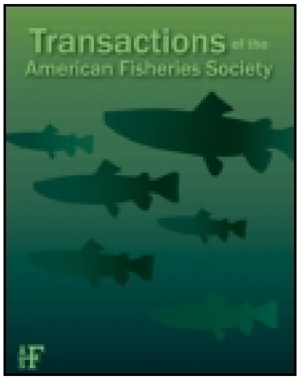

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Movements and Demography of Spawning American Shad in the Penobscot River, Maine, prior to Dam Removal

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ARTICLE

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Abstract
We conducted a baseline study to better understand the migratory movements and age and spawning histories of American Shad *Alosa sapidissima* in the Penobscot River, Maine. The Penobscot River is currently undergoing a major dam removal project that is focused on restoring migratory connectivity and recovering diadromous fish populations including American Shad. This study addresses key data gaps for a previously unstudied native population of shad prior to restoration. A combination of radio- (n = 70) and acoustic telemetry (n = 14) was used to investigate the movements of migratory adult fish in 2010 and 2011. Scale-based analyses were used to assess spawner age and iteroparity. Radiotelemetry results indicated that few tagged fish (5–8%) approached the head-of-tide dam. Tagged fish exhibited three general patterns of movement in the accessible freshwater river habitat: use of the upper river reach, the lower river reach, or both. Mean freshwater residence time ranged from 9.1 to 14.0 d. Congregating fish were observed at two sites in the upper river reach and spawning activity was observed. Freshwater survival and survival to the estuary were at least 71%. This observed high survival was consistent with the estimated age and spawning histories of tracked fish, which indicated that 75–95% of the sampled fish were repeat spawners. Estimated age of adult migrants ranged from age 4 to age 9. Postspawning acoustic-tagged American Shad exhibited a series of prolonged upstream and downstream reversals upon entering the lower estuary. These movements have been previously unreported, and suggest that estuarine residency after spawning is important to osmoregulatory acclimatization for re-entry into salt water and the resumption of postspawning feeding activity.

The American Shad *Alosa sapidissima* is a large clupeid native to the Atlantic coast of North America from the St. Johns River, Florida, to the St. Lawrence River, Canada. Although historically abundant in eastern coastal river systems, populations are in decline throughout the species' native range (Limburg and Waldman 2009; Hasselman and Limburg 2012). Reasons for this decline include habitat loss resulting from dam construction, overfishing, and pollution (Limburg et al. 2003; Moring 2005).

Through the mid-1800s, American Shad were abundant in the Penobscot River system, Maine, with annual catches estimated at up to 2,000,000 adults (Foster and Atkins 1869). The construction of the Bangor Dam in the 1830s (Walburg and Nichols

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1967), followed by the Veazie Dam in 1910, prevented access to the vast majority of spawning habitat located upriver (Saunders et al. 2006). The resulting reduction in migratory connectivity is thought to have impacted the abundance and distribution of 11 species of native diadromous fishes, including American Shad (Trinko Lake et al. 2012).

Little is known about the abundance, behavior, or demography of American Shad in the Penobscot River. The current-day run is of unknown size, but was previously assumed to consist of only 1,000–2,000 adults (Saunders et al. 2006; MDMR 2009). Recent hydroacoustic work by Grote et al. (in press) recorded large numbers of American Shad at the base of the Veazie Dam, suggesting that the run is larger than was suspected. Multiple age-classes of juveniles have been captured in the lower Penobscot River estuary (C. Lipsky, National Oceanic and Atmospheric Administration [NOAA]–Fisheries, unpublished data), indicating successful and sustained reproduction in the system.

The Penobscot River American Shad run persists, despite the substantial reduction of accessible habitat to just 48 river kilometers (rkm) downstream from Veazie Dam. Although Veazie Dam was equipped with a vertical-slot fishway, American Shad did not frequently navigate it; only 16 adults passed through the fishway from 1978 to 2012 (O. Cox, Maine Department of Marine Resources [MDMR], unpublished data). American Shad spawn in freshwater (Massmann 1952; Weiss-Glanz et al. 1986) and do not tolerate full-strength saltwater rearing conditions (Zydlewski and McCormick 1997). Thus, both spawning habitat (15 rkm) and rearing habitat ($\sim$50 rkm) are limited for this migratory fish in the Penobscot River.

American Shad exhibit an increased incidence of iteroparity in northern latitudes (Leggett and Carscadden 1978). Repeat spawning data from other northern rivers suggest that iteroparity in the Penobscot River system should range from 50% to 80% (Limburg et al. 2003); however, no repeat spawning data have been collected for the Penobscot River. 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). One component of iteroparity is postspawning survival to the estuary, but little is known about the movements and behavior of postspawning American Shad in any river system.

The Penobscot River is the subject of an intensive river restoration effort, and data collection in advance of restoration provided an opportunity to establish population baselines. Under the Penobscot River Restoration Project (PRRP), the two lowest dams in the system, Veazie Dam (rkm 48) and Great Works Dam (rkm 60), have been removed (Figure 1). Great Works Dam was dismantled in the summer of 2012, and Veazie Dam was breached in July 2013. Additional PRRP restoration measures include the construction of a new fish passage system at Howland Dam (rkm 100) and the installation of a fish elevator at Milford Dam (rkm 62). It is anticipated that American Shad will benefit from increased access to 552 rkm of additional freshwater habitat (Trinko Lake et al. 2012). Baseline data on the current population will be useful in assessing American Shad response to the restoration efforts (Kibler et al. 2011).

This study used a combination of radio- and acoustic telemetry and scale (age and spawning history) analysis to document behavioral and demographic baselines of the adult Penobscot River American Shad before dam removal. The purposes of this study were to (1) describe American Shad movements and use of accessible freshwater (spawning) habitat, (2) determine the frequency and duration of approaches to Veazie Dam, (3) characterize age and spawning histories, and (4) investigate postspawning behavior and survival during seaward migration.

METHODS

Study site.—The Penobscot River watershed drains roughly 22,200 km^2 in northern and central Maine. For the purposes of this study, the lower Penobscot River "system" consists of the Penobscot River estuary and the interior of Penobscot Bay (Figure 1). The estuary extends from the head of tide at Veazie Dam (rkm 48) to just below the southern end of Verona Island (rkm 0), and the interior bay is defined as the 25 rkm south of rkm 0.

Water levels in the Penobscot River estuary vary widely with both tidal excursion and upriver hydropower regulation. The freshwater portion of the system is divided by the remnants of the Bangor Dam (rkm 43). Although the dam is breached, legacy portions of the structure remain, with the result that the former dam site acts as a hydrologic "step" above which the current does not reverse. A series of ledges and riffles that extend from the Veazie Dam tailrace to Graham Station (rkm 46) also differentiate the uppermost reach of the estuary, as these features are inundated only at high tide.

Fish passage in the Penobscot River has long been impeded by an extensive network of dams. The head-of-tide structure, Veazie Dam, was a 7.6-m-high concrete dam with an installed hydroelectric capacity of 8.4 MW. Fish passage structures at this facility included a vertical-slot fishway located midchannel between the forebay and spillway, and a derelict, nonoperable, pool–weir fishway on the eastern shore. The MDMR maintained a fish trap at the exit of the operable fishway. The trap was tended daily from May through October to collect Atlantic Salmon *Salmo salar* hatchery broodstock and to document passage of other fishes.

Tagging.—Adult migratory American Shad were captured via boat electrofishing at three locations: Eddington Bend (rkm 47), Graham Station (rkm 46), and the Bangor Dam remnants (rkm 43) in the Penobscot River estuary. Sampling was constrained by both boating operations (safe electrofishable flows below 340 m^3/s [12,000 ft^3/s]) and the presence of listed species, and was therefore directed and nonrandom. Sampling occurred between June 4 and June 9 in 2010 and between June 9 and June 24 in 2011. Fish immobilized by the electrofisher were netted and allowed to recover one at a time in a live well that contained

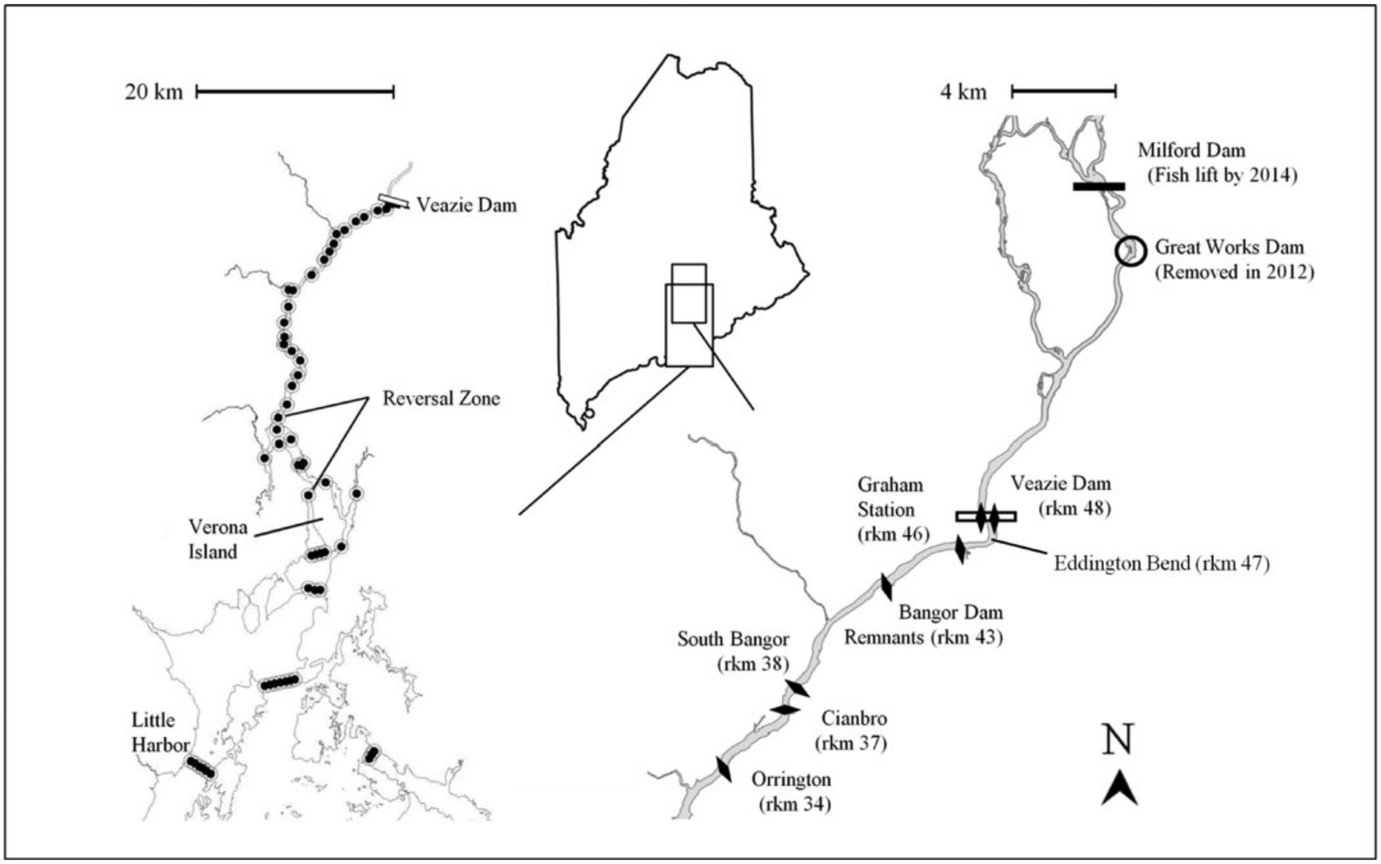

FIGURE 1. The lower Penobscot River and inner Penobscot Bay, with Veazie Dam and radio and acoustic receiver locations in 2011. Ringed circles (left panel) denote acoustic receiver sites in the estuary and interior of Penobscot Bay; black diamonds (right panel) denote radio receiver sites in the upper estuary and dam locations slated for passage improvements under the Penobscot River Restoration Project.

oxygenated river water at ambient temperature. Fish in good condition (minimal descaling and/or wounds) were tagged and sampled, whereas individuals in marginal condition were only sampled.

American Shad were implanted gastrically with radio or acoustic transmitters. Tags were gently inserted into the stomachs of the fish with a plastic straw according to the methods of Bailey et al. (2004). After tagging, fork and total lengths were measured, scale and caudal tissue samples were collected, fish sex was evaluated, and the fish were released. Beginning in 2011, we revised our tagging procedure to minimize handling time; tags were inserted while the fish was held upright in the live well, with the operculum just below the water line to allow unimpeded ventilation and to reduce the time fish were exposed to air (Smith et al. 2009). Fish were released immediately after tagging and downstream (within 150 m) of their original capture location.

Coded radio transmitters (Lotek Wireless, Newmarket, Ontario) were used in both 2010 (model NTC-4-2 L; frequency, 150.780 KHz) and 2011 (model NTC-4-2S; frequency, 150.750 KHz). The radio tags were programmed with burst rates ranging from 2.8 to 3.2 s, resulting in an expected battery life of 84–89 d. In addition, acoustic tags (Vemco, Halifax, Nova Scotia) were used in 2011 (model V7-2X; frequency, 69.0 KHz). Tag life for the acoustic tags was estimated at 69 d. Transmitters weighed 1.4–2.1 g in air, and all transmitters weighed less than 1% of the body weight of the smallest study fish.

Radiotelemetry.—Radio transmitters were monitored to assess American Shad movements near Veazie Dam and to identify areas of fine-scale habitat use. Shore-based radio receivers were deployed along the freshwater portion of the estuary from Orrington (rkm 34) to Veazie Dam (rkm 48; Figure 1). Radio signals attenuate in salt water, and the lowest radio receiver in the array was therefore placed just upstream of the upper edge of the mixing zone. In 2010, five stationary radio receivers were deployed, and in 2011 the radio array was expanded with two additional sites. Shore-based radio sites consisted of two Yagi antennas, one oriented upstream and the other downstream, and a single data-logging Lotek receiver (SRX 400 or SRX DL).

In both study years, two radio receivers were installed in the center of the river on the Veazie Dam. A coarse-scale radio array monitored tagged fish approaching the dam by means of three antennas oriented towards the east bank, west bank, and downriver. A fine-scale array with one aerial Yagi antenna and one underwater (stripped cable) antenna monitored the fishway entrance; the gain settings for these antennas were adjusted such that only transmitters within 3 to 4 m of the fishway entrance were detected. Fish logged at either receiver were classified as approaching the dam, whereas only those detected on the fine-scale underwater array were classified as locating the fish fishway.

In 2010, the radio receivers operated continuously from June 3 to July 21. In 2011, five of the seven receivers operated from May 27 to July 21, while two others were operational beginning June 21. Receivers were operated for a minimum of 11 d after the last transmitter detection to ensure that study fish had exited the array and to collect baseline noise occurrence data.

In addition to the stationary sites, radio-tagged fish were also monitored with boat and shore-based mobile tracking. Mobile surveys were conducted 2–3 times per week using an SRX400 receiver and a handheld Yagi antenna. When flows and tides permitted, the area between Eddington Bend and Veazie Dam was searched by boat to improve transmitter position estimates. As flows diminished over the course of the season, this section of the river was searched from shore. American Shad spawn at night (Liem 1924) or in low light conditions (Massmann 1952); therefore, most surveys were conducted in the afternoon and evening in an attempt to locate spawning areas. A total of 14 spawning surveys were conducted in 2010 and 13 were conducted in 2011.

False detections due to noise were logged by the radio receivers during both years. Many of the noise detections did not match study tag codes, but were recorded two to five times within 10-min windows at a single radio receiver. The occurrence of these "false positives" called into question the use of commonly used telemetry detection criteria, where "true" detections are identified based on an arbitrary frequency of occurrence within an arbitrary timeframe (Grothues et al. 2005).

To address the problem of identifying true detections from false noise detections, the radio detection data were evaluated using a probabilistic framework that identified radio detection events that were unlikely to be produced by random noise. This analysis was based on the approximation that false positives in the radio data could be modeled as the result of a stationary uniform random process; this approximation allowed the probability of multiple random events occurring within a given time period to be predicted using a Poisson distribution as follows:

$$P(N,T) = \text{Poisson}\,(\lambda,\ N), \tag{1}$$

where $P(N,T)$ is the probability that a random process occurs N times within a period of time T, λ is the mean rate of occurrence of the random process within time T, and N is the number of occurrences. Because the radio receivers were operated during times when there were no tags in the system, the rate of occurrence of random detections was measured and λ calculated for each tag code. Equation (1) was used to classify "true" and "noise" detection events based on a 0.99 certainty threshold. This classification process was implemented in MATLAB (2012).

Acoustic telemetry.—Acoustic transmitters were used to document American Shad movements throughout the Penobscot River estuary and Penobscot Bay. Unlike radio signals, acoustic transmissions do not attenuate in salt water, and acoustic telemetry can therefore provide detection information from the wide range of salinities encountered by postspawning adults. Acoustic tag data were screened for detections from the same transmitter recorded simultaneously at different receivers. Any detection event consisting of a single detection greater than 10 rkm from the previous legitimate detection event were considered false and filtered out of the data set.

The Penobscot River acoustic array is jointly maintained by the U.S. Geological Survey (USGS) Maine Cooperative Fish and Wildlife Research Unit, the University of Maine, and NOAA Fisheries. An array of up to 83 stationary acoustic receivers (VR2 and VR2W, Vemco) was deployed over 39 acoustic monitoring sites in the lower river system (Figure 1). In 2011, an extra receiver was deployed at the base of Veazie Dam to monitor fish entrance to the fishway. Several of the downstream sites were configured with multiple receivers to ensure "bank-to-bank" detection coverage. In 2011, the receivers in the estuary and the interior of Penobscot Bay were deployed throughout the study, but the outermost receivers in the Bay were removed on June 28 and 29. Acoustic receivers were omnidirectional, and typically exhibited minimum detection ranges of about 500 m (Holbrook et al. 2009). River and estuary receivers were moored to the channel bottom, whereas receivers in the bay were fixed approximately 10 m below the water surface.

Movement analysis.—Capture histories were generated and plotted for all tagged fish to describe their positions (rkm) in the system over time. The first and last detections at a given receiver were used to generate these histories so that both presence of the detected transmitter and the duration of the detection could be inferred. Tags were assumed to be stationary (either ejected or mortalities) if they were detected continuously at a single receiver for over 36 h and were not subsequently detected at any other station, or if they were detected in the same location by mobile tracking surveys over 2 weeks and were not subsequently detected at any other station.

Residence time was calculated for radio-tagged fish and was defined as the time elapsed from release after tagging to the final detection at either a fixed or mobile receiver. Transit time to the mouth of the estuary was calculated for acoustic-tagged fish and was defined as the time elapsed from release to first detection at the Fort Knox site (rkm 8.5). In both study years, a small number of radio-tagged fish ($n = 2$ each year) departed the system very rapidly, exiting the radio array less than 24 h posttagging. Many alosine telemetry studies report significant "fallback" after handling (e.g., Bailey et al. 2004), but there is limited information on whether this behavior is due to handling effects or "normal" migratory egress behavior (Frank et al. 2009). With no a priori criteria to discriminate between these

TABLE 1. Radio-tagging data, including tag type, number (*n*), sex (M = male, F = female, U = undetermined), median FL (and range), tag date, and tag location for American Shad tagged in the Penobscot River, Maine, in 2010 and 2011.

			Sex					Tag site		
Year	Tag type	*n*	M	F	U	FL; cm (range)	Tag date	Eddington Bend	Graham Station	Bangor Dam
2010	Radio	20	15	4	1	43.0 (38.0–49.0)	Jun 4–12	12	5	3
2011	Radio	50	15	9	26	44.0 (34.0–51.0)	Jun 9–20	43	7	0
2011	Acoustic	14	9	2	3	40.5 (37.0–46.0)	Jun 20–24	14	0	0

behaviors, we conservatively included these fish in the residence time analysis.

Scale analysis.—Scales were collected from the right side of each captured fish, below and slightly posterior to the dorsal fin. The number of readable scales for each fish ranged from one to six. Whole scales from each individual fish were combined in a single microscope slide mount and were reviewed using a microfilm reader. Three experienced readers worked together reviewing scales and generated consensus estimates for the numbers of annuli and spawning checks using Cating's (1953) criteria. A fourth experienced reader was used as a "tie-breaker" when estimates differed. Freshwater marks were not readily apparent in many of these scales, which made identifying the first annulus, using Cating's (1953) transverse groove approach, infeasible (Duffy et al. 2011). The lack of clear freshwater marks in these scales was not surprising, given that juvenile American Shad from multiple year-classes have recently been documented to use the Penobscot River estuary (Lipsky, unpublished data). Juvenile scales collected from the lower Penobscot River were used to identify a range of scale sizes for age-1+ American Shad. These juveniles were collected during and immediately after the spawning run in 2011 and were too large (146–210 mm FL) to be young of the year (age 0). Size templates from age-1+ fish were used, in conjunction with transverse grooves where available, to help identify the first annulus in the adult scales. Subsequent obvious annuli and spawning checks were used to age each fish (Duffy et al. 2011).

Environmental data.—Mean daily water temperature was obtained from the USGS Eddington Bend gauging station (rkm 47). Gauge elevation from the Eddington Bend station was used to describe both the daily mean water level and the tidal stage in the section of river from Veazie Dam to the Bangor Dam remnants. Water elevation from the USGS Bangor gauge (rkm 41) was used to infer tidal stage in the estuary downriver from the breached Bangor Dam site. All USGS data were downloaded from the National Water Information System website (http://waterdata.usgs.gov/nwis). Daytime and nighttime calculations for the diurnal-effects analysis were based on average sunrise and sunset times over the survey period in Bangor, Maine.

Statistics.—A Welch's two sample *t*-test with no assumption of equal variance (Welch 1947) and an alpha level of 0.05 was used to evaluate differences in mean egress timing between acoustic- and radio-tagged fish.

RESULTS

Upper Estuary

A total of 84 adult American Shad were tagged over the course of this study: 20 in 2010 and 64 in 2011 (Table 1). In both years, the majority of study fish were captured and tagged in the shallows at Eddington Bend (rkm 47) just below the Veazie Dam (rkm 48), and fewer fish were collected at Graham Station (rkm 46) and at the remnants of the Bangor Dam (rkm 43).

All radio-tagged fish were detected during both study years, whereas 12 of 14 acoustic-tagged fish were detected during 2011. The two missing acoustic tags were assumed to be functional, but the fish may have become stationary near the tagging site where they were out of range of the nearest receiver. In 2010, study fish were detected in the freshwater portion of the estuary from June 4 (the first day of tagging) to June 30 (the last active detection in the radio array). In 2011, study fish were detected from June 9 to July 9. During these times, daily mean water temperature ranged from 17.5°C to 24.1°C in 2010 and from 17.3°C to 24.4°C in 2011, and mean daily gauge height varied from 0.95 to 1.99 m in 2010 and from 1.08 to 1.50 m in 2011.

Within the upper array, tagged American Shad were regularly detected over extended intervals (longer than 2 h) at both the Bangor Dam remnants at rkm 43 and Graham station at rkm 46. Radio mobile tracking surveys confirmed that tagged fish frequently congregated in the pool immediately upstream from the Bangor Dam remnants. In 2010, three radio-tagged fish were detected in this location during a single evening when chase activity behavior associated with spawning was observed at the surface. In 2011, between four and seven tagged American Shad were located at this site on six different mobile survey occasions. Mobile tracking surveys also identified Eddington Bend at rkm 47 as a location frequented by tagged fish. In 2010, three fish were repeatedly detected in the riffles below the Veazie Dam tailrace, and in 2011 six fish were detected in Eddington Bend on multiple occasions.

While 82% of American Shad in the study were captured or located in Eddington Bend, relatively few tagged fish were detected 1 km upriver at Veazie Dam. In 2010, only 1 of 20 radio-tagged American Shad (5%) was detected at the Dam. This fish was detected by both the proximity and the fishway entrance antennas, and was present near the dam over the course of 2 d. In 2011, 4 of 50 (8%) radio-tagged fish approached the dam, and three of these went on to locate the fishway entrance. No acoustic-tagged fish were detected at the dam.

Persistence near the dam was variable: three fish were detected over 2 d, and one fish was present on 14 d. American Shad activity near the dam appeared greatest around midday, although tagged fish were present in the vicinity of the Veazie Dam during all hours of the day. Activity at the fishway likewise appeared greatest during the afternoon, with fishway detections occurring exclusively in daylight hours. Both male ($n = 2$) and female ($n = 2$) American Shad approached the dam, as did one fish of unknown sex.

During both study years, the majority of tagged fish were detected moving downstream after capture, and only a small percentage initially remained at or above the tagging sites. In 2010, 85% of the study fish were detected at the Bangor Dam remnants (rkm 43), 3–4 rkm below the tagging sites, within 24 h of tagging. Likewise, in 2011 90% of the study fish were detected downstream at the Bangor Dam remnants within 24 h of tagging. Rapid initial seaward movements were observed farther downstream as well, but not to the same extent. In 2010, 70% of tagged fish were detected downstream (rkm 42–34) of the breached Bangor Dam within 36 h after tagging, and in 2011 that proportion decreased to 43%.

American Shad movement histories were classified according to detection location (and inferred fish position) within the radio array (Table 2). During both years, the majority of histories were associated with one of three movement patterns: (1) remaining in the upper array (at or above rkm 43) before egress, (2) moving downstream and remaining in the lower array near rkm 34 until egress, or (3) using the entire array (Figure 2). While the majority of tagged fish followed these patterns, some did not. Several radio tags ($n = 2$ in 2010, $n = 6$ in 2011) were detected and then disappeared from the system, or were identified as stationary by mobile tracking surveys. It was assumed that the "missing" study fish were depredated (and may have been removed from system) and that stationary tags were either mortalities or expelled. These missing and stationary fish were identified as "other" in the movement histories and were excluded from subsequent analyses.

The percentage of radio-tagged fish that survived to exit freshwater ranged from 80% in 2010 to 72% in 2011. Of the 14 radio tags that were not detected leaving the radio array in 2011, five were last detected at the Bangor Dam remnants and were not recorded by mobile tracking surveys. Acoustic-tagged fish exhibited similar freshwater survival, as 71% were detected leaving the upper estuary. Mean posttagging residence time for radio-tagged fish was shorter in 2010 (9.1 d) than in 2011 (14.0 d) (Table 3), but minimum and maximum posttagging residence times were similar. Although the acoustic-tagged fish were tagged several days later than the radio-tagged fish, mean timing of freshwater egress at rkm 33 did not appear to differ between the groups ($P = 0.165$).

TABLE 2. Radio-tagged American Shad movements summarized by predominant use area: Upper (upstream from rkm 43), Lower (downstream from rkm 34), Both, and Other (depredated and stationary tags), in the Penobscot River, Maine, in 2010 and 2011.

	Lower		Upper		Both		Other		
Year	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	Total *n*
2010	3	(15.0)	7	(35.0)	8	(40.0)	2	(10.0)	20
2011	12	(26.0)	7	(14.0)	24	(48.0)	6	(12.0)	49

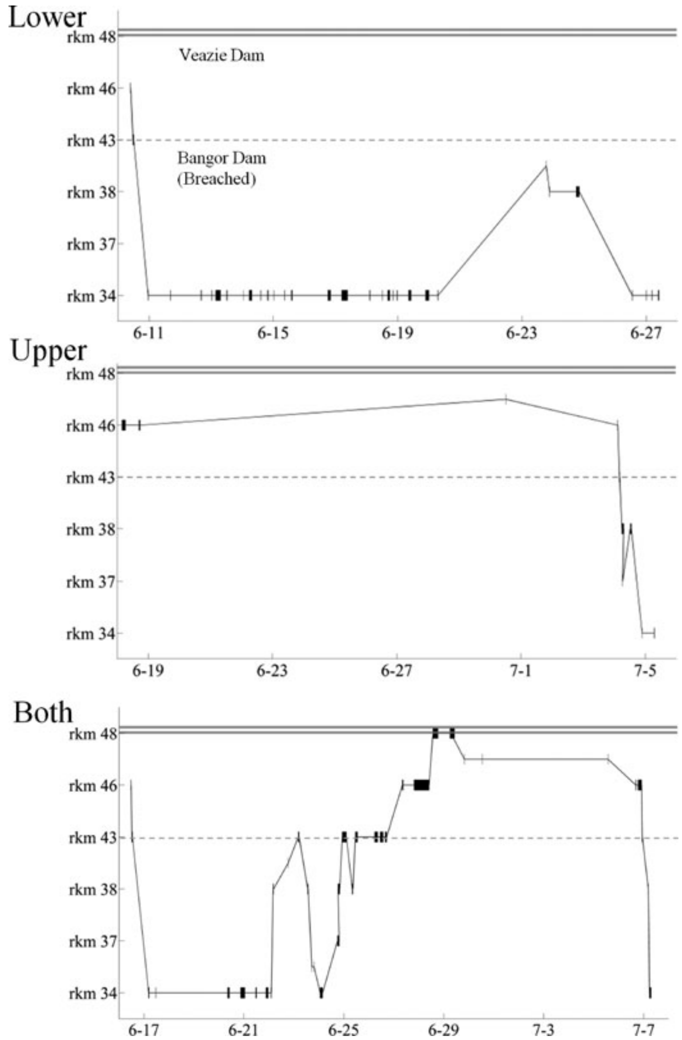

FIGURE 2. Radiotelemetry movement histories (Lower array, Upper array, Both arrays) of individual radio-tagged American Shad in the freshwater zone of the Penobscot River estuary in relation to Veazie Dam (double line) and the remnants of the Bangor Dam (dashed line).

Lower Estuary

Ten American Shad with acoustic tags were detected migrating from the tagging site at rkm 46.5 to the estuary mouth at rkm 8.5, resulting in an apparent survival rate to the estuary of 71%. Transit time to the estuary ranged from 2.7 to 17.3 d; mean transit time was 10.6 d (SD = 4.3). Shad with active transmitters

TABLE 3. Residence time (days) for radio-tagged American Shad in the Penobscot River, Maine, during the spring of 2010 and 2011.

Year	Mean	Range	SD	*n*
2010	9.1	0.5–25.4	6.6	17
2011	14.0	0.3–23.6	6.4	44

were detected in the lower estuary and bay from late June until the first week of August 2011.

Of the 10 acoustic-tagged fish that exited the freshwater zone, nine exhibited repeated upstream and downstream reversals in the lower estuary between Drachm Point (rkm 18.0) and Fork Knox (rkm 8.5; Figure 3). These movements appeared tidal, with fish moving upstream on flood tides and downstream on ebb tides. Time of day did not appear related to reversal movements, as fish moved upstream and downstream both during the day and at night, and often a single excursion would occur during both daylight and nighttime hours. The mean duration of the lower estuary reversal phase was 10.9 d (SD = 7.3) and ranged from 2.5 to 25.4 d.

Following the reversal phase, three acoustic tags were detected sequentially at the Harriman Cove site (rkm 12.1), suggesting that fish with these tags became stationary (Figure 3). Three more tags were last detected within the reversal zone, indicating that tag ejection or mortality had also occurred in this area but out of range of a receiver. The four remaining acoustic-tagged fish were detected moving out into Penobscot Bay, and two of these were later detected as far south as Little Harbor at rkm −23.8 (Figure 1). One fish returned back to the lower estuary after 15 d in the bay and resumed reversals.

Age and Spawning Histories

Scale-based age estimates of American Shad ranged from 4 to 9 years old, and the majority of sampled fish were estimated as 5 or 6 years old (Table 4). Mean age in 2010 was 5.6 years (SD = 1.0), while mean age in 2011 was 5.9 years (SD = 1.1). We identified high numbers of repeat spawners during both 2010 (95.0%) and 2011 (75.4%; Table 5). The mean number of spawning checks was 2.4 (SD = 0.7) in 2010 and 2.2 (SD = 1.0) in 2011. The maximum number of spawning checks observed was five.

DISCUSSION

This study investigated a previously uncharacterized population of American Shad in an unusual study system. American Shad were documented using, moving between, and, in one case, spawning in specific freshwater habitats below the Veazie

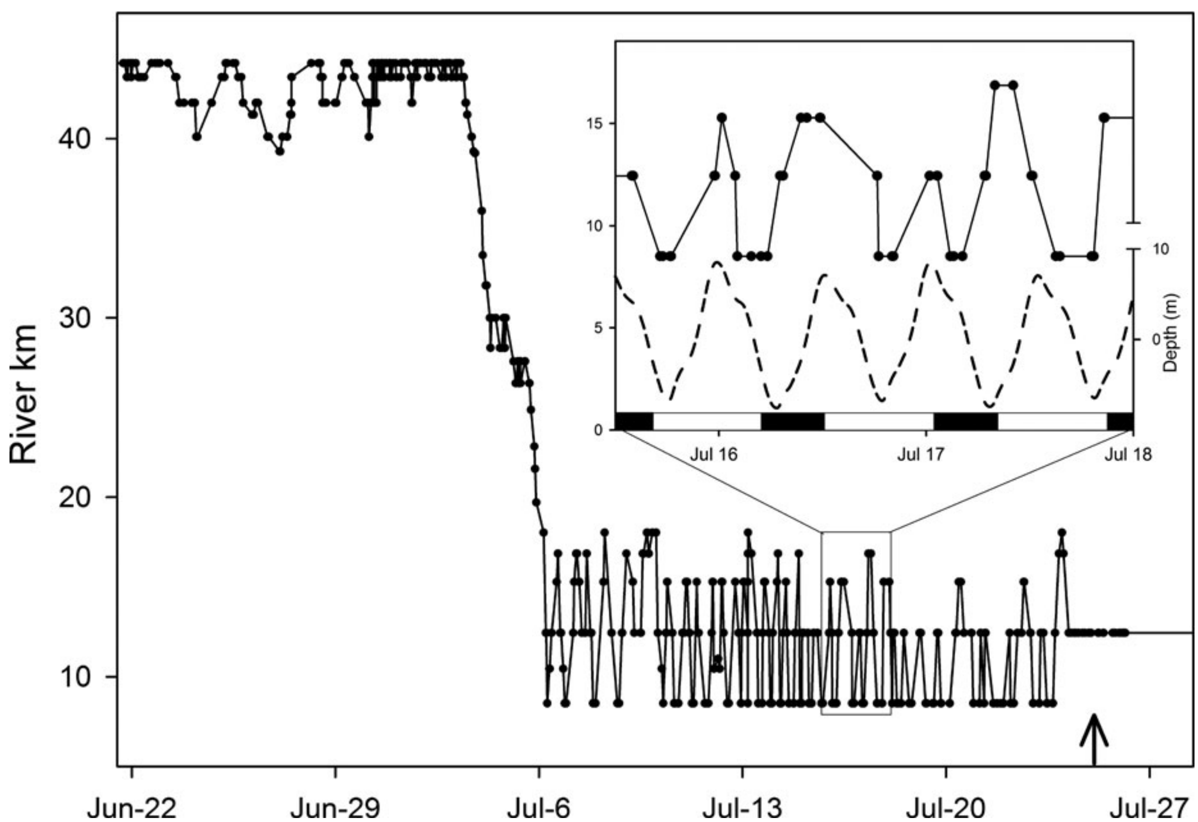

FIGURE 3. American Shad detection history in freshwater followed by egress to and reversals in the lower estuary and repeated detections of a stationary tag. The inset shows reversals movements in the lower estuary (solid line with dots) versus tidal stage (dashed line) and the time of day (black–white bars). The arrow denotes a change in fish detections from multiple receivers and locations, to a single receiver at rkm 12.1, indicating the tag had become stationary.

TABLE 4. Scale-based age (years) distributions of adult American Shad captured in the Penobscot River in June 2010 and 2011.

	Age 4		Age 5		Age 6		Age 7		Age 8		Age 9		
Year	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	Total *n*
2010	2	(10.0)	8	(40.0)	6	(30.0)	3	(15.0)	1	(5.0)	0	(0.0)	20
2011	6	(9.2)	20	(30.8)	21	(32.3)	13	(20.0)	4	(6.2)	1	(1.5)	65

Dam in the Penobscot River. American Shad were documented throughout the system, although only a small percentage of tagged fish (5–8%) approached the dam. Survival in freshwater was high (71–80%), as was survival to the estuary (71%). These results suggest high rates of iteroparity in this population, as does the large proportion of repeat spawners (75–95%). This study documented a persistent reversal movement pattern in the lower estuary that was previously unreported for American Shad. These movements appear tidal, and may be associated with physiological adaptation to salt water or with the resumption of feeding activity.

Radiotelemetry identified "hotspots" of freshwater habitat use below Veazie Dam. Tagged shad routinely congregated at Eddington Bend (rkm 47) and the old Bangor Dam headpond (rkm 44) throughout the day and into the evening. Although riffles are more representative of preferred American Shad spawning habitat (Marcy 1972; Stier and Crance 1985; Beasley and Hightower 2000), no diurnal migrations were observed from the slow, deep, headpond habitat up into the Eddington Bend quickwater. Multiple individuals were present at the Bangor Dam headpond at all times of day, and an evening spawning chase was observed there in 2010. Use of this area for spawning suggests Penobscot River shad utilize diverse and possibly suboptimal spawning sites, possibly as a result of freshwater habitat limitation.

While extensive freshwater habitat use was documented downstream, few tagged American Shad (5–8%) appeared to investigate the Veazie Dam, and only 5–6% of the study fish sucessfully located the fishway. This result is somewhat surprising, given the large number of adult encounters recorded with a multibeam sonar detector at the fishway entrance in a companion study (Grote et al., in press). In that study, over 31,000 presumptive American Shad sonar observations were made from a 5% subsample of recorded data. If a small proportion of shad approached the dam, and generated the large number of sonar observations, then the American Shad population present in the Penobscot River may be much larger than the 1,000–2,000 fish that was previously estimated (MDMR 2009).

Alternatively, the number of American Shad approaching Veazie Dam may have been underestimated. Detections from the spring of 2011 may not have been recorded when one of the Veazie proximity receivers was inactive for approximately 9 d. Marked fish may have incurred handling (Bailey et al. 2004) or tagging effects (Corbett et al. 2012) that made them less likely to approach the dam, or may have been deterred by the turbulence and shadows created by the dam itself (Haro and Castro-Santos 2012). Lastly, study fish may have approached the dam prior to capture and may have progressed to downstream spawning sites (Maltais et al. 2010) by the time they were tagged and monitored.

The timing of radio detections from the proximity and fishway receivers has implications for future fish passage and management in the Penobscot River system. While American Shad held near the dam for all 24 h, they were only detected at the fishway entrance during daylight. This behavior corroborates the temporal pattern observed for presumptive American Shad targets in the same system (Grote et al., in press) and is consistent with what has been reported for the timing of passage in other rivers (Haro and Castro-Santos 2012). These approach data highlight the need for future American Shad passage efforts to be focused on daytime operations and may provide information to fisheries management at the Milford Dam fishway following the removal of the Great Works and Veazie dams.

Between 85% and 90% of study fish initially moved downstream following tagging. Similar downstream movements, or "fallback," are well documented for American Shad (Moser and Ross 1993; Beasley and Hightower 2000; Bailey et al. 2004; Aunins and Olney 2009). Although posttagging downstream movements have typically been attributed to adverse handling effects (Barry and Kynard 1986; Hightower and Sparks 2003), downstream migration may be a part of normal alosine migratory behavior (Frank et al. 2009). Without information on

TABLE 5. Scale-based spawning histories of adult American Shad captured in the Penobscot River in June 2010 and 2011.

	1 Spawn		2 Spawns		3 Spawns		4 Spawns		5 Spawns		Iteroparous		
Year	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	Total *n*
2010	1	(5.0)	11	(55.0)	7	(35.0)	1	(5.0)	0	(0.0)	19	(95.0)	20
2011	16	(24.6)	26	(40.0)	15	(23.1)	7	(10.8)	1	(1.5)	49	(75.4)	65

the physiological state of study fish, the mechanisms behind the downstream movements of tagged American Shad are unclear, and movements that occurred outside of the 24–36-h stress response time frame (Shrimpton et al. 2001) were likely migratory and not related to fallback.

Barring fallback, residence times and movement histories indicate that most study fish remained in freshwater for at least 9 d. After freshwater residency, these fish exited spawning habitats and commenced seaward migration. Radio and acoustic tag detections throughout the upper estuary suggest over 71% survival through freshwater and to the mouth of the estuary. This high percentage of postspawning survival is similar to the yearly estimates of iteroparity (75.4–95.0%) from the scale data. American Shad exhibited high rates of iteroparity, which were similar to rates reported in other northern rivers and what would be predicted based on the latitudinal cline of reproductive behavior in this species (Leggett and Carscadden 1978).

The age structure of American Shad in the Penobscot River appears similar to, or slightly older than, those historically reported for other northern systems (Walburg and Nichols 1967; Collette and Klein-MacPhee 2002). However, recent work in northern systems including the Hudson River (Limburg et al. 2003) and Connecticut River (Leggett et al. 2004) suggest that considerable interannual variability occurs in mean spawning ages; thus, comparisons between systems are difficult without additional years of data. While the use of scales to estimate age and spawning history may not be as accurate as otolith-based analyses (Duffy et al. 2012), the estimates they produce still provide a useful starting point for a previously uncharacterized population. Our estimates are likely biased towards underestimating the age of older fish (McBride et al. 2005), as annuli and spawning checks may be resorbed at the scale margins. Nevertheless, the confirmation of fish that were at least 8 and 9 years old, with some having spawned four or five times, is notable.

The observed greater age and high levels of iteroparity in American Shad may be related to the total length of their annual migrations. Migrations are energetically costly for a variety of reasons, including movement over long distances, reduced foraging opportunities, and gamete production. Migratory American Shad may lose up to 60% of somatic fat reserves and 40% of somatic protein reserves to reach the spawning grounds (Glebe and Leggett 1981). Those traveling farther use more of their energy reserves (Leonard and McCormick 1999).

Adults originating from the Penobscot River have a relatively short distance to cover to reach their summer feeding grounds in the Gulf of Maine (Talbot and Sykes 1958), and the close proximity of this system to marine feeding areas may be what makes a repeat spawning strategy possible (Leggett and Carscadden 1978). At the same time, the freshwater migrations of Penobscot River American Shad are also constrained by the current lack of passage in the system. In other northern rivers, including the Hudson River (Limburg 2001), Connecticut River (Watson 1968), and St. Lawrence River (Bouchard 1976), American Shad routinely migrate between 100 and 200 km upriver to spawning grounds before reversing course. Migration in the Penobscot River is currently limited to the 48 rkm downstream of Veazie Dam, and this short distance may also reduce migrants' energy expenditures related to spawning with resulting high levels of iteroparity.

Although American Shad in other systems have demonstrated an ability to recolonize newly accessible habitats (Bowman 2001; Weaver et al. 2003; Burdick and Hightower 2006), the overall population-level effect of dam removal in the Penobscot River remains to be evaluated. It is anticipated that American Shad will benefit from improved access and additional diverse spawning and rearing habitats associated with a longer migratory route (Limburg et al. 2003) as they have in the Santee River, South Carolina (Cooke and Leach 2003). Improved fish passage and increased habitat may negatively impact this population, however, as downstream delays at dams (Castro-Santos and Letcher 2010) and longer freshwater migrations (Leggett et al. 2004) may diminish the survival and reproduction of iteroparous individuals. It is unclear if improved passage and access will reduce iteroparity in Penobscot River American Shad, and future monitoring will be needed to evaluate this species' response to the PRRP.

Little is known about the seaward migrations of postspawn clupeids, and investigations into the postspawn movements of other iteroparous fishes have yielded conflicting results. Postspawning transit times and travel direction both appear highly variable. Movement studies with Brown Trout *S. trutta* have documented short (one or two tidal cycles) and highly directed egress through the estuary (Bendall et al. 2005), whereas Atlantic salmon employ a variety of seaward migration strategies (Hedger et al. 2009) including extensive estuarine reversals and delays (Hubley et al. 2008). We observed a systematic and persistent pattern of reversals in the lower estuary, which was previously unreported for American Shad. This behavior may be preparatory for return to the marine environment, compensatory for weeks spent spawning in freshwater, or both.

Dodson et al. (1972) tracked American Shad as they entered the Connecticut River estuary and found that the fish "meandered" for 24–53 h at the onset of freshwater migration. They reported that these movements were not a "typical behavioral response" to tidal fluctuation, and speculated that the fish were maintaining position at the leading edge of the saltwater wedge in order to adapt to freshwater (Dodson et al. 1972). Seaward movements by American Shad in the James River, Virginia, were also associated with tidal phase (Aunins and Olney 2009). This pattern may be related to the transition from freshwater to salt water, as suggested by the Connecticut River work on prespawning shad, or may be due to increased feeding opportunities and the resumption of feeding activity.

Better information exists on the osmoregulatory development for juvenile than for adult American Shad. Juvenile osmoregulatory acclimatization takes from 5 to 10 d (Zydlewski and Wilkie 2013) and typically occurs months before juveniles migrate out of freshwater into the estuary (Zydlewski et al. 2003). It is unclear whether adults are able to “preadapt” their osmoregulatory function in advance of leaving freshwater, or if this process is accomplished during their estuarine reversal phase. If adult American Shad acclimatize to elevated salinity in only a few days, then the extended duration of the reversal phase observed in the Penobscot River estuary suggests this behavior is due to more than just osmoregulatory acclimatization.

In addition to acclimatizing for re-entry into salt water, adults may use the reversal phase to replenish diminished energy reserves. American Shad were previously thought to cease feeding during spawning migration (Liem 1924; Moss 1946). More recent information indicates that riverine plankton may be too small for adults to capture effectively (Atkinson 1951) and that American Shad may feed opportunistically in freshwater when presented with suitable prey (Chittenden 1969).

Walter and Olney (2003) investigated the feeding behavior of migrating American Shad in the York River, Virginia, and found that feeding activity resumed during seaward migration, with stomach fullness increasing by 92% at midestuary (rkm 24). Mysid shrimp, *Neomysis americana*, comprised 97% of stomach contents in postspawning fish captured in the estuary, and this prey source was not available to American Shad farther upstream in freshwater (Walter and Olney 2003). While information on mysid shrimp populations in the Penobscot River system is lacking, sampling by Wilson (1978) indicated that copepods are more abundant at the mouth of the estuary than upriver in freshwater. American Shad movements in the reversal zone may be related to both the size and abundance of zooplankton prey, and future work could investigate the diets of postspawning American Shad to further evaluate feeding behavior and habitat use during seaward migration.

If feeding in the estuary, postspawning American Shad may optimize growth potential by maintaining position with respect to favorable environmental gradients. Throughout the summer of 2011, physical conditions in the lower estuary and reversal zone fluctuated with tidal cycle, with subsurface temperatures at rkm 15.3 ranging from 11°C to 23°C and salinity ranging from 5 to 26 ppt (M. O’Malley, NOAA–Fisheries, unpublished data). Tidal movements may offer optimal salinity (Jia et al. 2009) and temperature (Leggett and Whitney 1972; Neves 1979) for growth, along with reduced osmoregulatory costs in isosmotic conditions (Zydlewski and Wilkie 2013). Without additional information on the physical conditions experienced by postspawning American Shad, the driving mechanisms behind this tidal reversal behavior cannot be determined, and future research in this system may investigate this aspect of postspawning behavior and implications for iteroparity.

The implementation of the PRRP provides an important opportunity to evaluate alosine responses to dam removals in a northern river. Currently, American Shad are limited by impoundments in the lower river, but dam removal is anticipated to greatly expand access to suitable spawning habitat. This anticipated increase is entirely dependent upon effective upstream passage at what will become the lowermost impoundment in the system, Milford Dam. As a result, information of passage efficacy at this dam will be vital to management in the system. Future work on American Shad in the Penobscot River has obvious utility in assessing the relative success of the PRRP. In addition, the demographics of spawning runs, when compared with our work, may inform the relationship between migratory distance and iteroparity in American Shad.

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