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ARTICLE

River Reach Restored by Dam Removal Offers Suitable Spawning Habitat for Endangered Shortnose Sturgeon

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Abstract
The lowermost dam on the Penobscot River, Maine, was removed in 2013, making new habitat available for migratory fish. There is no evidence that endangered Shortnose Sturgeon *Acipenser brevirostrum* have spawned in the Penobscot River in recent years, but dam removal has facilitated access to potential freshwater habitat essential for spawning. Spawning success also depends on the quality of the available habitat. We sought to describe the distribution and amount of suitable spawning habitat in the first 5-km reach upstream of the removed dam. Previously collected river elevation and bottom substrate data were used to create two-dimensional hydrodynamic simulations of the reach for spring discharge levels ranging from 310 to 1,480 m^3/s using the program River2D. Simulations were validated and adjusted using field-collected data. Suitable spawning habitat was predicted based on literature-informed suitability curves of depth, velocity, and bottom substrate. Between 41% and 63% of the study area offered usable spawning habitat, depending on river discharge. Velocity was the most limiting characteristic to overall suitability at all modeled discharges. Embeddedness was minimal at suitable sites. Based on the habitat characteristics considered, the newly accessible reach of the Penobscot River could support Shortnose Sturgeon spawning, offering critical habitat for this endangered species.

Access to suitable freshwater habitat for spawning is vital for diadromous fish species' persistence. The restriction of movement in rivers by dams has detrimentally affected numerous species (e.g., Sea Lamprey *Petromyzon marinus*, Atlantic Salmon *Salmo salar*, and American Shad *Alosa sapidissima*; Liermann et al. 2012). Dams have contributed substantially to declines in Shortnose Sturgeon *Acipenser brevirostrum* populations by restricting access to freshwater spawning habitat required by the species (Limburg and Waldman 2009; Jager et al. 2016). Across the species' range (from the St. John River, New Brunswick, to the Altamaha River, Georgia (Dadswell et al.

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1984; Kynard et al. 2016), dam construction as well as other human impacts, like habitat degradation and fishing pressure (as bycatch), contributed to population declines over the last two centuries (Kynard 1997; Limburg and Waldman 2009; NMFS 2015). The species has been federally listed as endangered in the United States since 1967 throughout its range (NMFS 1998).

Kynard (1997) demonstrated a positive relationship between the abundance of adult Shortnose Sturgeon in northern and north-central populations and the maximum upriver spawning location, underscoring the negative impact dams impose on the species. Dam removals offer the potential for recovery of depleted populations by restoring access to upstream freshwater habitat that is critical for both spawning and growth. Larvae require adequate amounts of freshwater habitat downstream of spawning grounds to settle in areas where they are not exposed to salt water before they gain salinity tolerance at around age 1 (Jenkins et al. 1993). Dam removals on two large northern rivers offer some of the first opportunities to study how such restoration activities could impact the species. The removal of the Edwards Dam from the Kennebec River, Maine, in 1999 restored access to almost 30 km of habitat. Within 10 years of the removal, Shortnose Sturgeon spawning was confirmed in the restored habitat (Wippelhauser et al. 2015). More recently, two dam removals from the Penobscot River, Maine, facilitated access to 14 km of historic Shortnose Sturgeon habitat (Figure 1). The Great Works Dam (river kilometer [rkm] 58) removal was completed over the summer of 2012, and the Veazie Dam (rkm 46.8) removal occurred from July to November 2013. Milford Dam (rkm 62) is now the lowermost dam on the river, and it sits at a natural falls that would have been impassable to Shortnose Sturgeon even prior to dam construction (Opperman et al. 2011; PRRP 2016).

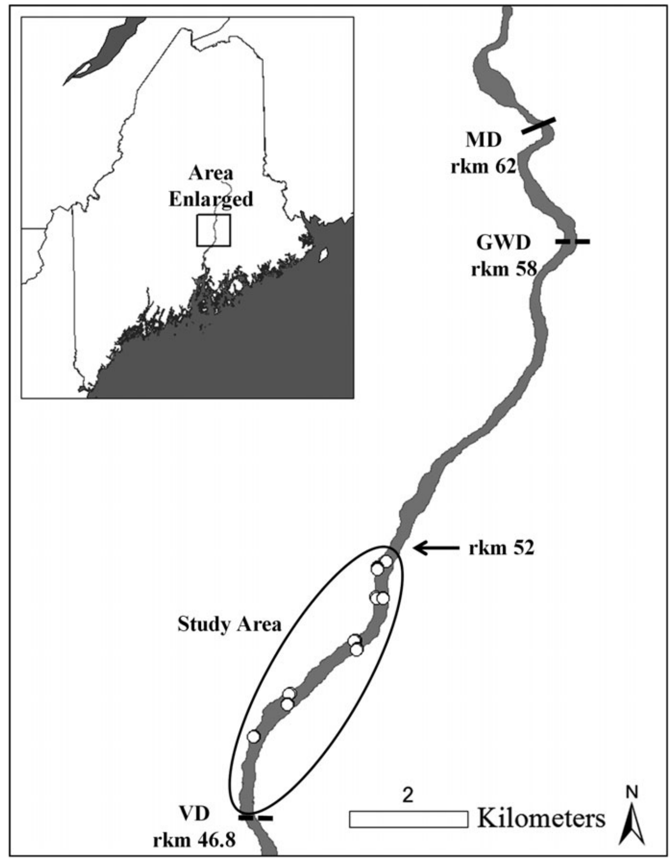

FIGURE 1. The lower Penobscot River, Maine. Removed dams are represented by dashed lines (GWD = Great Works Dam, removed in 2012; VD = Veazie Dam, removed in 2013). Milford Dam (MD) is now the lowermost dam on the main-stem Penobscot River. The study area (rkm 47–52) is circled. Calibration data collection points are shown in white (multiple sampling points occurred in close proximity at each location shown).

Migratory fish movement in the Penobscot River has been impacted by dams since the 1820s (Opperman et al. 2011). The Penobscot River Restoration Project (PRRP) dam removals (Opperman et al. 2011) restored access to 100% of the Shortnose Sturgeon's historic range in the Penobscot River, but whether individuals will spawn in the newly accessible habitat is unknown. The first documented use of habitat upstream of the former Veazie Dam (rkm 46.8) occurred in October 2015, when three acoustically tagged fish moved into the first 5 km of restored river (Johnston 2016), but spring movements upstream of the former Veazie Dam have not been documented (Johnston 2016). Females with late-stage eggs have been captured in the Penobscot River during summer and fall (Fernandes et al. 2010; Dionne et al. 2013; Johnston 2016); based on the species' migratory behavior in other northern rivers like the Connecticut River, these females would be expected to remain in-river until spawning the next spring (Buckley and Kynard 1985; Kynard 1997; Kynard et al. 2016). However, no evidence of spawning in the spring has been collected, and after overwintering in the Penobscot River, these maturing females were often detected on spawning grounds 140 km away in the Kennebec River during the spring spawning period (Fernandes et al. 2010; Zydlewski et al. 2011; Dionne et al. 2013; Wippelhauser et al. 2015; Johnston 2016). A central question is whether mature Shortnose Sturgeon will continue to migrate to the Kennebec River to spawn or will begin to use the newly available freshwater habitat in the Penobscot River. Spawning in the Penobscot River could benefit Shortnose Sturgeon recovery in the region, but that outcome would depend on the availability of areas with physical characteristics that meet the species' spawning requirements (Kynard 1997). This research focused on describing the quality of habitat made available by the PRRP Veazie Dam removal.

Suitable water temperatures and flow conditions must be present to trigger the final maturation of Shortnose Sturgeon eggs and induce spawning activity (Buckley and Kynard 1985). In other northern river systems, Shortnose Sturgeon spawn after peak spring flows, when discharge returns to moderate levels (Buckley and Kynard 1985; Kieffer and Kynard 1996; Kynard 1997). Suitable river temperatures range from 9°C to 15°C (Taubert 1980; Dadswell et al. 1984; Kynard 1997). These conditions are annually present in the Penobscot River, but Shortnose Sturgeon spawning has not been documented (Fernandes et al. 2010; Wegener 2012; Johnston 2016).

Although river discharge and temperature are considered key determinants of the timing of Shortnose Sturgeon spawning, the location of spawning activity is governed by bottom substrate and by water depth and velocity. Spawning typically occurs in the main channel of a river at water depths ranging from 1.2 to 10.4 m (Richmond and Kynard 1995; Kieffer and Kynard 1996). Suitable water velocities for northern populations of the species range from 0.36 to 1.2 m/s based on research conducted in the Connecticut, Merrimack, and Androscoggin rivers (Buckley and Kynard 1985; Squiers et al. 1993; Kieffer and Kynard 1996). The survival of Shortnose Sturgeon's adhesive eggs has been postulated to depend on suitable water velocities. At high velocities, eggs might not adhere to substrate; at low velocities, eggs could deposit in clumps, inhibiting oxygen uptake and increasing the risks of predation and fungal growth (Buckley and Kynard 1985; Crance 1986). Survival of larvae is dependent on velocities of 0.4–1.2 m/s, which allow sufficient downstream drift to rearing habitat (Buckley and Kynard 1981; Richmond and Kynard 1995).

River bottoms composed of substrate with large interstitial spaces have been described as critical for successful spawning because they provide protection from currents, surface area for egg adhesion, and protection from predators (Kynard 1997; Cooke and Leach 2004). Substrate grain size-classes considered most suitable for spawning include boulder, cobble, and gravel (grain sizes ≥8 mm; Dadswell 1979; Taubert 1980; Buckley and Kynard 1985). Highly embedded river bottoms (e.g., bottoms composed of cobble with a large volume of sand grains interspersed) are not suitable for Shortnose Sturgeon spawning because the fine sediment fills the interstitial spaces that are important for egg and embryo retention and concealment (Richmond and Kynard 1995; NMFS 1998).

The goal of this study was to describe the distribution and amount of suitable spawning habitat in the Penobscot River upstream of the lowermost dam removal site. We used hydrodynamic modeling validated with field measurements to address this goal. We focused on the 5-km reach just upstream of the former Veazie Dam site from rkm 47 to rkm 52 (Figure 1). Specific objectives included (1) creating hydrodynamic simulations of the study area at representative spring river discharge rates; (2) applying field-measured water depth, velocity, and bottom substrate grain size data to validate and adjust simulations; (3) predicting suitable spawning habitat for Shortnose Sturgeon based on combined depth, velocity, and bottom substrate grain size; and (4) refining suitable habitat predictions by incorporating bottom substrate embeddedness.

STUDY SITE LOCATION AND GEOMORPHOLOGY

The Penobscot River watershed is the largest in the state of Maine, draining over 22,000 km^2 (Figure 1). Its largest tributaries, the East and West branches, join at rkm 160 to flow south into Penobscot Bay (rkm 0 is defined as the southern end of Verona Island). The river valley traverses through two physiographic settings dominated by igneous rock types, with the river channels set within metamorphosed rocks. The headwaters of the East and West branches flow through the Central Maine Highlands, which has mountainous terrain, including Mt. Katahdin (Denny 1982). Downstream of the confluence of the East and West branches, the main stem of the Penobscot River flows across the Coastal Lowlands, where the river valley is relatively wide and there are numerous depositional features, such as sediment bars and terraces, inspiring identification as the Island Division (Kelley 2006). The fluvial portion of the river between rkm 62 and rkm 36, identified as the Rapids Division (Kelley 2006), contains the study area. This downstream-most reach of the fluvial system is characterized by multiple rapids and few depositional features compared to the upstream reach (Dudley and Giffen 1999). River kilometer 52 was chosen as the upstream limit for several reasons: (1) the reach from rkm 47 to rkm 52 is the first habitat that sturgeon will encounter upstream of the former dam site, (2) it lies just downstream of a set of rapids (FERC 1997) that may create a velocity barrier to Shortnose Sturgeon passage at certain river discharges (Wegener 2012), and (3) bathymetry and substrate data for areas upstream of these rapids were not available. The active channel width is approximately 200 m along the reach, and some manmade structures related to log drive activities remain in some locations, creating local obstructions to flow in portions of the channel width.

The present-day morphology of the river, including the bottom sediment characteristics, is derived from a sequence of events related to the deglaciation approximately 12,000 years ago (Borns et al. 2004) that affected the competence and capacity of the fluvial system to carry sediment. Down-cutting through glacial outwash deposits continued down to bedrock outcrops that provide the modern base-level control along the river profile. A large amount of sediment was conveyed downstream to what is currently a paleo-delta in the tidal portion of Penobscot Bay. However, the sediment supply was reduced as the glacial deposits were progressively eroded away. Remnant terrace and floodplain deposits are still observable today in the Island Division upstream of rkm 62. Visual observations of contemporary river conditions indicate that they are rarely mobilized in large quantities over short time periods through large-scale river bank erosion and morphodynamics. Transport capacity was reduced after isostatic rebound following glacial retreat, causing a substantial reduction (estimated ~25%) in the extent of the Penobscot River drainage area contributing to surface flows (Kelley et al. 2011). Isostatic adjustments linked to glacial retreat and evacuation of outwash deposits also decreased the longitudinal gradient of the river, reducing sediment transport competence—specifically the ability of the flow to move gravels and larger-sized sediment particles (Hooke et al. 2017).

The slope and water discharge rates in the Rapids Division, which holds our study area, are steep enough to efficiently pass the fine-sediment grain sizes but are not large enough to entrain the coarse grain sizes (large gravel and cobbles) that dominate the bed of the river where bedrock outcrops are not present. Fine grain sizes of sand size or smaller are supplied to the main stem of the river at low rates, far less than the capacity of the river flows. The fine-grained sediment supply is further limited by the minimal thickness of soil and regolith produced since deglaciation of the landscape. Deposits of gravel-sized or smaller sediment that do exist are mostly stored in the Island Division of the river, where bedrock outcrops have created gentle gradients (Kelley 2006; Hooke et al. 2017).

No large floodplain sediment deposits or bar formations have been observed in the study site. Extensive deposits of fine-sediment grains were not observed upstream of Veazie Dam prior to its removal, and most of the head pond bottom was dominated by cobble, boulders, and exposed bedrock (CR Environmental 2008). The notable absence of fine-grained deposits upstream of the dam is unique compared to the relatively large amount of sediment commonly stored behind dams in other physiographic settings, such as the Mid-Atlantic Piedmont, where watersheds have relatively high modern sediment yield conditions (Collins et al. 2017). Some portions of both shorelines in the study reach do contain sand- and gravel-sized sediment, presumably created by the few relict deposits on the valley sides, relatively low flow velocity conditions, and delivery of sediment from bank erosion to the river channel in those areas. An eroding bluff is located on the east side of the river at rkm 47 and is a potential source of sand- and gravel-sized sediment. These conditions generally make nearshore side areas of the channel highlighted targets for detecting changes after dam removal. In particular, changes in sediment grain sizes and deposition thickness in nearshore areas can result from impoundment drawdown effects on shoreline stability.

The U.S. Geological Survey (USGS) stream gauge at West Enfield, Maine (station 01034500), is approximately 53 km upstream of the study area and is the closest gauge recording river discharge. The drainage area at the West Enfield station is 17,278 km^2. The mean annual flow there is 345 m^3/s for the period of record (1903–2015). The range of flows during the spring season (i.e., the period of interest, during spawning) varied from approximately 130 to 960 m^3/s. For the 10-year period from 2006 to 2016, the mean spring flow was 576 m^3/s.

METHODS

Hydrodynamic simulations were generated using River2D, a two-dimensional, depth-averaged model based on a conservative form of the St. Venant equations (Ghanem et al. 1996; Steffler and Blackburn 2002; Waddle 2010). Data used to create the hydraulic model domain included georeferenced bed elevation points (from bathymetry data) and associated bed roughness height at each point (from substrate data). A computational mesh was created with R2D_Mesh by defining the perimeter of the study area and boundary condition parameters: inflow discharge, inflow elevation, and outflow elevation. The simulation was run to convergence, and results were compared to field-measured data to calibrate and validate the simulation. Inflow and outflow water surface elevations were adjusted to build the final simulations used to acquire habitat suitability predictions. An additional examination of spawning habitat suitability was accomplished by examining composite suitability and embeddedness data using ArcGIS for Desktop version 10.2.2 (Environmental Systems Research Institute [ESRI], Redlands, California). Statistical analyses were performed in R version 3.3.2 (R Core Team 2015).

Bathymetry and substrate data collection and validation.— Bathymetry and substrate data used in the River2D simulations were collected in 2007, prior to dam removal (CR Environmental 2008). A SyQwest Hydrobox precision echosounder (SyQwest, Inc., Cranston, Rhode Island) and a Trimble DGPS (Trimble, Sunnyvale, California) were used to collect bathymetry data. A side-scan sonar (Edgetech Model 560; Edgetech, Inc., West Wareham, Massachusetts), sediment sampling, and video surveys were used to generate a bottom substrate map (for more detailed data, refer to CR Environmental 2008). Because our interest was in postdam-removal conditions, we assessed the validity of using the predam-removal data collected in 2007 to simulate postdam-removal conditions. To do this, we estimated the conditions necessary for incipient motion of the river bottom sediment

(Wilcock et al. 2009) using the U.S. Forest Service's Bedload Assessment for Gravel-Bed Streams (BAGS) program to calculate bed load transport rates (Pitlick et al. 2009) and to estimate the grain sizes most likely to move under the discharge conditions experienced since 2007 (see the Supplement available in the online version of this article for details). Although we also used the 2007 bed elevation data, we assumed that only water surface elevations relative to the river bottom would change after dam removal.

After validating the applicability of the 2007 survey data to postdam-removal modeling, the 2007 survey map delineating substrate facies was georeferenced in ArcMap (ESRI), and the facies polygons were digitized into a layer of dominant substrate types. Each point in the River2D input file was assigned a substrate type by performing a spatial join of the substrate data to the bed elevation data set. The bottom substrate conditions were included in the River2D input file as a roughness height (k_s) by using half the median diameter of the dominant substrate at each point in the data file.

River2D simulations.— Discharge rates for River2D simulations were chosen to characterize suitable habitat availability under a range of conditions representative of spring flow rates in the Penobscot River. Discharge data were collected for spring dates on which water temperature was suitable for Shortnose Sturgeon spawning (9–15°C), and five discharge conditions associated with the 5th, 25th, 50th, 75th, and 95th percentiles were determined (Supplement).

Inflow and outflow water surface elevation values were specified as input parameters to each spring discharge simulation and were acquired using USGS gauge data (Supplement). Field-collected depth and velocity data were used to calibrate and validate each simulation. Paired *t*-tests were used to compare simulated values with field-collected values for a simulation run for the discharge on the day of calibration data collection (678 m^3/s). Linear regression was performed to test for correspondence between measured and simulated values, and a hypothesis test was performed to determine whether the slopes of the relationships were equal to 1. Depth values associated with each spring discharge rate were also calibrated based on the field measurements and USGS gauge data. See the Supplement for details.

Predicting habitat suitability.— Habitat suitability index (HSI) curves for Shortnose Sturgeon spawning habitat were used for calculating habitat suitability in River2D (Figure 2). Habitat suitability index values from 0.7 to 1.0 were considered highly suitable, HSI values from 0.40 to 0.69 were deemed moderately suitable, and HSI values from 0.0 to 0.39 represented low suitability. We created HSI curves for depth, velocity, and channel index (the metric used to represent bottom substrate) based on Wegener (2012), Crance (1986), and Squiers et al. (1993). Two velocity HSI curves were created: the original curve based on literature reports; and a second, adjusted curve, which was derived by applying the measured versus simulated velocity regression equation (Figure 3B, inset) to the velocity values of the original curve.

After model creation and validation, habitat suitability at each spring discharge was estimated using the PHABISM weighted usable area (WUA) approach in River2D (Bovee 1982). The HSI curves were loaded into River2D, and linear interpolation was used to determine the HSI value for each characteristic at each node. The minimum calculation approach (Steffler and Blackburn 2002; for each node of the mesh, the minimum value for the three separate suitability indices) was used to determine combined suitability. The WUA was calculated by multiplying the combined suitability value at each node by the area associated with the node and summing the WUAs for all nodes. Percent WUA is the WUA relative to the total area of the wetted study reach.

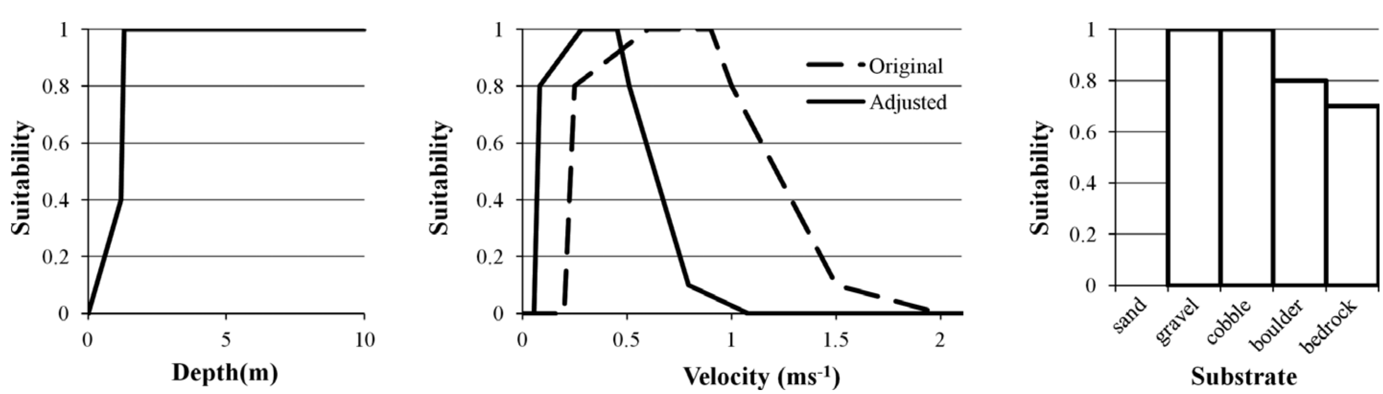

FIGURE 2. Shortnose Sturgeon spawning habitat suitability index curves for depth (m), velocity (m/s), and bottom substrate (represented by channel index in the model).

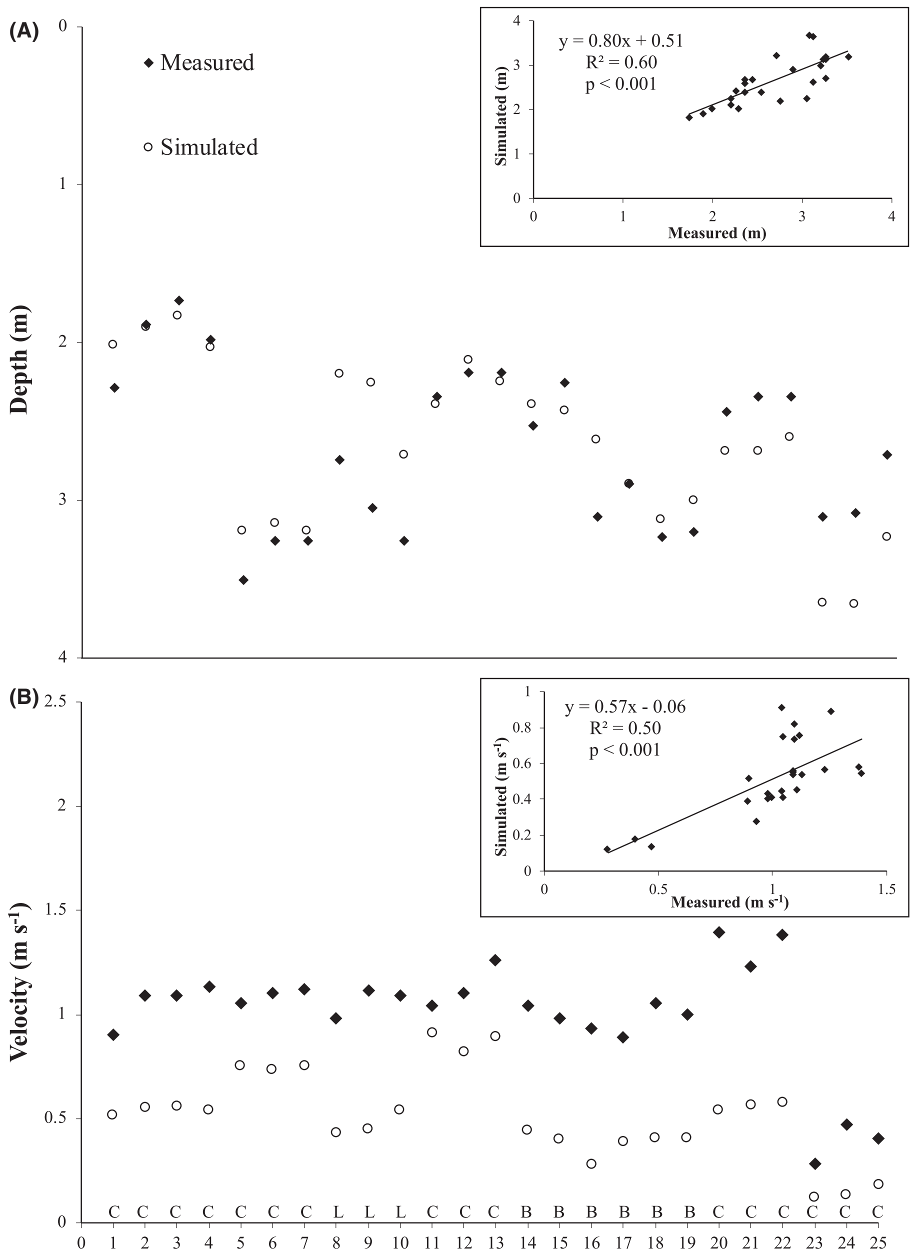

FIGURE 3. Measured and simulated **(A)** depths (m) and **(B)** velocities (m/s) at 25 sites (*x*-axis) within the study reach of the Penobscot River for a discharge of 678 m^3/s. The inset graphs are linear regressions of measured versus simulated depths (A) and velocities (B). Letters associated with each site indicate bottom substrate type: cobble (C), bedrock (B), or boulder (L).

The suitability results were examined to determine which of the three habitat characteristics (depth, velocity, or bottom substrate) was most limiting under each discharge condition. For the five simulated discharges, the habitat characteristic that produced the smallest percent WUA value was the most limiting characteristic to combined suitability.

Habitat suitability analyses in ArcMap.— For each spring discharge simulation, the suitability results files were imported to ArcMap for additional analyses. The combined suitability value of each simulation node was used to assign cell values to an output raster, with the mean value option used when more than one node fell within a cell. Raster cell size was 10.4 × 10.4 m. Raster-based WUA was calculated by multiplying the cell's suitability value by the cell area and summarizing the entire study area. Total area was calculated by summing the area of polygons created from the raster. The process was repeated using each spring discharge habitat suitability raster, and the percent WUA resulting from each method was compared to confirm that this method corresponded closely to the approach used in River2D to calculate WUA. The mean difference between percent WUA values calculated from the rasters versus River2D was 0.5%. Rasters for the five spring discharges were averaged to create a composite map of habitat suitability for all simulated spring discharges. To test for a relationship between the distance upstream of the former Veazie Dam and composite suitability, the "Locate Features Along Routes" tool (ESRI) was used to determine the distance of each of the simulation nodes upstream of the dam. Pearson's product-moment correlation was used to test this relationship (Harrell and Dupont 2018).

Combining embeddedness with habitat suitability.— Because HSI curves for embeddedness have not been computed for Shortnose Sturgeon, but embeddedness could be an important determinant of spawning habitat suitability (Richmond and Kynard 1995; NMFS 1998), we separately mapped embeddedness throughout the study area (rkm 47–52) for joint consideration with HSI predictions. Embeddedness data collection was based on a modified system described by Cooke and Leach (2004). Embeddedness measurements were taken along both shores of the river during late summer of 2015, when river flow stage was at its minimum, exposing habitat that would be covered during the spring spawning season. A tape measure was extended perpendicular to the river along the shoreline from the vegetation line down to 1 m into the river. A meter stick was laid parallel to the river at each meter along the tape measure, alternating in the upstream or downstream direction. A sediment particle immediately adjacent to each 10-cm mark along the meter stick was examined to determine its extent of embeddedness. The percent coverage by fine sediment was summarized using a rating system from 1 to 5 (Platts et al. 1983); 75–100% coverage with fine grains corresponded to a rating of 1, and less than 5% coverage by fine grains corresponded to a rating of 5. The overall embeddedness rating at each transect (n = 20) used for analysis in this study was the median value for each site.

A spatial join was performed to relate each site where embeddedness was measured to composite suitability. Embeddedness survey sites were assigned the composite suitability value of their closest raster cell, and the joined attribute table was exported for statistical analysis. Pearson's product-moment correlation was used to test the relationship between embeddedness rating and composite suitability value.

A separate index, "Embeddedness + HSI," was calculated using embeddedness rating and composite habitat suitability. To do this, we scaled the embeddedness ratings for each site to the same 0–1 range as habitat suitability by dividing the embeddedness values by 5. We added the scaled embeddedness rating for each site to the composite suitability value associated with it and divided by 2.

RESULTS

Substrate Data Validation

Results of the BAGS incipient motion analyses suggested that substrate data collected in 2007 could be used to predict postdam-removal habitat suitability (Supplement). There was no difference in the pre- and postdam-removal geometric mean grain size for the upper or lower reach cross sections; the geometric mean grain sizes transported in the upper and lower cross sections were 38 and 32 mm, respectively, for all discharge scenarios. This consistent result suggests that changes in substrate composition since 2007 would be limited to the movement of very coarse gravel and smaller grains. Only 4% of the total study area was reported to be covered by gravel and sand (CR Environmental 2008), and the site remains fine sediment limited due to its glacial history (Borns et al. 2004). Based on these facts, changes to the area since 2007 were assumed to be limited, and the 2007 survey data were used for the River2D modeling of suitable spawning habitat. See the Supplement for additional results.

Model Calibration and Validation: Depth and Velocity

The five discharge levels used to represent spring river conditions were 310, 422, 667, 972, and 1,480 m^3/s (Table 1). All spring discharge simulations were calibrated to predict depths comparable to field-measured depths (Table 1; Figure 3A). For the calibration day simulation, linear regression confirmed a significant correspondence between measured and simulated depths (Figure 3A, inset; $n = 25$, $R^2 = 0.60$, $P < 0.001$). The slope of the regression line (95% confidence interval [CI] = 0.518–1.083) was not significantly different from 1.0, indicating a lack of skew ($P = 0.157$).

Simulated depth-averaged velocity predictions differed from field-measured depth-averaged velocities, even after bed roughness values and eddy viscosity coefficients were adjusted in River2D (Steffler and Blackburn 2002). Predictions were consistently lower than measured values (Figure 3B; $n = 25$, paired t-test: $P < 0.001$). Measured and simulated velocities were correlated, with an R^2 value of 0.50 and a difference of 0.49 m/s (Figure 3B inset; $P < 0.001$). A hypothesis test for determining whether the slope of the regression line (95% CI = 0.326–0.815) was equal to 1.0 pointed to skew ($P = 0.001$). The SDs of measured and simulated velocities were 0.27 and 0.21 m/s, respectively. When the velocity validation results were considered along with bottom substrate type (see the Supplement), mean differences between measured and simulated velocities ranged from 0.43 to 0.59 m/s. When only bottom velocity (rather than depth-averaged) measurements were compared to simulated values, they still differed by 0.25 m/s (Supplement; paired *t*-test: $P < 0.001$). As such, velocities predicted by the five spring discharge simulations were found to be underpredicted.

To adjust for the difference between actual and simulated velocities, two velocity HSI curves (original and adjusted) were used to evaluate combined suitability at the five spring discharge levels. An adjusted velocity HSI curve (Figure 2) was created by applying the measured versus simulated velocity regression equation (Figure 3B, inset) to the original curve to account for the model's underprediction of velocity. The original velocity HSI curve resulted in greater percent WUA for all discharge rates compared to the adjusted curve (Figure 4). The mean difference between percent WUA at each discharge level using the original and adjusted velocity curves was 18.2 ± 5.4% (mean + SE). Because the adjusted velocity HSI curve was most representative of field-measured conditions and resulted in the most conservative estimate of WUA, it was used for the remaining assessments of habitat suitability.

Habitat Suitability Predictions

Habitat suitable for Shortnose Sturgeon spawning was predicted to be present throughout the length of the study reach at all discharge levels considered (Figure 4) and generally expanded with increasing discharge ($R^2 = 0.77$, $P = 0.05$). Percent WUA was least for the 5th and 10th percentile discharge simulations, with 41% of the study area being usable (Table 2). Percent WUA was greatest for the 75th percentile discharge simulations, with 63% of the study area being usable. Within all simulations, suitability was generally low along the western shore of the study area between rkm 48.25 and rkm 49 (Figure 5). Suitability at all discharges was also limited (to varying degrees depending on the discharge) around the bend in the river at rkm 50.75 and within the main channel of the river upstream of the bend around rkm 51 and downstream of the bend around rkm 50.

Velocity was the most limiting characteristic for suitable spawning habitat in the study area at all spring discharges (Table 2). Percent WUA based on velocity ranged from 55% to 77%, percent WUA based on depth ranged from 75% to 100%, and percent WUA based on bottom substrate stayed constant at about 82%.

The composite suitability map of all five spring discharges indicated that 51% of the study area offered usable habitat for spawning (Figure 6). Two regions provided the highest suitability at all flows: the most upstream portion of the study area (around rkm 52); and the mid-channel habitat between rkm 47.5 and rkm 49. There was a significant but weak relationship between distance upstream of the former Veazie Dam and composite suitability. Pearson's product-moment correlation between distance and composite suitability was significant ($P < 0.001$), with a coefficient (Pearson's *r*) of −0.1.

Embeddedness

Sites with suitable levels of embeddedness (i.e., little to no fine sediment dispersed in larger substrates, or a rating of 4 or 5) were distributed throughout the study area on both shores of the river (Figure 6). East shore sites had a median embeddedness rating of 4.1, while the west shore sites had a median embeddedness of 3.1. The mode for all sites was 5, and the average was 3.5 ($n = 20$). Locations where embeddedness measurements were collected that were within areas of high (0.7–1.0) composite suitability exhibited low levels of embeddedness (ratings of either 4 or 5; Figure 6). In areas with moderate (0.40–0.69) composite suitability, 70% of the sites had low embeddedness, and in areas with low composite suitability (0.0–0.39), 33% of the sites had low embeddedness. Embeddedness decreased as the composite suitability value for a site

TABLE 1. Depth calibration paired *t*-test results (CI = confidence interval). Mean difference is the difference between simulated and measured depths for the lower Penobscot River.

Percentile	Discharge (m^3/s)	Mean difference (m)	95% CI	*P*
Calibration day	678	0.03	−0.12, 0.17	0.70
5th	310	−0.10	−0.22, 0.03	0.14
25th	422	−0.11	−0.25, 0.03	0.13
50th	667	−0.002	−0.14, 0.14	0.98
75th	972	0.28	−0.06, 0.62	0.10
90th	1,480	0.34	−0.06, 0.74	0.09

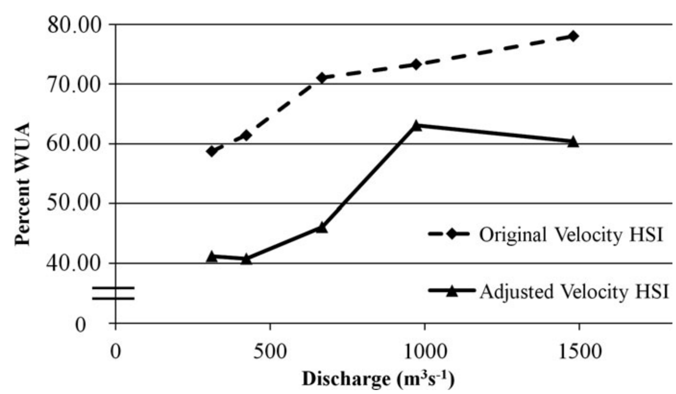

FIGURE 4. Percent weighted usable area (WUA) at five spring discharge levels (m^3/s) in the lower Penobscot River. Results using both the original velocity habitat suitability index (HSI) curve and the adjusted curve are shown.

increased (Pearson's $r = 0.47$, $P = 0.037$). Overall, 10 of the 20 embeddedness sites had joint Embeddedness + HSI index values of 0.7 or greater, indicating the predominance of highly suitable habitat.

DISCUSSION

Suitable habitat for Shortnose Sturgeon spawning was predicted to be available in the first 5 km of newly accessible habitat in the Penobscot River. Spawning by Shortnose Sturgeon has yet to be documented in the Penobscot River (Fernandes et al. 2010; Wegener 2012; Dionne et al. 2013; Johnston 2016), but with an increase in available freshwater habitat after dam removal and with the predicted presence of suitable spawning habitat, spawning is more likely. Successful reproduction in the Penobscot River would indicate progress toward recovery of this endangered species in the Gulf of Maine. In the Kennebec River, Shortnose Sturgeon returned to historical spawning habitat within 10 years of the Edwards Dam removal, and spawning was confirmed in the restored reach by the collection of early life stages (Wippelhauser et al. 2015). Shortnose Sturgeon in the Penobscot River were first confirmed to access newly available habitat as far upstream as rkm 52 in fall 2015 (Johnston 2016). However, in the spring, when we expect spawning to occur, individuals have not been documented moving upstream of the former Veazie Dam site at rkm 46.8 (Johnston 2016). By focusing on the study area from rkm 47 to rkm 52, we were able to determine that suitable habitat is available in the reach that would be first accessed by Shortnose Sturgeon if they return upstream of the former Veazie Dam during spring to spawn.

TABLE 2. Percent weighted usable area (WUA) by habitat characteristic for each spring discharge rate using the adjusted velocity habitat suitability index curve. Values denoted by asterisks are the lowest percent WUA for that spring discharge rate and represent the habitat characteristic that is most limiting to combined suitability (presented in the bottom row).

	Spring discharge (m^3/s)				
Characteristic	310	422	667	972	1,480
Depth	75	77	91	97	100
Velocity	58*	56*	55*	77*	74*
Bottom substrate	82	82	83	82	82
Combined suitability	41	41	46	63	60

Shortnose Sturgeon have been described using 1- or 2-km-long reaches for spawning in other rivers (Kieffer and Kynard 1996; Wippelhauser and Squiers 2015). The 5-km study area described in this research may represent the reach most likely to support spawning because the rapids at rkm 53 could present a velocity barrier to Shortnose Sturgeon during times of high river discharge. Our results indicate that between 41% and 63% of this reach is usable habitat for Shortnose Sturgeon spawning. Although the present study focused on the first 5 km of this newly available habitat, future research on the reach from rkm 52 to Milford Dam (rkm 62) would enhance understanding of the quality of habitat made available by the PRRP dam removals because, as a whole, the 14-km reach restored

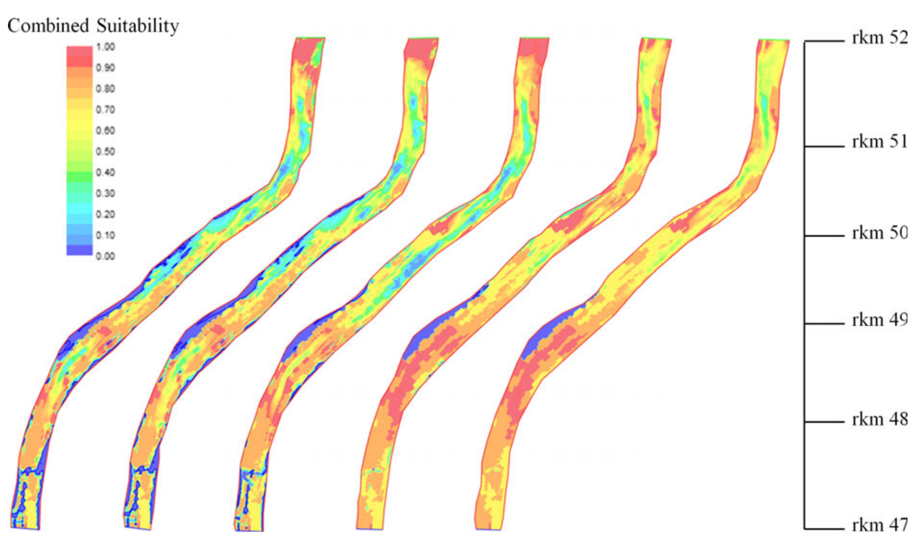

FIGURE 5. Spawning habitat suitability maps for the five spring discharge levels (using the adjusted velocity habitat suitability index curve) in the lower Penobscot River. Areas with the highest combined (depth, velocity, and channel index) suitability are shown by the warmest colors. The far-left simulation is for the discharge of 310 m^3/s, and each progressive map represents simulations with increasing discharge (422, 667, 972, and 1,480 m^3/s [far right]).

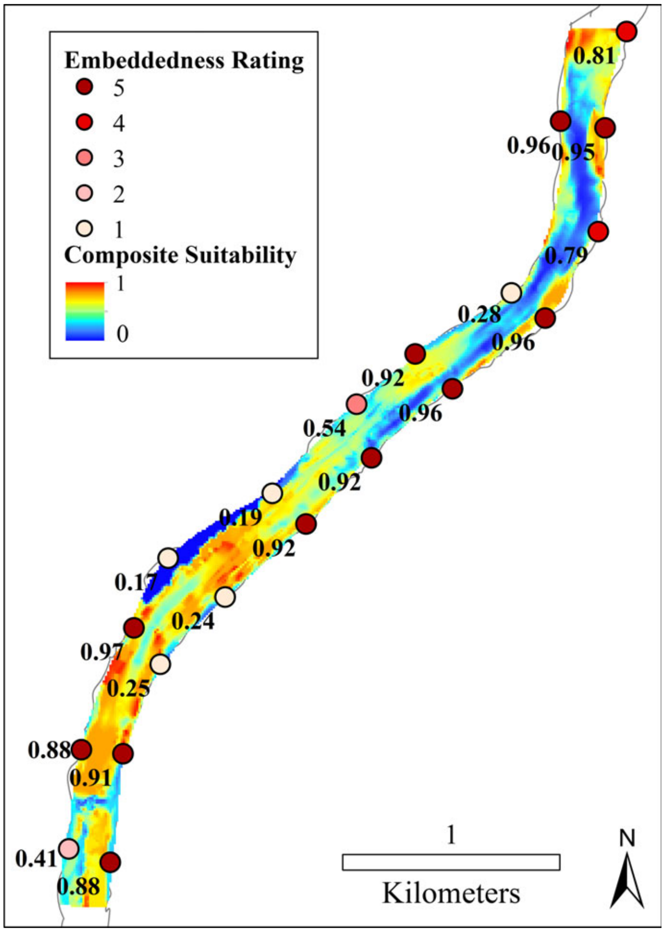

FIGURE 6. Composite map of habitat suitability within the lower Penobscot River study area at all spring discharge rates. Areas with the warmest color are predicted to offer highly suitable habitat at all five spring discharge rates. Areas with the coolest color do not offer suitable spawning habitat at any discharge. Embeddedness data points are shown along the shore, with a color gradient representing the median rating of embeddedness at each site. Darkest red is least embedded (most suitable for spawning habitat); light pink is highly embedded with fine sediment (not suitable). Values associated with each embeddedness point represent the Embeddedness + HSI index (HSI = habitat suitability index).

by the removals of Veazie Dam and Great Works Dam represents a substantial increase in the amount of critical freshwater habitat for Shortnose Sturgeon in the Penobscot River. If spawning commences, the survival of larval and young-of-the-year Shortnose Sturgeon will depend on adequate freshwater habitat downstream of the spawning site to allow them to grow without exposure to salt water (Dadswell 1979; Jenkins et al. 1993). Shortnose Sturgeon larvae have been reported to travel between 15 and 25 km from spawning grounds to downstream rearing habitat (Taubert 1980; Bath et al. 1981). In the Penobscot River, salt water has been reported to reach rkm 20 or rkm 30 during the spring, while in drier summer months, salt water can reach rkm 32 or rkm 42 (Haefner 1967; Stich et al. 2016). Prior to the PRRP dam removals, access to freshwater spawning and rearing habitat was limited by the Veazie Dam at rkm 46.8. Now, if spawning commences within the study area or upstream as far as rkm 62, up to 42 km of freshwater habitat would be available to fish for rearing, depending on the intrusion of salt water.

Our model predicts that Shortnose Sturgeon would find the greatest amount of usable spawning habitat during springs with high discharge. In 7 of the last 10 years, discharge rates exceeded the 75th percentile discharge; in 2 of the 10 years, values exceeded the 90th percentile discharge. A Shortnose Sturgeon that lives to be 50 years old, perhaps spawning five or six times in its life (Dadswell 1979; Kynard 1997), might encounter discharges close to the 75th percentile value twice and discharges around the 90th percentile value once. Usable spawning habitat will be most prevalent in the study area at these high discharges; however, lower discharges also provide conditions offering usable habitat.

Water velocity, which is thought to be the most important habitat characteristic determining spawning habitat suitability (Kieffer and Kynard 1996; Kynard 1997), was the most limiting characteristic for all spring discharge simulations. Spawning habitat choice has been related to the water velocity requirements for egg and larval survival (Kieffer and Kynard 1996; Kynard 1997). Water depth and bottom substrate were less limiting for combined suitability. Bottom substrate consistently provided a high percent WUA for all discharges, while depth provided lower percent WUA values at the lowest discharges and became less limiting at the highest discharges. The composite suitability map reflects the limitations imposed on combined suitability at all discharges and illustrates that suitable spawning habitat is absent in the main channel within the upper part of the study area due to high velocities. Further collection of velocity measurements from the field would provide higher confidence in simulations predicting suitable spawning habitat and perhaps would address the skewed relationship between simulated versus field-measured velocities that we observed.

Spawning Shortnose Sturgeon in other rivers prefer bottoms composed of gravel, cobble, boulder, and ledge (Crance 1986; Squiers et al. 1993; Kieffer and Kynard 1996). In addition, spawning habitat is expected to contain low levels of embeddedness because fine grains within interstitial spaces can limit egg survival (Richmond and Kynard 1995; NMFS 1998). The reach upstream of the former Veazie Dam is dominated by suitable bottom substrates and, based on available data, is characterized by moderate to low levels of embeddedness. The limited embeddedness found at most sites is consistent with the geology of the Penobscot River, with its limited supply of fine sediment (Dudley and Giffen 1999; Borns et al. 2004).

Habitat suitability predictions from hydrodynamic simulations were based on calibrated and field-checked results. Field-collected measurements were used to successfully calibrate all spring discharge simulations for depth. The River2D model underestimated velocities (consistent with observations by Waddle 2010 and Wegener 2012). We addressed this by using a correction to adjust the HSI curve. Based on the percent WUA predicted using the original and adjusted velocity HSI curves (Figure 4), the adjusted HSI curve resulted in more conservative estimates of percent WUA. We also addressed our use of the 2007 substrate data to represent the river bottom and found that this was reasonable based on calculated incipient motion and transport rates (Supplement). Additionally, the geologic characteristics of the Penobscot River watershed support our use of predam-removal substrate data; the study site falls in an area defined as a high-energy reach with limited fine-sediment supply (Dudley and Giffen 1999; Borns et al. 2004; Kelley 2006). We also acknowledge that our embeddedness surveys were conducted along the shoreline and not across the entire width of the river, but because they were performed during a period of low flow in late summer and early fall, the surveyed area still represents what would be potential habitat during higher spring flows. Due to the high-energy nature of the Penobscot River, we expect that fine-sediment deposition in the deeper channel is less likely than deposition along the shore. Therefore, our prediction of the study area being suitable based on low embeddedness is likely conservative. Current-day substrate and higher-resolution embeddedness data would be effective in decreasing the uncertainty of using predam-removal data.

We acknowledge that the inclusion of depth, velocity, and bottom substrate as independent (or equally important) features of the environment is an assumption of our approach using River2D and deviates from reality. To compensate for the default equal weighting of these habitat characteristics in River2D, we examined the WUA predictions based on depth, velocity, and bottom substrate separately. This provided insight into how each characteristic contributed to the suitability predictions since researchers have suggested that each are separately important (e.g., Buckley and Kynard 1985). Better documentation of the physical conditions at spawning locations is necessary to inform more accurate HSI curves for Shortnose Sturgeon spawning, such as from the Kennebec, Androscoggin, and Merrimack rivers (Kieffer and Kynard 1996; Wippelhauser et al. 2015).

The methods used in this study allowed us to synthesize information concerning four habitat characteristics that influence Shortnose Sturgeon spawning habitat suitability: depth, velocity, bottom substrate, and embeddedness. Although the spatial resolution of the Embeddedness + HSI index locations was limited to 20 data points along the river shore, these methods could easily be applied to a larger embeddedness data set to provide finer-scale details on overall spawning habitat suitability. Researchers have previously employed River2D to model spawning habitat for Shortnose Sturgeon (Wegener 2012) and other species (Yi et al. 2010; Hatten et al. 2013), but our additional analyses using ArcMap could be useful in application to other systems to further refine River2D habitat suitability predictions for multiple fish species.

Habitat suitability analyses and field monitoring can be effectively paired to target sampling activities. The true confirmation of the value of the habitat highlighted in this study will occur when early life stage Shortnose Sturgeon are documented in the Penobscot River. The habitat suitability maps created in this study can be used to target directed sampling activities to areas where spawning is most likely to occur. Conversely, performing field monitoring (e.g., for eggs, larvae, and fish presence in a restored area) would allow for validation and refinement of the habitat suitability modeling. These joint efforts can be particularly valuable for researching the response of a fish species to restoration activities. Because of the imperiled status of Shortnose Sturgeon and the critical importance of suitable spawning habitat for the species' persistence, habitat assessment and suitability modeling could be used to increase the effectiveness of recovery efforts for this and other species of concern.

With the confirmation that Shortnose Sturgeon visited the area upstream of the former Veazie Dam during October 2015 (Johnston 2016), this study offers timely information on the suitability of the habitat for spawning. Shortnose Sturgeon in other northern rivers spend the winter in areas close to spawning grounds, moving from these staging areas a short distance upstream to spawn in the spring (Buckley and Kynard 1985). In the Kennebec River, Shortnose Sturgeon wintered as close as 2 km downstream of spawning habitat (Wippelhauser et al. 2015). In recent years, Shortnose Sturgeon wintered between rkm 43 and rkm 44 in the Penobscot River (Lachapelle 2013; Johnston 2016), conforming to the trend observed in other rivers that support spawning. Continued monitoring of acoustically tagged adults during the spring will be important to determine whether fish move upstream and use the newly available habitat. If Shortnose Sturgeon spawning does begin, it would represent the restoration of spawning that has likely not happened in the Penobscot River for more than a century, promoting future success for this endangered species in the Gulf of Maine.

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SUPPORTING INFORMATION

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