>224 mm TL; Nye et al. 2008). Each analysis was based on a capture history (CH) with rows for individual fish and columns for time in days. The matrix contained a "1" if one or more detections occurred for the selected date and contained a "2" to indicate a lack of detections. Because Weakfish had a staggered entry into the model, time periods in which a fish was not yet released or was unavailable to the model (i.e., the battery had expired) received a "0." The "0" allowed for the creation of a first and last vector that specified the periods during which an individual fish was available to the model. All Weakfish were assigned to the same year based on the actual day of release to allow for identification of seasonal patterns, and all were assumed to be alive on the day of release. To minimize concerns about mortality due to capture, handling, and tag implantation, the analysis period for each individual started 1 week after tagging, and fish were censored from the analysis if they were not detected alive after 7 d (Table 2). Weakfish that were detected alive after the probationary period were assumed alive when they first entered the model, and they received a "1" on day 8 regardless of an actual detection. All CHs were constructed using the library EasyMARK in R (Waller 2014; R Core Team 2019). The daily CHs were then condensed into a weekly time frame for estuarine survival models and into a monthly time frame for the pooled model. The period of analysis ranged from the first time a Weakfish was released until the last battery expired or when an array was retrieved. The analysis time period was 17 weeks for the Navesink River (June–October of year 1), 120 weeks for Great Bay (April of year 1 to November of year 3), 101 weeks for Bogue Sound (March of year 1 to February of year 3), and 28 months for the pooled estimate (April of year 1 to July of year 3).

Capture histories were analyzed using a multistate CJS model modified from Hightower et al. (2015), which estimates apparent survival (φ) and detection probability (p; Kéry and Schaub 2012). The multistate model distinguished between the true states of "alive" and "dead" based on observations of our CHs. We implemented the model using a Bayesian modeling framework through OpenBUGS software in R (Spiegelhalter et al. 2007; R Core Team 2019), in which individual Weakfish were treated as the unit of observation (Otis and White 1999). Preliminary modeling indicated variability in φ and p among time periods. Because we were specifically interested in seasonal patterns of survival, we modeled time-dependent φ as a fixed-effect factor and p as a random-effect factor on the logit scale. Following Kéry and Schaub (2012), we used uninformative prior distributions

TABLE 2. Detected emigrations and fates for telemetered Weakfish (censored from the model [censored fish] or included in the model [model fish]) across multiple estuaries (the Navesink River and Great Bay, New Jersey; Delaware Bay, New Jersey–Delaware; and the New River and Bogue Sound, North Carolina). Censored fish included those that (1) temporarily emigrated or died within 7 d, (2) were never detected, or (3) were never detected alive after 7 d. Model fish included those that (1) were alive in system until the receiver array was pulled; (2) exhibited temporary emigration after 7 d; (3) died due to predation, harvest, or an unknown cause; or (4) disappeared in the receiver array. For the Cormack–Jolly–Seber analysis, the capture histories of model fish within the death categories were altered to meet the assumption that all detections were from live animals.

	Navesink River		Great Bay		New River	Delaware Bay	Bogue Sound			
Variable or fate	2006	2007	2007	2008	2014	2015	Fall 2015	Spring 2016	Fall 2016	Total 2006–2016
Number released	15	26	26	33	13	18	92	60	59	342
Censored fish										
Emigration within 7 d		1	2	1	5	1	5	2		17
Death within 7 d			3	4			2	4	2	15
Predation								1		1
Cause unknown			3	4			2	3	2[c]	14
Not detected alive after 7 d			2	1	2[a]	3	1	1		10
Never detected			3	6	1	6				16
Total		1	10	12	8	10	8	7	2	58
Model fish										
Alive in system	1	4								5
Emigration after 7 d	9	9	13	18	4	4	40	42	33	172
Death after 7 d	1		2		1		18	5	19	46
Predation							1	2	9	12
Harvested			2				3[b]			5
Cause unknown	1				1		14	3	10	29
Disappeared in array	4	12	1	3		4	26	6	5	61
Total	15	25	16	21	5	8	84	53	57	284

[a]A single fish was confirmed dead through active telemetry.
[b]Two fish were harvested by recreational fisherman, and one fish was recaptured and gut-hooked by researchers.
[c]One "cause unknown" death was a tag expulsion because the fish was recaptured with an incision wound but no transmitter.

to estimate φ (uniform, 0–1) and p, with the latter being the logit-transformed sum of $\mu + \varepsilon_t$ ($\text{logit}^{-1}[\mu]$, uniform, 0–1; ε_t, normal, mean = 0, SD = uniform, 0–10). Low sample size ($n < 10$) precluded us from running analyses by year for each estuary and for Delaware Bay and New River Weakfish, as preliminary model estimates of uncertainty surrounding survival were biologically meaningless (ranged from ~0 to 1). For similar precision reasons, estimates were only shown when at least 10 fish were at risk or considered alive by the model. We explored different time intervals in preliminary modeling and found that weekly intervals among estuaries and monthly intervals pooled across estuaries allowed for biologically relevant insights.

Model assumptions.— The assumptions of the model are outlined below.

1. Survival rates are equal for all telemetered Weakfish, as tagged fish across all study sites had a relatively narrow size range (Table 1).
2. The probability of transmitter failure or expulsion is negligible. Although VEMCO transmitter failure has been reported or assumed (Dresser and Kneib 2007; Friedl et al. 2013), the majority of studies have reported no transmitter failures (e.g., Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Ellis et al. 2017). All NCSU transmitters passed a functionality test prior to implantation, of which three working transmitters were returned by anglers and five transmitters were recovered from Weakfish that were recaptured and subsequently released by researchers; furthermore, detections from our control tag until the end of its 513-d battery life suggested negligible transmitter failure. Manderson et al. (2014) implanted replica V-9 transmitters into Weakfish ($n > 12$) and did not witness any transmitter expulsion during an observation period of over 120 d. In one instance, NCSU researchers captured a Weakfish bearing surgery scars without sutures approximately 7 d after release;

however, necropsy did not reveal a transmitter. Based on scar tissue healing, the veterinarian performing the necropsy believed that transmitter expulsion occurred within 4 d of initial release, with the most likely cause being suture discharge due to incising through thin anchor muscle and skin, incision dehiscence, and ultimately transmitter expulsion (Craig Harms, North Carolina State University, personal communication). We assumed that transmitter expulsion was negligible after the 7-d probationary period, as many Weakfish were detected alive for many weeks after release, the single known transmitter expulsion occurred shortly after surgery, and there was no evidence of transintestinal expulsion based on tank holding studies (Marty and Summerfelt 1986; Manderson et al. 2014).

3. Tagging mortality is negligible. The aforementioned tank holding experiment by Manderson et al. (2014) demonstrated 100% survival of fish with transmitters. Field results from Turnure et al. (2015a, 2015b) indicated that 7 of 59 Weakfish ceased to move within 7 d of release, whereas 6 of 211 Weakfish from Bogue Sound (NCSU-tagged fish) likewise ceased to move in the same time period, suggesting possible surgery mortality or transmitter expulsion (Table 2). To meet the assumption of negligible tagging mortality, we implemented the 7-d probationary period.
4. All detections are classified without error. Because Weakfish were released by NCSU in Bogue Sound and the New River during relatively short time periods and often congregated on structure (e.g., bridges), the probability of false detections increased. All false detections, as indicated by the default settings of the VEMCO VUE False Detection Analyzer, were removed from the analysis ($n = 317$; Table 1). For Weakfish released in the Navesink River and Delaware Bay, we did not have the data to run the False Detection Analyzer, but we assumed negligible false detections based on the gradual release of fish across multiple locations. For Weakfish in Great Bay, where Lotek equipment was used, the detections were cleaned post hoc by using a temporal filter (contacts per interval; Grothues et al. 2005). All detections need to come from living fish; thus, for any fish that survived the probationary period but died from "predation" or an "unknown cause," the detections after the death date were changed to nondetections (from 1 to 2 in the CH). All harvested fish (i.e., whose transmitters were returned and inserted into new fish) were coded as "2" from the date of harvest until the battery expiration.
5. Bias in estimated survival due to the timing of tagging or detections is negligible, given the short interval (weekly or monthly) for detection relative to the period of analysis (17 weeks, 101 weeks, 120 weeks, or 28 months). Although most fish egressed within 3 months, the detection probabilities (p) were high during those time periods, minimizing the timing bias in weekly and monthly estimates.
6. The fate of a tagged fish is independent of the fates of other tagged fish. The assumption may be violated because Weakfish aggregate on structure (i.e., bridges or deep holes) during the spring and fall for long periods of time (>1 month), but the extent of aggregation is not known. We often released Weakfish during relatively short time periods (89 of 92 Weakfish from Bogue Sound were released during a 24-h period in fall 2015) and found that while many resided by structure with other transmitter-tagged fish, just as many moved to other estuary locations or emigrated within days of release. Violations of this assumption lowers precision but does not cause bias (Pollock et al. 2004).
7. There is no permanent emigration out of the study area. With the development of cooperative telemetry networks, the sampled area consisted of the entire range of Weakfish.

RESULTS

In total, 342 telemetered Weakfish were released during 2006–2016, with sample sizes differing by estuary (Table 1), and the median size was 361 mm TL across all studies (range = 224–864 mm TL; Table 1). Overall, 178 long-lived transmitters contained batteries lasting greater than 300 d, of which 11 were released in 2007 and 18 were released in 2008 within Great Bay by Rutgers. For NCSU-released Weakfish in Delaware Bay, all 18 transmitters were long-lived; in Bogue Sound, 12 long-lived transmitters were released in fall 2015, 60 were released in spring 2016, and 59 were released in fall 2016 (Table 1). Weakfish were detected 1,987,559 times across all studies, varying by estuary and temporal release (Table 1). Of the total detections, 158 were provided by the Smithsonian Environmental Research Center from within the Bogue Sound array (Figure 2B); no other detections were provided by cooperative telemetry networks. The majority of detections occurred between spring and fall, with a few fish apparently overwintering in Bogue Sound (Figure 3), although only two individuals released with long-lived transmitters were detected after their overwintering period in the following spring and fall (Figure 3). The daily detections of the control transmitter indicated a seasonal difference, with the highest number of detections occurring during winter and the lowest number occurring in summer (Figure 4A), and the number of false detections increased with an increasing number of transmitters present in a given area (Figure 4B).

The fates of fish varied by estuary and season (Table 2). Overall, 58 fish were censored from the analysis: 17

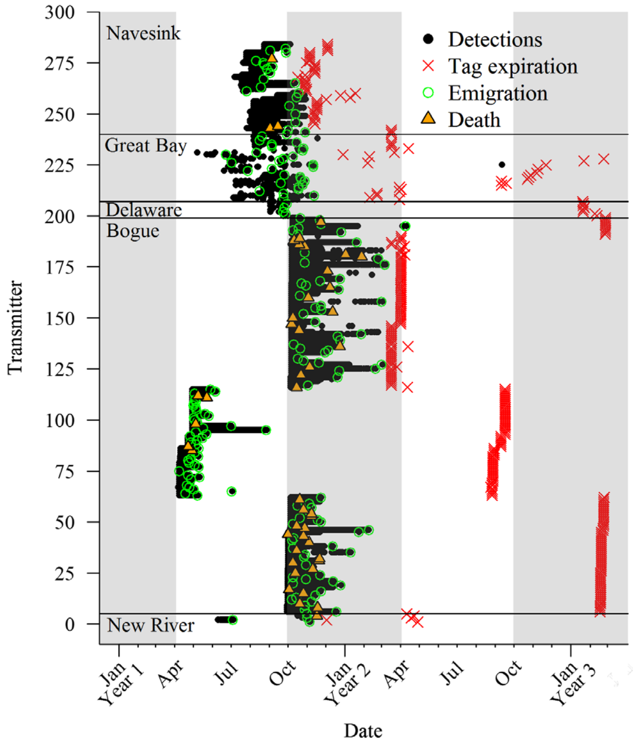

FIGURE 3. Abacus plot of daily Weakfish detections across five estuaries arranged from north to south and by release date across 3 years within each estuary (the Navesink River, Great Bay, Delaware Bay, Bogue Sound, and the New River). The red ×-symbols indicate when the transmitter was assumed to have expired, green circles represent the date of emigration, orange triangles denote deaths, and gray shading indicates the Weakfish overwintering time period (from October 1 to the end of March). For the Navesink River, the array was pulled in October before batteries expired.

emigrated within 7 d of release, and the remaining 41 died or were not detected after the probationary period (Table 2). Overall, 284 Weakfish were included in the modeling, of which 149 had transmitters with battery lives greater than 300 d. The fates of fish were as follows: 172 emigrations, 46 deaths, and 61 disappearances within the array (Table 2). Furthermore, the CHs of 46 fish were updated to reflect deaths from "predation," "cause unknown," and "harvested," as noted in assumption 4 (see Methods).

Emigration was evident across all estuaries (Table 2) and was steady across multiple weeks (Figure 5). For modeled fish, 61% were considered emigrations (Table 2). In estuaries from Delaware Bay and northward, egress peaked around the third week of September (week 39) and ended by the third week of November (week 47; Figure 5A). For North Carolina Weakfish that were released in the spring, egress peaked around the second week of May (week 19) and ended for most fish by the third week of June (week 25; Figure 5B). For North Carolina Weakfish that were released in the fall, egress peaked by the first week of November (week 45) and continued throughout the winter and into the early spring (weeks 53–67). The duration between the release of a Weakfish in Bogue Sound and its emigration out of the estuary varied based on the season of release, as reflected by those released in the spring demonstrating the lowest median value of detection days at 22, as compared to fall 2015, with 47 detection days, and fall 2016, with 38 detection days (Table 1).

Weekly estimates of φ were similar among estuaries, as evidenced by overlapping 95% credible intervals (CrIs; Figure 6B, D, F). The number of "fish at risk"—or those estimated to be alive by the model—decreased with seasonal emigration out of estuaries to areas on the shelf without receiver coverage (Figures 5, 6B, D, F). Mean weekly median φ estimates (when the number of fish at risk was ≥ 10) were 0.84 (95% CrI = 0.80–0.89) for the Navesink River, 0.87 (95% CrI = 0.83–0.91) for Great Bay, and 0.78 (95% CrI = 0.74–0.82) for Bogue Sound. Weekly median values of p (when the number of fish at risk was ≥ 10) were high among all estuaries: 0.91 (95% CrI = 0.87 to 0.95) for the Navesink River, 0.82 (95% CrI = 0.78–0.86) for Bogue Sound, and 0.50 (95% CrI = 0.44–0.57) for Great Bay, with Great Bay having the most uncertainty (Figure 6A, C, E). Both the median and precision of φ and p-estimates decreased as the number of fish at risk decreased.

For the model that pooled telemetry-tagged Weakfish across all estuaries, monthly estimates of survival were used to better inform coastwide management. Monthly φ estimates varied across time (Figure 7B) and decreased with increases in detected emigrations (Figure 7). Specifically, φ of Weakfish released in Bogue Sound during the spring decreased from 0.77 to 0.17 between April and May (months 4 and 5; Figure 7B); 44 of 60 Weakfish from Bogue Sound were detected as emigrating during that same period (Table 2; Figure 5B). The average median p was high at 0.78 but declined as the number of fish at risk decreased through emigration in the spring and fall (Figure 7). The 95% CrIs widened for both φ and p when the number of fish at risk decreased (Figure 7). The highest value of fish at risk at 174 in September of year 1 dwindled to 1 by the following April, which corroborates the extremely low annual estimate of φ at 0.001 (95% CrI = 0.002–0.0003) or an apparent instantaneous total mortality (Z') of 7.25 (95% CrI = 6.28–8.05).

DISCUSSION

We documented Weakfish emigrating from estuaries in autumn. However, we found almost no evidence of fish returning to spawn. The most likely explanation for the low number of Weakfish detections after emigrating from estuaries is their movement to continental shelf waters with limited receiver arrays. However, Weakfish are

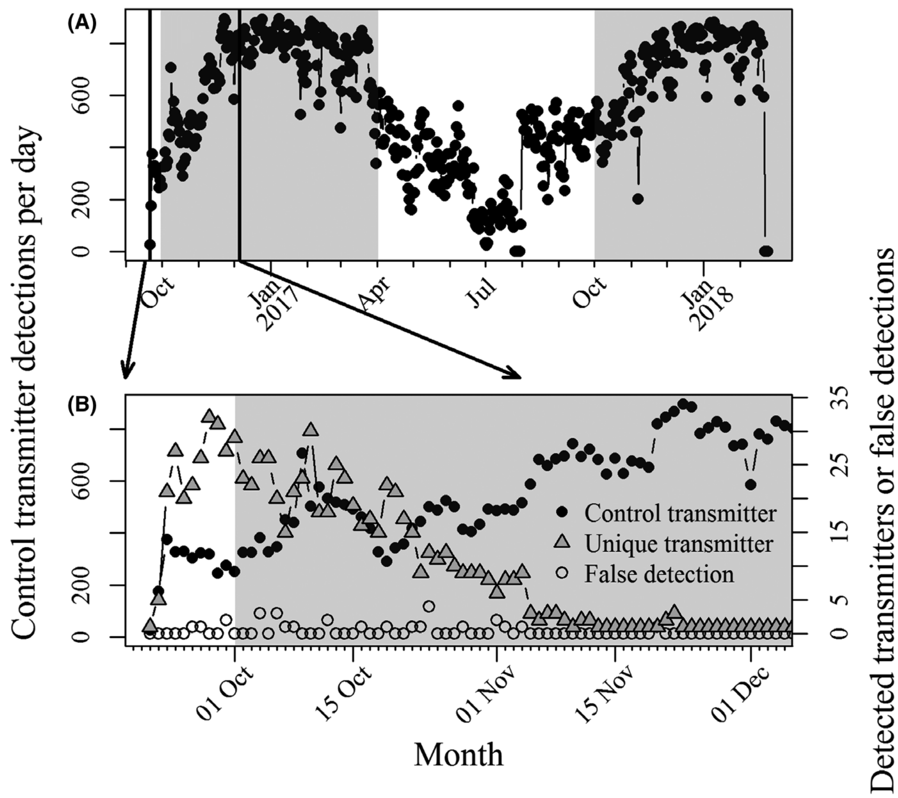

FIGURE 4. **(A)** Daily detections of the control transmitter on a single receiver in Bogue Sound across the life of the transmitter; and **(B)** inset of daily control transmitter detections from September 20 to December 6, 2017, compared to the number of unique transmitters detected and the number of false detections of Weakfish. Gray shading indicates the Weakfish overwintering time period.

estuarine spawners and have estimates of spawning site fidelity ranging from 60% to 81% (Thorrold et al. 2001); thus, we would expect telemetered Weakfish to be detected the following spring in estuaries, as all tagged fish were sexually mature and there is no evidence suggesting that Weakfish exhibit skipped spawning (Merriner 1976). Contrary to predictions based on spawning, only 2 of 149 fish with long-lived tags returned to estuarine release sites in subsequent years. Despite increased coverage across multiple estuaries from collaborative network receiver arrays, we observed no additional detections beyond the general vicinity of the tagging array in which the fish were released. The lack of detections is not attributable to nonsharing of detections by other investigators, as most fish were released by NCSU, which actively participates in local collaborative receiver networks. Other potential reasons for the small number of telemetry-tagged Weakfish returning to estuaries the following spring include surgery mortality, tag expulsion, and tag malfunction. In the assumptions section (see Methods), we provided evidence against each of these possibilities as a dominant source of loss. Harvesting of telemetered Weakfish may cause attrition of those fish, but fishing mortality has been low since 2006 due to management regulations and primarily occurs in estuaries or near-estuary habitats (ASMFC 2016; Krause 2019). Given the network of acoustic receivers on the U.S. East Coast, the most parsimonious explanation for the small number of Weakfish detections the following spring and summer is low survival.

Multiple studies support the hypothesis of low survival. The stock assessment's average Z for the period 2006–2014 was estimated as 2.42—an annual mortality rate of 91% (ASMFC 2016). A catch curve from Pamlico Sound based on fisheries-independent data estimated a Z of 2.62 (95% CrI = 1.83–3.70) for 2016, and annual median Z-values for 2002–2016 ranged from 1.04 to 3.92 (Krause 2019). Multiple conventional tagging studies focused on Weakfish have had low return rates, which can result from low reporting rates (sometimes caused by low rewards) or tag loss but can also occur due to high mortality. From 1996 to 1999, the Virginia Game Fish Tagging Program released 8,980 T-bar-tagged, low-reward Weakfish, of which only 65 were returned (a 0.7% return rate), resulting in the eventual termination of the study (Lucy et al. 2000; Lucy and Bain 2001). In 2007, the Delaware Division of Fisheries and Wildlife released 840 T-bar-tagged Weakfish, with no returns (Clark 2008). North Carolina State University released 3,672 high-

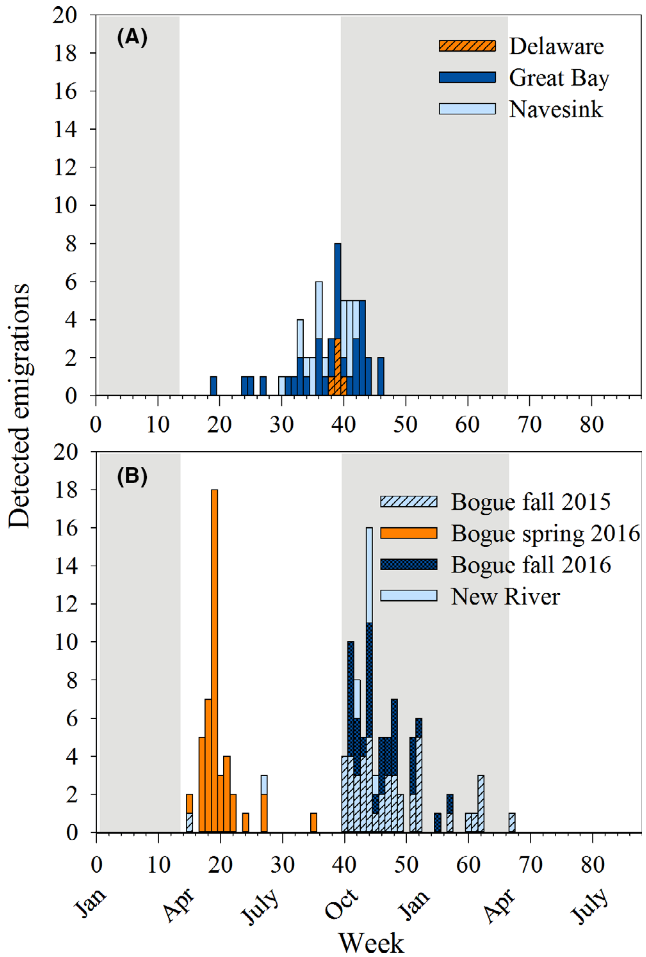

FIGURE 5. Detected weekly temporary emigrations of Weakfish released **(A)** north of Virginia (Delaware Bay, Great Bay, and the Navesink River) and **(B)** in North Carolina (Bogue Sound and the New River). Gray shading indicates the Weakfish overwintering time period.

reward (US$100), conventionally tagged Weakfish coincident with the release of telemetered individuals from Bogue Sound and had 140 returns (a 3.8% return rate). Although a higher return rate was measured in this study than in previous ones, 92% of the tag returns occurred within 100 d of release, which was reflected in an estimated annual Z of 5.78 (95% CrI = 4.46–7.47; Krause 2019) for the period 2014–2017; this value of Z was similar to our telemetry-based estimate of apparent Z', as both estimated over 99.7% annual mortality on a discrete scale. In summary, prior research supports our result of low φ, which likely represents true survival in the U.S. East Coast stock of Weakfish.

Weakfish mortality most likely occurred during the timespan between the fall emigration from estuaries and the spring return to estuaries. Our fate assignment determined that at least 61% of Weakfish emigrated out of the estuary, and a further 21% of modeled fish disappeared in the array, meaning that we could not determine a fate. If the Weakfish from the latter category represented undetected emigrations, the percentage of estuarine emigrants could be as high as 82%. The model estimated lower φ in periods when emigration away from estuarine receiver arrays occurred. Although spring-released telemetered Weakfish emigrated rapidly away from estuarine receivers, returns from spring-released Weakfish that were conventionally tagged by NCSU indicated that many of these fish were migrating eastward and northward and surviving until the fall (Krause 2019). Our finding is supported by the Virginia conventional tagging study, in which only 1 of 65 total Weakfish tag returns went through an overwintering period (Lucy and Bain 2001). Similarly, only 4 of 140 conventionally tagged Weakfish returns from the NCSU study overwintered (Krause 2019).

In the fall, Weakfish begin to aggregate and move offshore in conjunction with their predators, which have similar migration and overwintering behaviors (e.g., Striped Bass: Overton et al. 2008; common bottlenose dolphin: Hayes et al. 2018). Recent work has shown that the predatory demand of Weakfish predators has increased. The biomass attributable to M from the Weakfish stock assessment (ASMFC 2016) was similar to predator consumption of Weakfish during winter periods, suggesting that predation mortality is the most likely mechanism for low survival (Krause 2019). The phenomenon of predation mortality affecting stock size and structure is not unique to Weakfish, as shown by recent work with salmon and Atlantic Cod *Gadus morhua* (Wright et al. 2007; Swain and Benoît 2015; Thomas et al. 2016; Chasco et al. 2017; Neuenhoff et al. 2018).

The fall emigration of Weakfish is thought to commence with cooling water temperatures (Shepherd and Grimes 1984; Bigelow et al. 2002) and is supported by the initial telemetry work with Weakfish in Great Bay and the Navesink River, where egress began when water temperatures dropped below 24°C (Manderson et al. 2014; Turnure et al. 2015b). Bogue Sound Weakfish that were released in fall 2015 resided longer in the estuary, corresponding with high water temperatures in December and January, as compared to Weakfish that were released in fall 2016, which left earlier. During winter 2015 and into early 2016, some fish remained within Bogue Sound, suggesting estuarine overwintering—a phenomenon also noted to occur in Delaware Bay (Weinstein et al. 2009).

Our work indicates that Weakfish emigration is gradual, especially in the fall, suggesting a process that is driven by a more complex mechanism than solely a change in water temperature. Manderson et al. (2014) found that egress was a product of salinity regimes and fish size as well as temperature. Out of four telemetered Weakfish released in Great Bay during spring 2007, the two largest (838 and 864 mm TL) egressed within 4 d of tagging,

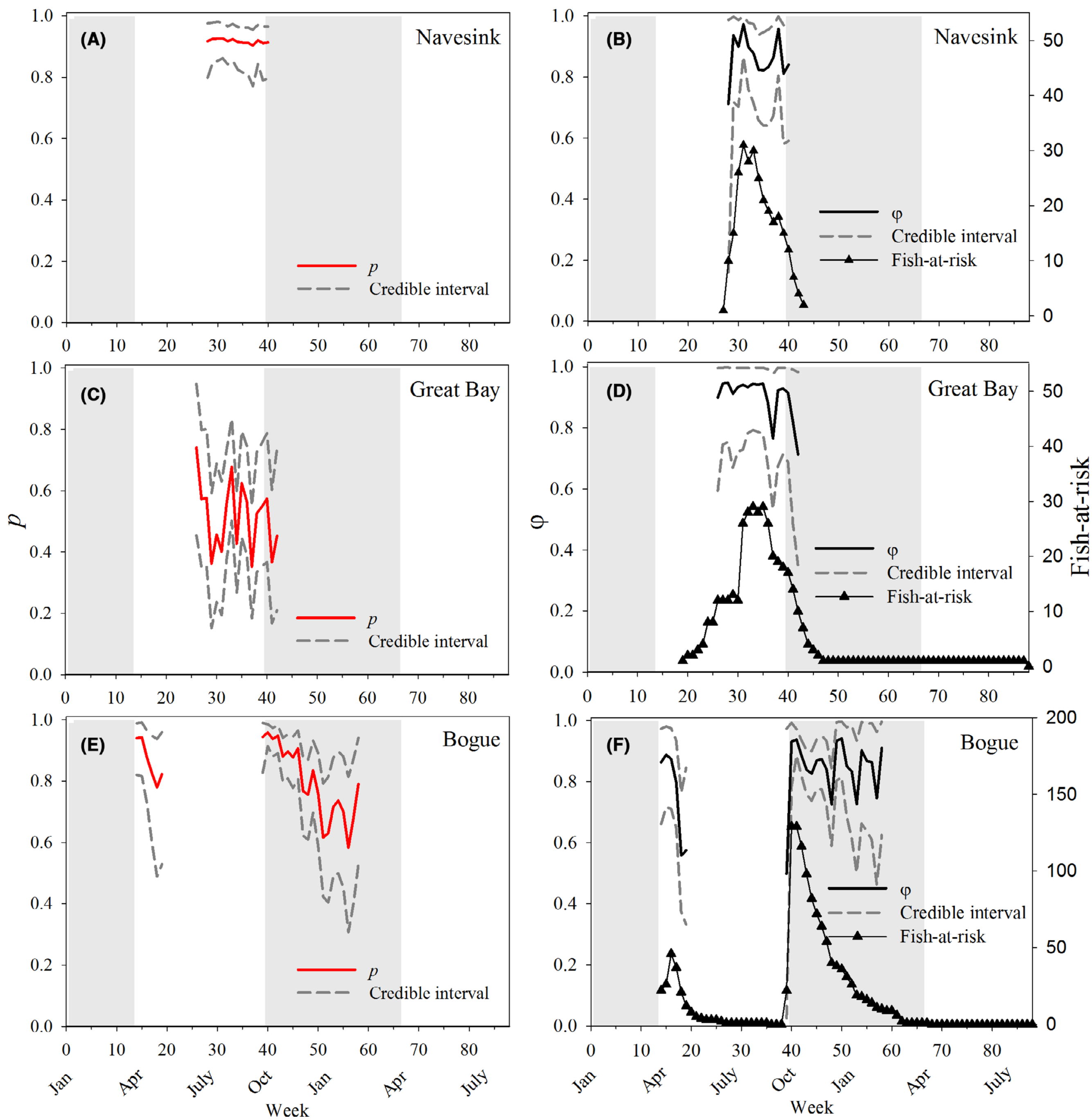

FIGURE 6. Weekly detection probabilities (p) in red and apparent survival (φ) estimates (with 95% credible intervals) for telemetry-tagged Weakfish in three estuaries: **(A)**, **(B)** the Navesink River; **(C)**, **(D)** Great Bay; and **(E)**, **(F)** Bogue Sound. Estimates are provided for those weeks in which at least 10 fish were at risk. Fish-at-risk data are presented for all time periods over which the model was run. Gray shading indicates the Weakfish overwintering time period.

whereas the smaller fish (381 and 648 mm TL) resided for 3–5 weeks posttagging (Turnure et al. 2015b). Although limited by small sample size, the size-based emigration supports the hypothesis that older fish may spawn first in estuaries and egress immediately thereafter (Shepherd and Grimes 1984). Weakfish that were released in Bogue Sound during the spring had the shortest residence time, which may be due to rapidly increasing water temperatures or may indicate that tagging occurred during the fish's northbound migration.

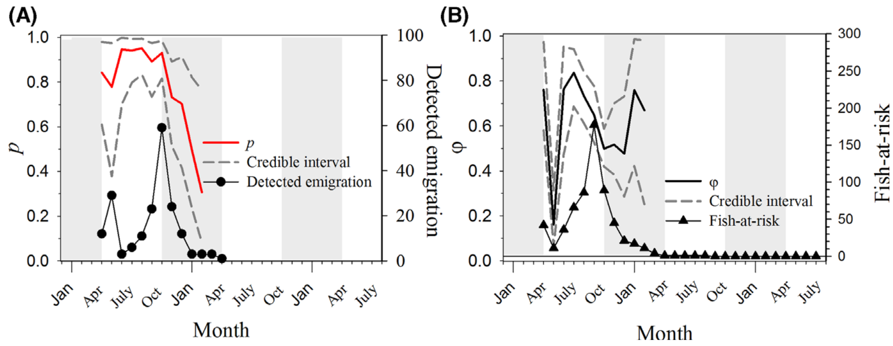

FIGURE 7. Monthly **(A)** detection probabilities (*p*) in red and **(B)** apparent survival (φ) estimates (with 95% credible intervals) for telemetry-tagged Weakfish pooled across all estuaries. Detected emigrations ($n = 190$) include all Weakfish that showed clear signs of emigrating from estuaries (panel A). Estimates of φ and *p* are provided for those months in which at least 10 fish were at risk; fish-at-risk data are presented for all time periods over which the model was run (panel B). Gray shading indicates the Weakfish overwintering time period.

Trends and magnitudes in Weakfish φ and *p* were similar among estuaries. Time-varying φ estimates were punctuated by downward spikes that matched the occurrences of Weakfish emigrations, with the timing of spikes occurring earlier in northern latitudes. The values of *p* were generally high at over 0.4, with Great Bay Weakfish having the lowest *p*, as Great Bay had six to nine stationary receivers as compared to the Navesink River and Bogue Sound arrays, which had over 25 receivers. Hightower et al. (2015) investigated annual φ estimates for Atlantic Sturgeon and found them to be similar between four southeastern U.S. rivers. In that study, time-dependent *p* was around 0.2 while Atlantic Sturgeon were in coastal waters during the winter and then *p* increased to approximately 0.7 as the fish returned to estuaries during spring and summer. A similar *p* pattern was evident with Weakfish in estuarine and coastal waters. Lindley et al. (2008) examined migrations of Green Sturgeon *A. medirostris* along the Pacific coast of North America and found that detections were highest as the fish exited and entered rivers but declined as the fish moved to marine overwintering grounds without receivers.

Apparent survival can be lower than true survival, as the former is confounded by permanent emigration. We assumed that permanent emigration was negligible due to extensive receiver coverage across the range of Weakfish, at least for the majority of telemetered (NCSU-released) Weakfish, since the number of receivers in collaborative telemetry networks has increased substantially in recent years (www.theactnetwork.com). The use of Lotek equipment reduced the possibility that Great Bay Weakfish would be detected outside of that estuary because there were few such compatible receiver arrays deployed relative to VEMCO arrays. As described above, fish moved to areas with minimal to no receiver coverage during their overwintering period. Normally, the fate of a tagged individual is made clear upon its return in the spring or summer (Williams et al. 2002), which makes long-term φ estimates unlikely to be biased by the low *p* in winter. However, Weakfish did not return for estuarine spawning as expected, even with good receiver coverage in major East Coast estuaries. More than half of Weakfish had long-lived battery tags, and Weakfish longevity is up to 17 years (Lowerre-Barbieri et al. 1995). Therefore, the model accurately interpreted the low winter values of *p* and subsequent lack of spring detections by estimating a low annual φ that, in the case of Weakfish, may approximate true survival.

Although this was not a fates-driven model (e.g., natural mortality and fishing mortality), we required some fate assignments to properly build the CJS observed-states matrix. The subjectivity of assigning these fates was minimized by having individual CHs read by a consistent pair of readers and maintaining an array until all transmitter batteries had expired. The ability to assign a fate increased with the number of receivers in an array, as was seen across seasonal releases in Bogue Sound (the number of fish categorized as “disappeared in array” decreased). For our model, only the CHs of dead fish (i.e., predation and cause unknown) were altered to reflect the assumption that detections only come from live fish. Although assigning predation may be the most subjective, we could discern non-Weakfish behavior by using metrics such as fish speed and location (e.g., Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Friedl et al. 2013; Ellis et al. 2017). Estuarine and temporal differences in the number of assigned deaths occurred (e.g., there were fewer assigned deaths in northern estuaries than in southern estuaries) and may be a result of differences in study design (e.g., receiver coverage) or real differences (e.g., increased predation or catch-and-release mortality in southern estuaries). Bias caused by erroneous assignment of death fate or the date of death was deemed minimal, as the behavior leading to the assignment predominately occurred during the last detection day and the daily detections were condensed to weekly or monthly time steps.

We could have improved our study by using conventional tags and denser receiver coverage at the mouths of estuaries. If all fish had received high-reward external tags, additional information regarding catch-and-release and fishing mortalities could have been acquired (Kerns et al. 2016; Hightower and Harris 2017), a condition that was only applicable to some of our telemetered Weakfish. Many of our study estuaries were spatially large and had porous gates, which did not give us the ability to confidently assign a fate for 21% of all released fish that disappeared within the array; therefore, we were unable to confidently subtract emigration from φ to estimate true survival (Scheffel et al. 2020). In addition, emigration was consistent in spring and fall time periods, so it was not possible to choose φ estimates from time periods with no emigration to estimate emigration by difference from φ with emigration. Instead, emigrations offered insight into the temporal variation in φ estimates and allowed us to conclude that the bulk of fish emigrated out of estuaries.

Our modeling approach allowed for coastwide survival estimates and provided insights into Weakfish population dynamics. The multistate CJS framework requires large amounts of data, including sufficient resights and sample sizes, in order to determine whether an animal is present and not detected (i.e., p) during a specific time period or whether it has transitioned to another state (e.g., from alive to dead; Joe and Pollock 2002; Coggins et al. 2006). For the model, an adequate total sample size is more important than the number of detections obtained for each individual (Otis and White 1999; Patterson and Pillans 2019), and this requirement was reflected in the lack of precision in estimates from time periods with less than 10 fish at risk. The combination of multiple studies increased the precision of our φ estimates as well as the spatiotemporal scope of our findings. Lastly, resights from telemetry allowed for higher values of p as compared to traditional mark–recapture methods, in which fish must be physically recaptured (Pine et al. 2001; Hewitt et al. 2010; McMichael et al. 2010; Dudgeon et al. 2015). The higher values of p from telemetry studies increase parameter precision, allowing for less restrictive models that can better detect trends (e.g., temporal) in mortality estimates, diagnose the causes of mortality, and direct effective management options (Johnson et al. 2010; Rudd et al. 2014).

Conclusions

Survival estimates are paramount to understanding population dynamics, especially for Weakfish, whose stock has not rebuilt despite harvest reductions (ASMFC 2016). Incorporating previously published telemetry data allowed for coastwide φ estimates that can be used to inform management (Crossin et al. 2017). Telemetry-tagged Weakfish emigrated from estuaries and did not return in subsequent years, indicative of an extremely low φ (<1%). Our estimate supports the low average annual survival probability from the 2016 Weakfish stock assessment (ASMFC 2016). Telemetry also provided insight into the timing of mortality given the observed fall emigration from estuaries and the lack of spring detections. Conventional tagging studies and catch-curve mortality estimates support the timing and magnitude of mortality (Lucy et al. 2000; Lucy and Bain 2001; Clark 2008; Krause 2019) and, when combined with our telemetry findings, increase the power of our results and can be used to formulate hypotheses for the cause of Weakfish stock decline, such as predation mortality (Krause 2019).

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