A variety of data needs challenge the successful restoration and management of alosine populations, including information on the migration, mortality, behavior, demographic rates, and distribution of fish, both in riverine and marine environments. Radiotelemetry with gastric-implanted transmitters has typically been used to answer some of these questions; however, observing alosines over extended periods and in the marine environment has remained beyond the limitations of this technology and implantation technique. To address these issues, we conducted an acoustic telemetry study on American Shad *Alosa sapidissima* by using surgical implantation methods. We tagged fish during 2015 (*n* = 46) and 2016 (*n* = 52) in the Charles River, Massachusetts, an urbanized watershed where American Shad were believed to be extirpated prior to restoration efforts beginning in 2006. Surgical implantation produced rates of in-river mortality (40% overall) and posttagging fallback (39% overall) that were comparable to those from traditionally used gastric implantation methods. Data from American Shad that were retained for statistical analyses (*n* = 59) demonstrated that Watertown Dam (at river kilometer 14.3) impeded upstream migration and that New Boston Dam and Locks (at the mouth of the river) delayed postspawn emigration from the river. In total, 49 American Shad were detected outside of the Charles River. The distribution and low number of total detections, despite a large number of nearshore arrays, suggest that American Shad occupy waters farther offshore during their marine phase. American Shad were detected as overwintering on the Scotian Shelf (*n* = 5) and the Mid-Atlantic Bight (*n* = 1). In 2017, 10 of the individuals that were tagged in 2016 returned to spawn, providing the first reported data on total migration timing and migratory behavior free of handling effects. Surgical implantation of acoustic telemetry tags is an effective method that can provide necessary and previously unattainable data on a species of conservation need.

Modern restoration efforts begin with a basic understanding of the biology and ecology of populations as a whole. These fundamental building blocks are difficult to obtain when dealing with highly migratory populations in which individuals move across varied habitats and multiple management regimes. Anadromous fish populations are notable both for their highly variable migratory patterns and for the large reduction in their population sizes over the last 200 years (Limburg and Waldman 2009; Hall et al. 2012). Management and restoration of
anadromous populations depend on multiple in-river factors, including spatial distribution, residence time, number of spawning events, and migratory success (upstream and downstream), as well as out-of-river factors, including movement and habitat usage in the near-coastal and marine environments.

The American Shad *Alosa sapidissima* is an anadromous clupeid native to the East Coast of North America from the St. Johns River, Florida, to the St. Lawrence River, Canada (Leim 1924; Collette and Klein-MacPhee 2002). Since the late 1800s, a suite of factors, including habitat loss, pollution, and overfishing, has caused a decline in stocks of American Shad along the East Coast (Dadswell and Rulifson 1994; Limburg and Waldman 2009), with the loss of as much as 50% of historic populations (Limburg et al. 2003). Reductions in American Shad and other alosine species have likely exerted negative effects on freshwater and marine food webs (Ames 2004; Mattocks et al. 2017; Dias et al. 2019). Riverine spawning migrations of American Shad are relatively well characterized; fish passage preferences and information from directed fisheries and historical landings have also been examined (Moser et al. 2000; Limburg et al. 2003; Bailey et al. 2004; Haro and Castro-Santos 2012; Grote et al. 2014; Raabe and Hightower 2014; Waldman et al. 2014). However, less is known about the interannual survival, movements, and behavior of postspawn American Shad outside of rivers (Leggett 1977; Melvin et al. 1986; Dadswell et al. 1987) despite a need for such information (ASMFC 2010; Hightower and Harris 2017; Stich et al. 2019). Efforts to improve fish passage (where possible), closures of directed fisheries, and management of bycatch in nondirected fisheries have had limited success, with most individual river stocks still being at or near historic lows (ASMFC 2007). The continued decline of American Shad and other alosines suggests that vital information about the ecology and life history requirements of these species remains unknown.

Acoustic telemetry is a relatively recent but well-accepted methodology for observing movement and migration patterns of fish (Cooke et al. 2013). Advances in and widespread adoption of the technology have led to marked leaps in understanding of the ecology and movements of migratory fish species (Dionne et al. 2013; Secor 2015), and acoustic telemetry has been adopted by researchers globally, leading to extensive data-sharing networks (Harcourt et al. 2019). The proliferation of acoustic telemetry studies and receivers in coastal waters has led to an improved understanding of fish species large and small (Skomal et al. 2017; Bishop and Eiler 2018). For anadromous species, the technology can be extremely informative because, unlike radiotelemetry, it works across all salinity levels, allowing individual fish to be tracked across coastal waters, estuaries, and freshwater environments during their annual migrations (DeCelles and Zemeckis 2014). The environmental flexibility of acoustic telemetry technology and the rapid proliferation of receiver coverage have led to studies that have better defined the ecology and life cycle requirements of iconic anadromous species, such as Striped Bass *Morone saxatilis*, Atlantic Sturgeon *Acipenser oxyrinchus*, and a number of salmonids (e.g., Hayes et al. 2011; Goetz et al. 2013; Kneebone et al. 2014; Gaughan et al. 2015; Breece et al. 2016; Altenritter et al. 2017).

In contrast, studies of alosines have been predominately focused on the time spent in rivers by spawning adults (e.g., Barry and Kynard 1986; Hightower and Sparks 2003; Bailey et al. 2004; Sprankle 2005; Harris and Hightower 2011; Grote et al. 2014; Raabe et al. 2019). Alosines are considered relatively “fragile” fish (Hendricks 2003); as a result, historic and recent telemetry studies of these species have used gastric tagging (e.g., Dodson et al. 1972; Acolas et al. 2004; Frank et al. 2009; Grote et al. 2014; Eakin 2017; McCartin et al. 2019) or external tagging (Brine et al. 2017) methods, although Bolland et al. (2019) tagged a small number of Twait Shad *Alosa fallax* surgically. While all tagging methods incur some risk to the health of the fish, surgical methods are often considered more stressful than other methods (Nielsen 1992; Winter 1996; Castro-Santos and Vono 2013), but no formal examinations exist for many species. The predominance of the gastric implantation method in alosine telemetry theoretically places less stress on fish but often results in shorter time periods of tracking, as tags are either regurgitated or can lead to feeding complications (Winter 1996; Browncombe et al. 2019). Surgical implantation may place more acute stress on fish but can result in higher tag retention and multiple years of movement history. With reductions in tag size and battery size due to the miniaturization of components (Cooke et al. 2013), expansive cooperative arrays to augment coastal tracking (Crossin et al. 2017; Harcourt et al. 2019), and analytical approaches that allow for many traditional in-river applications, the risks associated with surgical implantation of acoustic tags are often outweighed by the amount and types of information that can be gained, even for fragile species (Eiler and Bishop 2016). For alosines, surgical implantations should allow studies to follow individuals’ and cohorts’ migrations between freshwater and coastal environments over multiple years, providing information about marine movements, interannual survival, and in-river movements free of handling effects.

During 2015–2017, we used acoustic telemetry to investigate the movement and passage of American Shad in the Charles River, Massachusetts, and marine waters. At the time of European contact, the Charles River hosted impressive populations of anadromous fish, but the
American Shad population was one of the first in Massachusetts to be extinguished due to anthropogenic impacts and was long considered unsalvageable (Belding and Corwin 1921). Decades of water quality improvements led to the resurgence of river herring (i.e., Alewife Alosa pseudoharengus and Blueback Herring Alosa aestivalis), White Perch Morone americana, Rainbow Smelt Osmerus mordax, and American Eel Anguilla rostrata populations, but American Shad appeared absent. In 2006, the Massachusetts Division of Marine Fisheries (MADMF) and the U.S. Fish and Wildlife Service (USFWS) began a joint program to restore American Shad to the Charles River. From 2006 to 2018, 500,000 to more than 7 million larvae were stocked into the Charles River annually. In 2011, the agencies began monitoring for adult returns and collecting otolith samples to examine hatchery production and track population demographics (Sheppard and Chase 2011). In 2013 and 2014, video monitoring at the Watertown Dam fishway observed only 87 American Shad—but more than 300,000 river herring—exiting the ladder in each year (Sheppard and Chase 2014, 2015). Concurrent electrofishing sampling below the dam clearly demonstrated a larger population available for passage.

Faced with an immediate objective to improve in-river restoration efforts and the longstanding need for information on the marine phase of alosine life history and ecology, we surgically implanted acoustic tags in American Shad. Our goals were to demonstrate the viability of the technique as well as to answer typical ecological and management questions associated with anadromous fish restoration, including upstream and downstream passage, riverine habitat use during spawning migrations, movements in the coastal and marine environments, and potential survival and behavior in the years after tagging.

METHODS

Study site.—The Charles River is a 128-km-long, urbanized watershed that drains 495 km² in eastern Massachusetts. There are 20 dams along the main stem of the river, which originates in Newton and terminates in Boston. This study was primarily conducted between New Boston Dam, which lies at the terminus of the river in downtown Boston, and the next upstream barrier, Watertown Dam (Figure 1A). New Boston Dam was constructed in 1978 and has three navigational locks and a powerful pumping system with a combined ability to pump over 226.53 m³/s (8,000 ft³/s). The dam serves the dual purposes of maintaining a stable water surface level in the Charles River basin to protect city infrastructure as well as preventing saltwater intrusion into the basin. Sited at the interface of the river and Boston Harbor, New Boston Dam effectively removes all tidal influence and estuarine habitat within the Charles River below Watertown Dam. New Boston Dam was originally constructed with a modified vertical slot fish ladder, but this was deemed to provide ineffective passage early in the dam’s history and was eventually fully decommissioned in 2014. All fish passage into and out of the Charles River now occurs through the three navigation locks. In the 1980s, the dam operators began following a lock opening protocol that has been modified as more information has become available. Although untested, the locking protocol appears to facilitate passage for migratory fish in the Charles River (Brady et al. 2005).

Wooden dams or fish weirs had been constructed on the site of Watertown Dam (river kilometer [rkm] 14.3; rkm 0 = the mouth of the Charles River) as early as the 1630s and would often fail in high flows, allowing for fish passage in the spring. The current dam is a 60-m-long, 1.8-m-high, ogee-crest concrete dam, which was constructed in 1966. The dam features a 1.2-m-wide Denil fishway on river right that provides fish passage for some species despite being located on the opposite side of the river from the thalweg. As a result, fish passing upstream must transit a wide, shallow riffle below the toe of the dam to access the ladder entrance.

Fish capture and tagging.—Collection and tagging of fish used in this research followed the general methods and guidelines of the Massachusetts Division of Marine Fisheries. American Shad were primarily captured by using a Smith-Root boat electrofisher. A single fish was captured by using hook and line. Fish were tagged between May 21 and June 8, 2015, and between May 24 and June 10, 2016. The density of American Shad in the Charles River is low, so sampling was targeted and nonrandom. All tagged fish were captured within 1.5 km of Watertown Dam, and 90% were caught within 0.4 km of the dam. Upon capture, the fish were immediately placed in a large, in-boat, flow-through live well. The boat was then brought to shore as expeditiously as possible. Prior to tagging, fish were examined for any capture-related or preexisting trauma, such as infections, wounds, or heavy scale loss. Any fish that was visibly traumatized or impaired was retained for biological samples but was excluded from the study. Immediately before tagging, TL was measured in millimeters, caudal tissue samples were taken, and the sex of the fish was evaluated by applying light pressure to the abdomen to express milt or eggs. If no gametes could be expressed, the fish’s sex was classified as “undetermined” at the time of tagging.

Prior to tagging fish in the field, we conducted post-tagging mortality studies comparing gastric and multiple surgical implantation methods at the USFWS North Attleboro National Fish Hatchery (M. M. Bailey and B. I. Gahagan, unpublished data). The best performing surgical protocol developed through the comparisons was
then applied in this telemetry study (for video of the tagging procedure, see Supplemental Video S.1 available separately online). First, a vertical incision with a number-12 scalpel was made between the ribs on the left side of the fish, at the posterior edge of the pectoral fin when laid flat against the body. The length of the incision was as small as possible to allow insertion of the tag without tearing. Tags were inserted toward the anterior of the fish, at an angle parallel to the long axis of the body, to minimize potential damage to gonads and other internal organs. After tag insertion, a single suture (Ethicon J415H) was used to close the incision and improve tag retention (Video S.1). Active fish handling and surgery typically lasted approximately 90–110 s. Following surgeries, American Shad were immediately placed in the river and manually revived for a period of up to 5 min. If a fish did not revive within that period ($n = 5$), it was retained as a biological sample and the transmitter was implanted into a new individual. In 2015, surgeries were performed on a wetted surface with the fish surrounded

FIGURE 1. Acoustic receiver array in (A) the Charles River and Boston Harbor, Massachusetts, during 2015–2017 and (B) locations where tagged American Shad were detected outside of the Charles River during 2015–2017. The color of receiver locations within the Charles River (panel A) represents the habitat area (purple = above Watertown Dam; red = below Watertown Dam; orange = upper river; yellow = open river; green = inside New Boston Dam Locks; blue = outside New Boston Dam Locks). The shape of receiver locations within the Charles River represents the years for which records exist (circles = all years; squares = 2015; diamonds = 2016; upward triangles = 2015 and 2016; downward triangles = 2016 and 2017). Watertown Dam and New Boston Dam are represented by red vertical bars. Light gray lines denote U.S. and state highways. Marine detection locations (panel B) are grouped into six geographical areas. The number in parentheses denotes the number of unique individuals detected in that area, and the color indicates the region (light blue = Boston Harbor; red = coastal Massachusetts; dark blue = Gulf of Maine; light purple = Minas Basin; dark purple = Scotian Shelf; cyan = Mid-Atlantic Bight).
by saturated towels, including over the eyes, gills, and opercula. In 2016, American Shad were tagged using an angled cradle, with lightly flowing water over the head and gills (Eiler and Bishop 2016).

We implanted shad with VEMCO V9-2L transmitters (Vemco, Halifax, Nova Scotia), which were 29 mm long, 9 mm in diameter, and weighed 4.7 g in air. The tags were programmed to emit a 146-dB, 69.0-kHz signal at a random interval between 60 and 90 s, with an estimated battery life of 472 d. This tag was selected to best accommodate the size of American Shad while maximizing the probability of meeting study goals—specifically detecting tagged fish within the Charles River, in the marine environment, and again within the river if they returned during the year after tagging (Use of Fishes in Research Committee 2014). Winter (1996) recommended that the tag weight in air should not exceed 2% of the fish’s body weight in air, which results in a minimum fish weight of 235 g for the V9-2L transmitter. Prior to tag selection, we collected 98 American Shad in the Charles River between 2011 and 2014. The minimum weight recorded was 582 g, meaning that the weight of the tag we selected was less than 1% of body weight in air for all American Shad sampled in the 4 years prior to the study.

Acoustic telemetry. — An array of Vemco VR2W receivers was deployed within the Charles River in 2015–2017, although the array size and configuration differed by year (Figure 1A). During all years, receivers were located in areas that would effectively cover the entire width of the river given the estimated detection range of the tags used (264–513 m; Vemco: https://vemco.com/range-calculator/). Estimated detection range and receiver deployments were based on conditions in seawater and could be considered conservative, as detection ranges in freshwater are generally greater than those in seawater (Eakin 2017). In total, nine receivers were used in 2015. Of those, three receivers were placed above Watertown Dam to track tagged fish that could potentially pass that dam and above other obstructions, five receivers were placed between Watertown Dam and New Boston Dam, and one receiver was stationed in Boston Harbor immediately outside of New Boston Dam. In 2016, 10 receivers were deployed, with only one receiver above Watertown Dam, eight receivers between Watertown Dam and New Boston Dam, and one receiver in the harbor beyond New Boston Dam. In 2017, five receivers were used; they were deployed on the upstream and downstream sides of Watertown and New Boston dams and at rkm 12.23.

Receivers deployed between the two dams in 2015 and 2016 delineated five approximate habitat areas. Receivers between rkm 0.0 and rkm 0.5 covered the area around New Boston Dam and Locks (Locks area); those between rkm 2.8 and rkm 11.8 represented deeper basin or channelized river (Open area); those between rkm 12.23 and rkm 13.10 were representative of shallower mud, sand, and aquatic vegetation (Upper area); and the receiver at rkm 14.1 was the last before the shallow riffle habitat below Watertown Dam (Dam area). In all years, a single receiver was placed above Watertown Dam to record successful passage events (Above Dam). Prior to restoration activities, MADMF and USFWS conducted a boat-based spawning habitat survey of the Charles River below Watertown Dam. American Shad spawning habitat is typically characterized by shoal areas, often of sand, gravel, or larger substrate, with moderate flows (Mansueti and Kolb 1953; Leggett 1976; Ross et al. 1993; Bilkovic et al. 2002; Hightower and Sparks 2003; Greene et al. 2009). During the survey, potential spawning areas were identified visually and by using onboard sonar equipment. The majority of American Shad spawning habitat below Watertown Dam was within the Dam and Upper river areas, while the Open and Locks areas—typically deep, slow moving, and muddy—appeared to have minimal to no spawning habitat. All American Shad that were tagged with acoustic transmitters were captured and released in the Dam habitat area. Receivers were deployed prior to tagging in 2015 and during late April in 2016 and 2017. Receivers were removed during late September or early October in all years.

Over the course of the study, three receivers were lost. In 2015, a receiver at rkm 11.8 in the Open habitat area was lost, along with all of its records. In 2016, a receiver at the same site was removed from the water on July 14 by a member of the public. During 2016, the furthest downstream receiver in the Open area (rkm 2.8) was lost after June 27. In 2017, the receiver on the Charles River side of New Boston Dam (Locks area) was lost, along with all of its records. Analytical methods were tailored to accommodate stations that had partial or no records within a given year by focusing on broader areas rather than on specific locations.

Receivers in Boston Harbor and coastal Massachusetts maintained by MADMF complemented the array within the Charles River (Figure 1A, B). The array in Boston Harbor was present during all years and was deployed in a line across the mouth of the outer harbor, running from Nahant in the north to Hull in the south. Unlike the array within the Charles River, receivers in coastal waters were spaced to detect tags with greater range or to provide incidental detections for different studies and target species. Here, they provide complementary and informative location data about American Shad in marine waters. Additional detections in the marine environment (Figure 1B) were reported by researchers associated with the Atlantic Cooperative Telemetry Network (www.theatnetwork.com) and the Ocean Tracking Network (www.otn.org).

Analysis. — The primary analytical objective was to determine the migration ecology of American Shad within
the Charles River and to provide a better understanding of impediments to American Shad restoration there. Upon download from receivers, all detection data were analyzed to identify potential false detections. Within the Charles River, any single detections of fish at a receiver from a given day were presumed to be false and were removed from the data set (Gahagan et al. 2015). Detections of transmitters in the marine environment were treated more liberally; single detections in a day were retained if they placed the fish in a feasible location given where it was detected prior to and after the detection in question. This rule was used to allow for the relatively small transmission range of tags used in this study and the need for providing information about American Shad marine migrations (ASMFC 2010; Stich et al. 2019).

Transmitters that were not detected as exiting the river but ceased to be detected on the Charles River array within 1 week of tagging were considered to be tagging-related mortalities and were removed from the study. Survival of tagged American Shad was defined as detections in all four habitat areas, indicating a complete downstream emigration. We compared posttagging mortality and in-river survival rates between years using Fisher’s exact test (Zar 1999). To better confirm in-river mortalities, we surveyed some portions of the river between receiver stations with a Vemco VR100 receiver during late fall 2015 and early spring 2017. This mobile tracking survey was boat based, with stations spaced approximately 400 m apart. Minimum listening time at each station was 3 min. Several tags became stationary for periods greater than 6 months within range of the receivers positioned on the river side of New Boston Dam, leading to the presumption that those fish had expired there. Because the actual time when those fish died on-site cannot be known, their records were truncated to meet the 95th percentile of time fish that successfully emigrated through the locks were detected at New Boston Dam. All remaining records were used in basic summaries of the total number of detections and the total fish detected at each receiver.

For analyses of residence times, swim speeds, and movement rates, the data set was further restricted to fish that were detected in all four habitat areas (i.e., Dam, Upper, Open, and Locks) during 2015 and 2016. All analyses were performed in R (R Core Team 2018). Unless noted otherwise, the significance level for tests was set at 0.05. In 2016, a single American Shad was detected at the locks at New Boston Dam for a long period (4 d) before reversing course and proceeding upriver. This transmitter was detected sporadically at multiple receivers throughout the late summer and early fall; although they were of interest, these detections were not considered in any analyses, as the individual represented an extreme outlier. Researchers have frequently described a “fallback” behavior in anadromous fish, wherein individuals are observed to move downstream after tagging (Moser and Ross 1993; Frank et al. 2009). Eakin (2017) further differentiated fallback behavior into terminal (i.e., the fish exits the downstream limit of the study area) and nonterminal (i.e., the fish resumes upstream migration after a short period) cases. Although this distinction is important, very few American Shad in our study exhibited nonterminal fallback behavior. As a result, any American Shad that moved down into the Open river area—presumably out of spawning habitat—soon after tagging was classified simply as a “fallback,” which allowed this behavior to be accounted for in analyses.

Differences in residence time among habitat areas in the Charles River were analyzed using a generalized linear mixed-effects model. This modeling approach is ideal for telemetry data, as it can help control for pseudoreplication as well as spatial and temporal autocorrelation (Bolker et al. 2009; Zuur et al. 2009; Brownscombe et al. 2019). The total time spent in a given habitat area by an individual American Shad was used as the response variable. For each fish, the time that elapsed between the first and last detections for every uninterrupted residence within an area (i.e., the fish was not detected in a different area) was summed for each habitat area. Separately, the time between departure from one area and arrival at the subsequent area for every transit was calculated and split evenly between the two areas. Using this method, a summed residence time was generated for every American Shad in each habitat area. Attempts to resolve residual heterogeneity through changes to the variance structure of fixed variables—the preferred method (Zuur et al. 2009)—were not successful; instead, residence times were log transformed, which adequately addressed this model diagnostic issue. The full model included categorical variables for habitat type, sex, tagging year, week of tagging (following the ISO [International Organization for Standardization] 8601 standard), and fallback classification; a continuous variable for TL; and meaningful two-way interactions. Fish ID was included a priori as a random term to account for the behavior of individual American Shad. Model selection of the fixed effects prioritized a parsimonious model based on the combination of a backward selection protocol and log-likelihood ratio tests using maximum likelihood estimation (described by Zuur et al. 2009), with a conservative alpha of 0.01. Models were fitted with the “lme” function in the “nlme” package (R Core Team 2018), and pairwise comparisons of habitat area use were performed with the “emmeans” package (R Core Team 2018).

Total residence time of tagged American Shad within the Charles River, defined as the time that elapsed between release after tagging and the final detection of an individual at the receiver on the river side of the locks, was compared in multiple ways. A Kolmogorov–Smirnov
test was used to determine potential differences in residence times between American Shad that displayed fallback behaviors and those that did not. Kruskal–Wallis tests (KWTs) were then used to examine differences among combinations of fallback classification and either sex or tagging year. For both sets of KWTs, differences among combinations were compared using a Nemenyi test for nonparametric post hoc multiple comparisons (Zar 1999).

Diel patterns of occupancy in the Dam habitat area were evaluated to determine how tagged American Shad interacted with Watertown Dam and available spawning habitat. Fish that displayed fallback behavior were omitted from the analysis of diel habitat use because they were not detected in the area except immediately after tagging. Detection histories for both years were summarized to hour of the day and then were standardized by dividing the number of days in which an individual was detected within an hour by the total number of days it was detected within the habitat area. Generalized linear models (GLMs) with a gamma error distribution and a log link function were then fitted to the standardized American Shad presence by hour using a candidate set of predictor variables that included tagging year, fish ID, and diel cycle as a circular variable (Zemeckis et al. 2019). The potential effect of tagging year was assessed by fitting a model with year as the sole predictor to test for statistical significance. To include the diel cycle in models, hour of day was transformed into circular variables by converting the value (i.e., 0–24) to radians and applying sine and cosine functions (Zar 1999). The best fitting models were selected from the set of candidate models by using Akaike’s information criterion (AIC).

Movement rate (Holbrook et al. 2011) was used to examine potential emigration delay of postspawn American Shad at New Boston Dam and Locks. Movement rate through habitat areas was defined as

\[ R_{ij} = \frac{L_{ij}}{T_{ij}} \]

where \( L_{ij} \) is the distance (km) between upstream receiver \( i \) and downstream receiver \( j \); and \( T_{ij} \) is the difference in time (h) between the first detections at sites \( j \) and \( i \). A similar detection range (300 m) was assumed at all receiver locations. To examine the effects of the locks on downstream passage, we compared the movement rate between the Open and Locks habitat areas with the movement rate between the Locks and Boston Harbor habitat areas (2015 and 2016) using the KWT. Differences among combinations of habitat area and year were compared by using a Nemenyi test for nonparametric post hoc multiple comparisons.

During each field season, the last in-river observations of tagged American Shad were characterized by a rapid downstream emigration, which allowed for the calculation of downstream swimming speeds that can be compared to results from other research and can be used in future modeling studies. Speeds were calculated by using the receivers within the Open and Locks areas so that they would not be affected by lock operations. This area is functionally an impoundment with minimal downstream flow. Swim speeds were calculated as the time that elapsed between the first and last detections at adjacent receivers within the Open and Locks areas as American Shad made their terminal downstream movement and were expressed as body lengths per second (bl/s). A mean swim speed was then generated for each individual from its receiver-to-receiver transits.

Detections of American Shad in the marine environment and within the Charles River during 2017 were considered separately from detections in the Charles River during 2015 and 2016. Marine detections of American Shad were classified to larger geographic areas to facilitate examination of potential migratory routes and destinations. Summary analyses were performed to describe the residence and behavior of fish that returned to the Charles River during the year after tagging, including residence time in different habitat areas, total residence time, and delay at the locks prior to entering the Charles River. For returning American Shad, total residence time was calculated as the time that elapsed between the first and last detections of an individual at the receiver immediately outside of the locks in Boston Harbor. Delay was defined as the time that elapsed between the first detection on the harbor receiver and the last detection at that receiver prior to being detected within the river.

RESULTS

Overall, 98 American Shad were tagged over the 2 years of the study: 46 in 2015 and 52 in 2016 (Table 1; for plot of all detections, see Supplemental Figure S.1 available separately online). In both years, the sex ratio was skewed toward males, but this trend was more pronounced in 2016 (Fisher’s exact test: \( P = 0.074 \)). There were two American Shad whose sex could not be determined at the time of tagging. One of these fish was classified as a posttagging mortality and was later located through mobile tracking and discarded from analyses. The second individual measured 535 mm TL, which was 10 mm longer than any sampled male (mean TL = 469.26 mm, SD = 28.09), and was classified as a female (mean TL = 523.93 mm, SD = 25.44) in applicable analyses. No tagged American Shad ascended the fish ladder at Watertown Dam during the year in which it was tagged.
Posttagging mortality was higher in 2015 (15 of 46 fish) than in 2016 (6 of 52 fish; Fisher’s exact test: $P = 0.014$); the difference was attributed to the introduction in 2016 of a cradle that kept the head of the fish completely submerged and maintained flow over the gills during tagging. All individuals were detected within the array at least once after tagging. Overall, 59 tagged American Shad (21 in 2015; 38 in 2016) were detected in all four habitat areas. Of those 59 fish, 23 displayed fallback behaviors (9 in 2015; 14 in 2016). In both years, the number of American Shad detected was highest in the Dam area, where tagging occurred, and was lowest in the Locks area (Table 2).

Of those 59 fish, 23 displayed fallback behaviors (9 in 2015; 14 in 2016). In both years, the number of American Shad detected was highest in the Dam area, where tagging occurred, and was lowest in the Locks area (Table 2). Excluding posttagging mortalities, survival from the Dam to the Locks was similar in both years (2015: 21 of 31 fish; 2016: 38 of 46 fish; Fisher’s exact test: $P = 0.172$). The Locks area had the most detections in both years, followed (in descending order) by the Dam, Upper, and Open areas.

### Residence Time in Habitat Areas

The generalized linear mixed-effects model process produced a parsimonious final model that illustrated significant differences in habitat use by tagged American Shad that was dependent on the posttagging behavior they displayed. From a global model that included 15 terms, the backward selection procedure indicated that habitat area and the interaction between habitat area and fallback classification were significant predictors of habitat area use (Table 3). Although not significant on its own, fallback classification was retained as a model term since it was involved in a significant interaction (Zuur et al. 2009). Habitat use by American Shad that did not display fallback behavior was significantly different (in all cases, $P < 0.001$) except in the Upper and Open habitat areas ($t$-ratio $= 0.098$, $P = 0.999$). These non-fallback American Shad spent the most time in the Dam area, followed by the Locks, Upper, and Open habitat areas of the Charles River (Figure 2A). American Shad that displayed fallback behavior spent the most time in the Locks, but this amount was significantly different only from the time spent at the Dam ($t$-ratio $= 3.430$, $P = 0.004$; Figure 2B). The differences between American Shad that did not display fallback behavior and those that did were significant in the Dam, Upper, and Open areas (in all cases, $P < 0.001$) but not at the Locks ($t$-ratio $= -0.072$, $P = 0.943$). Fish that did not display fallback spent more time

### Tables

#### Table 1. Acoustic tagging data for American Shad that were tagged in the Charles River, Massachusetts, during 2015 and 2016. Fallback classification was applied only to fish that were detected in all four habitat areas (Dam, Upper, Open, and Locks; defined in Methods).

| Year  | Tagging date | n   | Male | Female | Undetermined | Mean TL (mm; range) | Fallback |
|-------|--------------|-----|------|--------|--------------|---------------------|----------|
| 2015  | May 21–Jun 8 | 46  | 27   | 17     | 2            | 504 (423–563)       | 12 9     |
| 2016  | May 24–Jun 10| 52  | 41   | 11     | 0            | 469 (400–561)       | 24 14    |

#### Table 2. Total number of acoustic-tagged American Shad that were detected and the total number of detections in each habitat area (Dam, Upper, Open, and Locks; defined in Methods) of the Charles River, Massachusetts, in 2015 and 2016. Posttagging mortalities (i.e., fish that were undetected or became stationary within 1 week of tagging) are not included.

| Variable | 2015 | 2016 |
|----------|------|------|
|           | Dam  | Upper | Open | Locks | Dam  | Upper | Open | Locks |
| Transmitters | 30  | 29  | 24  | 21  | 46  | 41  | 39  | 38  |
| Detections  | 39,732 | 14,567 | 2,224 | 48,633 | 112,923 | 9,520 | 6,896 | 135,201 |

#### Table 3. Summary of results for the best performing generalized linear mixed-effects model of habitat area use by American Shad in the Charles River, Massachusetts, during 2015 and 2016. The model included fish ID as a random term.

| Model                                      | Explanatory variable | Likelihood ratio $\chi^2$ | df | $P$     |
|--------------------------------------------|----------------------|---------------------------|----|---------|
| $\log_2$(hours) ~ Habitat area + Fallback  | Habitat area         | 83.4112                   | 3  | <0.0001 |
|                                         | Fallback              | 0.8214                    | 1  | 0.3648  |
|                                         | Habitat area $\times$ Fallback | 90.0218                  | 3  | <0.0001 |
in the Dam area than those that exhibited fallback (t-ratio = 8.34, P < 0.001); fish without fallback spent less time in the Upper and Open areas than fish with fallback (Upper: t-ratio = −3.70, P < 0.001; Open: t-ratio = −2.75, P = 0.008).

**Total Residence Time and Diel Patterns**

The total amount of time for which American Shad remained in the Charles River after tagging was dependent on fallback classification (Figure 3A). On average, American Shad that did not display fallback behavior after tagging remained in the river for 27.8 ± 1.84 d (mean ± SE), which was significantly more than the 14.7 ± 1.59 d spent by fish that did exhibit fallback (Kolmogorov–Smirnov test: D = 0.62319, P < 0.001). Sex also affected the total residence time of tagged American Shad (KWT: χ^2 = 28.675, df = 3, P < 0.001). Males (mean ± SE = 31.5 ± 2.03 d) and females (19.2 ± 2.36 d) that did not display fallback behavior remained in the river for a longer period than fallback American Shad of either sex, but the difference was only significant for males (Figure 3B). Similarly, tagging year also affected total residence time (KWT: χ^2 = 25.183, df = 3, P < 0.001). Non-fallback American Shad tagged in 2016 spent significantly longer than fish that exhibited fallback in either year, whereas non-fallback fish tagged in 2015 were similar to all other combinations (Figure 3C). For fish that did not display fallback behavior, results for year of study and sex were difficult to separate because sample sizes were small and females were strongly represented in the 2015 sample (8 females; 4 males), while males dominated the 2016 sample (3 females; 21 males).

The presence of tagged American Shad (n = 36) below Watertown Dam was influenced by individual fish behaviors and time of day (Figure 4), with the highest degree of presence occurring from 2000 hours (sunset) to 0400 hours (1 h prior to sunrise). The GLM that included diel cycle and a fish ID term was the most supported model (AIC = −854.958). A GLM with diel cycle and year of study was less supported (ΔAIC = 345.712) and the year term was not significant (likelihood ratio test: χ^2 = 0.031, df = 1, P = 0.861), justifying the pooling of years in other models. The GLM with only the fish ID term was the least supported model (ΔAIC = 407.892).

**Movement Rates and Mortality at the Locks**

Movement rates of tagged American Shad were lower within the Locks habitat area than within the Open area (Figure 5). In both years, the movement rates at the Locks were similar to each other and significantly lower than the movement rates from the Open habitat area, which were also similar to each other (KWT: χ^2 = 75.306, df = 3, P < 0.001). A total of six tagged American Shad died within detection range of the receivers on the river side of the locks: three fish in 2015 and three fish in 2016. During 2016, an additional tagged fish appeared to abandon emigration efforts after 4 d and returned to the Open habitat area for the next 2 months before attempting to emigrate again in mid-September.
Downstream Swimming Speed

Swimming speed of tagged American Shad as they emigrated from the Charles River was variable. The overall mean downstream swimming speed was 0.742 bl/s, and the overall median was 0.489 bl/s. The slowest mean speed for an individual was 0.007 bl/s, while the fastest was 12.400 bl/s.

Marine Detections

In total, 49 tagged American Shad were detected outside of the Charles River; however, the number of detected fish dropped rapidly as distance from the river increased (Figure 1B). In the nearshore environment, most American Shad were detected on the northern half of the Boston Harbor array and on a receiver 30 km northeast of the harbor, off Gloucester, Massachusetts. After American Shad exited Boston Harbor, most detections occurred on receivers greater than 20 km from shore. Few records of continuous residence in an area were reported; rather, detections often occurred in a single day or over a short
sequence of days (Figure 6). Detections occurring between July and November were predominately in the Gulf of Maine, although one individual was located in the Minas Basin in late September. Two American Shad, one in each year, were detected in Massachusetts Bay during October. Between November and April, a total of five fish was detected on the Scotian Shelf. After April, two fish were detected on the Scotian Shelf and one was detected in the Mid-Atlantic Bight.

The vast majority of marine detections were at latitudes higher than Boston Harbor. Only two American Shad (1 female; 1 male) were detected south of Boston Harbor, both of which returned to the Charles River in 2017. The female was detected in the Mid-Atlantic Bight during early spring 2017, with previous detections in Boston Harbor and subsequent detections 50 km north of the harbor, near Cape Ann, Massachusetts, before returning to spawn. The male, which was detected multiple times off Nova Scotia between December 2016 and May 2017, made a rapid (13-d; >1.7-km/h) migration to coastal Massachusetts in May 2017 and was detected 70 km south of the harbor (near Provincetown) and then at the southern end of the Boston Harbor array prior to entering the Charles River.

Repeat Spawners

Of the 31 American Shad tagged in 2016 that emigrated from the Charles River, 10 fish were detected in the river during 2017 (Figure 7). All of these American Shad (4 females; 6 males) were detected outside of the Charles River between spawning events, although the number of days on which the fish were detected was relatively low (median = 9 d; minimum = 4 d, maximum = 36 d). Arrival date was highly variable, with fish first being detected at the locks between April 28 and June 19. The locks delayed entry for most of the returning American Shad (median = 1.95 d; minimum = 0.73 d, maximum = 5.55 d). Unlike prior years, tagged individuals successfully ascended the Watertown Dam ladder, with six fish (3 females; 3 males) detected above the dam. The delay caused by the dam for fish that passed was variable (median = 0.56 d; minimum = 0.35 d, maximum = 4.68 d) but less than the delay caused by the locks. Five of the six fish returned downstream of the dam after spending 14.4–26.6 d upstream (median = 15.7 d), and one of those five was last detected below the dam and presumed dead. Departure dates of
the eight surviving American Shad (3 females; 5 males) were also variable, ranging from June 10 to July 24. Total residence time of surviving fish ranged from 26.3 to 47.6 d (median = 33.9 d).

**DISCUSSION**

This telemetry study marks the first published results describing the successful surgical implantation of telemetry tags into alosines, with the tags providing continuous movement histories as the fish exited their spawning grounds, migrated through the marine environment, and returned to spawn during the subsequent year. Even within strictly riverine studies, we know of no records that have captured the true time spent by American Shad on a spawning migration, as most fish are tagged in-season and there is limited information on when the fish began their migration. We also performed a variety of analyses typical of in-river residency, habitat use, and fish passage to inform American Shad restoration in an urban river. Surgical implantation is a viable option for American Shad that, when paired with extensive acoustic telemetry receiver networks, provides necessary and heretofore unattainable data on a species of conservation need.

**Tagging Methodology**

The surgical tagging approach that was developed through the 2 years of the study resulted in levels of mortality and fallback behaviors comparable to those associated with gastric insertion of tags. Some studies conduct tagging very close to the downstream limit of the study area and are unable to separate tagging mortality from fallback behavior, making total mortality throughout the study a more common measure than postrelease mortality. In recently published work, total study mortality has varied from a high of 60–75% (Beasley and Hightower 2000; Aunins et al. 2013) to a low range of 17–18% (Bailey et al. 2004; Aunins and Olney 2009). In the present study, total mortality across both years was 40%, but after improving the tagging methods in 2016 the rate was reduced to 27%, which is equivalent to that observed by Grote et al. (2014). Similarly, fallback in prior work has been as low as 24% (Beasley and Hightower 2000) and as high as 71% (Aunins et al. 2013), with rates typically between 40% and 50% (Bailey et al. 2004; Aunins and Olney 2009; Grote et al. 2014). The overall fallback rate in our study was 39%, and the fallback rate was lower in 2016 (36%). The levels of mortality and fallback associated with surgical implantation of tags indicate that with thoughtful design and careful practice, surgeries do not appear to carry more risk than gastric techniques, while maximizing the amount of data and potential benefit of every fish tagged.

Surgical implantation allowed us to detect 10 American Shad that were tagged in 2016 returning to the Charles River to spawn in 2017. These 10 fish represented 20% of the total fish tagged in 2016 and nearly one-third of the fish that successfully emigrated at the end of that spawning migration. This rate of return is much higher than that reported from studies employing PIT tags, which have observed repeat spawning rates closer to 1% (Raabe and Hightower 2014; T. Castro-Santos, U.S. Geological Survey, personal communication). This difference could be affected by river-specific demographics or migration barriers as well as by the much larger range of acoustic tags but still indicates that surgical implantation successfully allows for individuals to be detected over multiple years. If returning fish are considered to be a true reflection of annual mortality, our results would indicate that given 46 available American Shad (after accounting for posttagging mortality), annual mortality was approximately 78% in our sample. No tagging results exist for comparison, but most scale-based estimates for rivers in New England vary from 18% to 92% (ASMFC 2007). A larger-scale study should be conducted to obtain realistic interannual mortality rates and other valuable demographic information (ASMFC 2009; Hightower and Harris 2017; Stich et al. 2019).

Data from the American Shad that returned to the Charles River in 2017 indicated that the behaviors of fish remaining in the river immediately after tagging were not greatly affected by the procedure, but tagging possibly influenced the probability of passage. American Shad that did not fall back in 2015 and 2016 remained in the Charles River for 27.8 d after tagging (Figure 3A), while returning American Shad in 2017—presumably free of tagging effects—were in the Charles River for roughly 1 week longer on average (34.7 d). These numbers are even more comparable since the total residence time of returning American Shad is biased higher relative to records within a tagging year, as the time the fish were in the river prior to tagging cannot be known. The estimates are also commensurate with those from other studies, which have reported mean residencies between 7.8 and 33.0 d (Beasley and Hightower 2000; Aunins and Olney 2009; Aunins et al. 2013; Grote et al. 2014; Raabe and Hightower 2014). The successful passage above Watertown Dam by 60% of the returning fish in 2017 raises concerns that swimming performance or migratory motivation of American Shad was compromised after surgeries; however, passage may have been influenced by differences in precipitation among years. The location of the fish ladder on the opposite side of the river from the thalweg likely presents a major obstacle under most flow conditions for deep-bodied fish like American Shad, as water depth can influence their movement (Haro and Castro-Santos 2012). In 2015 and 2016, total rainfall for the period April–June was 7.7 and 11.4 cm below the average for that period over the past 20 years, whereas rainfall during those months in 2017...
was 6.3 cm above average (National Weather Service: https://w2.weather.gov/climate/xmacis.php?wfo=box).

Increased flows and river depth would make the ladder, which is typically difficult to reach because of shallow depths between the thalweg and ladder entrance, more accessible to American Shad.

The effects of noise on fish are generally understudied, but research has confirmed that American Shad can hear within the frequency most commonly used by acoustic tags (Mann et al. 2002; Popper et al. 2004), leading to potential effects on behavior and survival. The behavior of tagged fish may have been altered, in both the short term and the long term, by their ability to hear the implanted tag, but this concern was lessened by the fact that tag power (146 dB) was lower than the threshold for observed behavioral changes (170 dB; Plachta and Popper 2003). It was also possible that tagging increased the risk of predation on observed American Shad, as seals can hear acoustic tags. In laboratory experiments, seals have been trained to associate the sound of an acoustic transmitter with food, indicating that they could learn this behavior in the wild (Stansbury et al. 2015). Conversely, an increasing number of large oceanic predators (e.g., White Shark *Carcharodon carcharias*) have been fixed with acoustic transmitters in Massachusetts waters (Skomal et al. 2017), so it is possible that seals may associate the noise of the tags with predation risk rather than opportunity. Although these concerns have merit, the ratio of tagged fish to the total number of fish available to marine predators is so infinitesimal that the learning of these behaviors in the wild seems unlikely. American Shad, although large, are forage fish, and some detections that we presumed to be American Shad may have been from predators that had consumed a tagged individual. Given the size of American Shad in our study, we assumed that any predator capable of swallowing an adult shad whole would pass a small transmitter through its digestive system and expel the transmitter in a relatively short period of time, lessening the chance of incorrectly interpreting detections. Supporting this assumption, Friedl et al. (2013) determined that small Striped Bass that ingested baitfish implanted with transmitters similar in size to those used in our study typically eliminated the tag within 15 d. Future studies could use tags that are capable of detecting predation events (e.g., Vemco V9D) to further explore predation-related mortality on adult American Shad and other alosines.

**American Shad in the Charles River**

This tagging study demonstrated that the restoration of American Shad in the Charles River is impeded by both Watertown Dam and New Boston Locks. Delays incurred at obstacles during spring migrations, both upstream and downstream, can reduce survival, migration success, and spawning success (Castro-Santos and Letcher 2010). American Shad that did not display fallback behavior after tagging were most commonly located below Watertown Dam. Abundant spawning habitat exists above the dam, and all larvae were stocked well above the dam at rkm 21. No American Shad were observed passing that structure during the year in which they were tagged, although a number of returning fish passed during 2017, a high-flow year. Even so, returning fish that did pass still experienced variable amounts of migratory delay at the dam, spending from 8 h to more than 4 d before ascending the fishway (Figure 7). Non-fallback American Shad spent more time below the dam than any other combination of fallback behavior and habitat area (Figure 2). These patterns are similar to other studies in which American Shad were observed to reach a dam and then continuously attempted to pass the structure for days or weeks (Bowman 2001; Hightower and Sparks 2003; Bailey et al. 2004). American Shad were detected below Watertown Dam during all hours of the day throughout the study, but there was a significant diel pattern to detections, with most detections occurring during the night (Figure 4).

American Shad may have been using this area for spawning, as they are known to spawn at night (Leim 1924; Massmann 1952) and suitable shoals were located within range of the receiver in both the upstream and downstream directions. Alternatively, American Shad typically have a diurnally passage pattern (Fisher 1997; Haro and Kynard 1997) and it is possible that they were dropping back to this area after failed passage attempts during the day or using the area for both hypothesized purposes. Regardless of the proximate explanation, Watertown Dam ultimately hindered migratory movements and limited American Shad to spawning habitat below the dam.

Multiple studies have examined upstream passage of American Shad at navigational locks, but they have been focused on semelparous populations, so downstream movements were neither recorded nor expected (Nichols and Louder 1970; Moser et al. 2000; Bailey et al. 2004; Smith and Hightower 2012). American Shad populations in New England are largely iteroparous (Leggett and Carscadden 1978). Repeat spawners tend to be older, larger, and more fecund than first-time spawners and are disproportionately important to the reproductive success and stability of iteroparous populations (Leggett and Carscadden 1978; Leggett et al. 2004). An important component of iteroparity is postspawn survival to the estuary, including downstream passage of adults at barriers (Castro-Santos and Letcher 2010; Bailey and Zydlewski 2013; Stich et al. 2019). In the Charles River, downstream migration was hindered by New Boston Dam and Locks. This trend was pervasive, affecting American Shad regardless of fallback status (Figure 2). Delays were also reflected in the rate of downstream movements, which were significantly
lower in the Locks area than in the Open habitat area (Figure 5). Stich et al. (2019), drawing on the hypotheses and modeling work of earlier studies (Leggett et al. 2004; Castro-Santos and Letcher 2010), found that in some cases downstream passage rates and delays can have a greater effect on population productivity than any other modeled factor. This is an intuitive outcome of American Shad often being at their most energetically depleted when they encounter downstream movement barriers (Leonard and McCormick 1999; Glebe and Leggett 2010).

We observed six American Shad that died within range of the receivers upstream of the locks and an additional individual that appeared to abandon attempts to emigrate in July before attempting again in September (Figure S1). Additionally, 41 (80%) of the 51 tagged American Shad that successfully emigrated from the river did not return the following year. Although many causes likely contributed to the degree of interannual mortality of tagged American Shad, latent mortality (Nieland et al. 2015) from delays at the locks may have contributed to marine losses. Based upon diet samples, Walter and Olney (2003) hypothesized that the ability to enter prey-rich brackish estuaries and feed immediately after spawning may be an important factor in limiting mortality during that period. Grote et al. (2014) reported that as postspawn American Shad entered the Penobscot River estuary, they displayed an oscillatory movement pattern that could have reflected osmoregulatory acclimation or a feeding pattern. The disruption of estuarine dynamics and resources is another potential negative impact of New Boston Dam and Locks for American Shad.

Posttagging downstream movements (i.e., fallback) are well documented for American Shad (Moser and Ross 1993; Beasley and Hightower 2000; Bailey et al. 2004; Aunins and Olney 2009). Fish that exhibited fallback behavior after tagging mostly demonstrated terminal fallback (Eakin 2017); only three fish that were detected below the Upper area eventually returned to the area of the dam. Although posttagging downstream movements have typically been attributed to handling effects (Barry and Kynard 1986; Hightower and Sparks 2003), downstream movement may be a part of normal alosine migratory behavior (Frank et al. 2009). In many studies, fish that experience fallback are able to move freely downstream into the estuary or out of detection range (Bailey et al. 2004; Aunins and Olney 2009; Aunins et al. 2013; Grote et al. 2014); however, in the Charles River the locks provide a barrier that effectively blocks this movement, making further comparisons difficult. An apparent difference in fallback behavior due to sex was confounded by potential year effects, as more non-fallback females were tagged in 2015 than in 2016 (Figure 3B). Female American Shad may spend shorter amounts of time on spawning grounds because the production of gametes and migration costs are more energetically costly for females, or at least larger fish, than for males or smaller fish (Leonard and McCormick 1999; Glebe and Leggett 2010; Raabe and Hightower 2014).

**American Shad in the Marine Environment**

Detections of tagged American Shad outside of the Charles River were not numerous, but they suggest that the distribution and migration of American Shad in the marine environment are likely more complex than previously thought. Dadswell et al. (1987) examined earlier mark–recapture studies and their own unpublished data to draw several conclusions about the coastal migration of American Shad: (1) there were separate winter and summer aggregation areas (with a focus on the Bay of Fundy as the dominant summer destination); (2) in the spring, spawning American Shad migrated close to shore, while nonspawning individuals migrated offshore; and (3) migration was generally northward in the spring and summer and southward in the fall and winter. Contrary to the historical emphasis, only one tagged American Shad was detected within the Bay of Fundy, although receiver coverage outside of the Minas Basin was sparse during our study period (Ocean Tracking Network: https://members.oceantrack.org/OTN/projects?sorts[collectioncode]=1). Instead, summer and fall detections were predominately from deeper waters in the Gulf of Maine or on the Scotian Shelf (Figure 1B). Two American Shad were observed in Massachusetts Bay during October and were most likely migrating southward closer to shore, as hypothesized by Dadswell et al. (1987), but the only detections that occurred during winter were of five American Shad in the Canadian Maritimes region, which has long been speculated as a winter aggregation area (Valdykov 1936, 1956). Taken together, these detections imply that American Shad from the Charles River, and perhaps those from other Gulf of Maine populations, do not uniformly select an overwintering aggregation and are distributed broadly in marine waters.

Much as previous mark–recapture studies were biased by where fishing activity occurred, the marine detections of American Shad were biased by where receivers were located during the study period. Given the large number of arrays close to shore and in embayments between Chesapeake Bay and Newfoundland (Ocean Tracking Network: https://members.oceantrack.org/OTN/projects?sorts[collectioncode]=1; Atlantic Cooperative Telemetry Network: http://www.theactnetwork.com/), it is informative that tagged American Shad were detected so infrequently (Figure 6). Detections of fish that survived a winter at sea and returned to spawn in 2017 illustrate this point. A total of six American Shad were detected on Jefferies Ledge in the Gulf of Maine, but only two fish were detected for multiple days or weeks, suggesting that the rest were transiting through the area. One of these fish was later
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**SUPPORTING INFORMATION**

Additional supplemental material may be found online in the Supporting Information section at the end of the article.