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Shortnose Sturgeon (Acipenser brevirostrum) Spawning Potential in the Penobscot River, Maine: Considering Dam Removals and Emerging Threats

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SHORTNOSE STURGEON (*ACIPENSER BREVIROSTRUM*) SPAWNING POTENTIAL IN THE PENOBSCOT RIVER, MAINE: CONSIDERING DAM REMOVALS AND EMERGING THREATS

By

Catherine Kelley Johnston

B.A. Bowdoin College, 2012

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology)

The Graduate School

The University of Maine

August 2016

Advisory Committee:

Gayle Zydlewski, Associate Professor of Marine Science, Advisor
Joseph Zydlewski, Professor of Fisheries Science
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Sean Smith, Assistant Professor of Earth and Climate Sciences

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By Catherine Kelley Johnston

Thesis Advisor: Dr. Gayle Zydlewski

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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Dam removals from the Penobscot River in Maine restored access to freshwater habitat critical for the life cycle of endangered shortnose sturgeon. Prior to the dam removals, shortnose sturgeon spawning activity had not been documented. Instead, evidence suggested that individuals emigrated from the Penobscot River to spawn in the Kennebec complex, 140 km away. A central question of this thesis was whether spawning activity would commence in the first two years following dam removal. Consistent with pre-dam removal movement patterns determined using acoustic telemetry, the majority (78%) of tagged individuals emigrated from the Penobscot River at some point over the study period and, of these, 71% were found on spawning grounds in the Kennebec complex. The high degree of connectivity with other coastal Maine rivers, along with the lack of documented spawning activity, suggests that shortnose sturgeon remain dependent on spawning in the Kennebec complex. For all individuals occupying the Penobscot River, seasonal distributions within the river were consistent

among years and similar to those observed pre-dam removal, with upstream/freshwater river use predominating in fall and winter and estuarine/downriver use dominating in spring and summer. In the fall of 2015, individuals were detected in the first 5 km made available by the Veazie Dam removal, offering evidence that shortnose sturgeon could return upstream during future springs to spawn.

Shortnose sturgeon require a suite of habitat characteristics to be present to spawn. Habitat suitability modeling was performed to assess the quality of the newly available habitat in the Penobscot River. Using a two-dimensional hydrodynamic model and ArcGIS, the first 5 km reach made available by the Veazie Dam removal was examined based on velocity, depth, and bottom substrate. Results indicate that at any discharge likely to occur during the spring spawning season, at least 40% of the area is usable for spawning. Velocity is the most limiting habitat characteristic at any simulated discharge. The habitat suitability maps generated could be useful for planning spawning sampling in future years.

Lessons learned from the first two studies were used to suggest future steps for research concerning shortnose sturgeon in the Penobscot River. To more fully describe how this endangered species responds to the recent dam removals, more acoustic tags should be deployed and further examination of habitat suitability should occur. In addition to continued telemetry and habitat assessments, researchers should consider how the emerging threat of climate change could impact shortnose sturgeon recovery. For example, how increased saltwater intrusion affects available habitat for spawning and juvenile rearing. Tracking the behavior and use of newly available habitat will help researchers and managers address threats to the species in the Penobscot River and to the wider population in the Gulf of Maine.

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Catherine Kelley Johnston, I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Dr. Gayle Zydlewski, Associate Professor of Marine Sciences Date

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Abstract

Dam removals from the Penobscot River, Maine, in 2012 and 2013 increased access to freshwater habitat that could support spawning of endangered shortnose sturgeon. Prior to the Penobscot River Restoration Project, a high degree of connectivity among Gulf of Maine rivers was observed, with shortnose sturgeon tagged in the Penobscot River regularly moving to other coastal rivers. In one, the Kennebec River, spawning was documented. The absence of tagged individuals making upstream movements in the spring and the lack of documented spawning activity point to the continued reliance on other Gulf of Maine rivers for spawning. Consistent with pre-dam removal patterns, the majority (78%) of tagged individuals emigrated from the Penobscot River at some point over the 2+ years they were tracked and, of these, 71% were found on spawning grounds in the Kennebec complex during spring. Seasonal distributions of tagged individuals occupying the Penobscot River were consistent among years and similar to those observed prior to the dam removals. Typically individuals occupied upstream/freshwater reaches in fall and winter and estuarine/downriver reaches in spring and summer. A notable exception to the general pattern of reach-use occurred in Fall 2015 when several shortnose sturgeon were tracked exploring a reach made available by dam removal. This marked the first time this reach was confirmed to be used since the construction of the Veazie Dam in the early 1900’s. Continued monitoring of shortnose

sturgeon movement patterns and seasonal distributions in the Penobscot River is critical to determine how the Penobscot River Restoration Project will influence this endangered species in the Gulf of Maine.

Introduction

Many diadromous fish species have experienced sharp declines in the last century due to human activities (Jager et al. 2016; Liermann et al. 2012; Limburg & Waldman 2009). Among these species is shortnose sturgeon, *Acipenser brevirostrum*, listed as endangered throughout its range since 1967 (Dadswell et al. 1984; National Marine Fisheries Service (NMFS) 1998). Shortnose sturgeon are found in coastal rivers from the St. John River in New Brunswick, Canada to the St. Johns River in Florida (Dadswell 1979). Throughout their range, shortnose sturgeon experienced population declines due to overfishing, habitat degradation, and blockage of access to upstream freshwater habitat by dams (Limburg & Waldman 2009; Kynard 1997; National Marine Fisheries Service (NMFS) 1998). In recent years, changes have been implemented to increase the potential for depleted shortnose sturgeon populations to recover. For example, water quality improvements promoted by the Clean Water Act of 1972 have decreased the threat of pollution (Dadswell 1979; NMFS 1998) and fishing moratoriums have decreased the frequency of shortnose sturgeon bycatch (Limburg et al. 2006). However, the species remains listed and, in many rivers, populations are still at depleted levels.

Dam removals offer an opportunity to restore shortnose sturgeon populations by facilitating access to upstream freshwater habitat critical for successful reproduction and have increased in frequency in recent years (O'Connor et al. 2015). Dam removals provide access to river habitat for numerous fish species and also initiate a suite of other changes such as increasing sediment and nutrient delivery to coasts, increasing invertebrate diversity, and promoting many other ecosystem improvements (Doyle et al. 2005; Hansen & Hayes 2012; O'Connor et al. 2015). Recent dam removals from the two largest watersheds in the Gulf of Maine, the Kennebec and Penobscot, offer the potential for recovery of shortnose sturgeon. In the Kennebec River, the Edwards Dam was removed in 1999, making an additional 29 km of freshwater habitat available to the species (Wippelhauser et al. 2015). Spawning by shortnose sturgeon upstream of the former dam site was confirmed within 10 years of the removal (Wippelhauser et al. 2015). On the Penobscot River, the removal of two dams in 2012 and 2013 restored access to 100% of historic habitat for shortnose sturgeon in the river. Shortnose sturgeon in the Gulf of Maine move frequently from the Penobscot River to the Kennebec River and other coastal rivers (Dionne et al. 2013; Fernandes et al. 2010; Zydlewski et al. 2011), indicating this species' dependence on habitat in multiple river systems for population persistence (Altenritter 2015). Therefore, increased access to freshwater habitat in the Penobscot River presents an important opportunity for shortnose sturgeon recovery not only in the Penobscot River, but in the broader Gulf of Maine.

The Penobscot River Restoration Project (PRRP) involved two dam removals, increased power generation at existing dams, the installation of a fish lift at the remaining lowermost dam, and construction of a bypass structure at another dam, all in an effort to improve fish passage and habitat access in the river (Opperman et al. 2011). Together, these efforts resulted in an increase of available freshwater habitat by 14 km and improved access to more than 100 km of habitat upstream of the lowermost dam on the river (Milford Dam, rkm 62; Figure 1.1). Prior to the restoration efforts, a knowledge-base of how diadromous fish species used the Penobscot River was built (Dionne et al. 2013; Fernandes et al. 2010; Kiraly et al. 2015; Lachapelle 2013; Stich et al. 2016; Trinko Lake et al. 2012). Shortnose sturgeon were observed occupying the river reaches below the lowermost dam throughout the year (Fernandes et al. 2010; Dionne et al. 2013; Lachapelle 2013); foraging was documented in certain estuarine reaches during summer months (Dzaugis 2013) and upstream freshwater river reaches (still below the dams) were used for wintering (Fernandes et al. 2010; Lachapelle 2013). However, despite the presence of individuals throughout the year, shortnose sturgeon were never documented spawning in the river (Dionne et al. 2013; Fernandes et al. 2010; Wegener 2012).

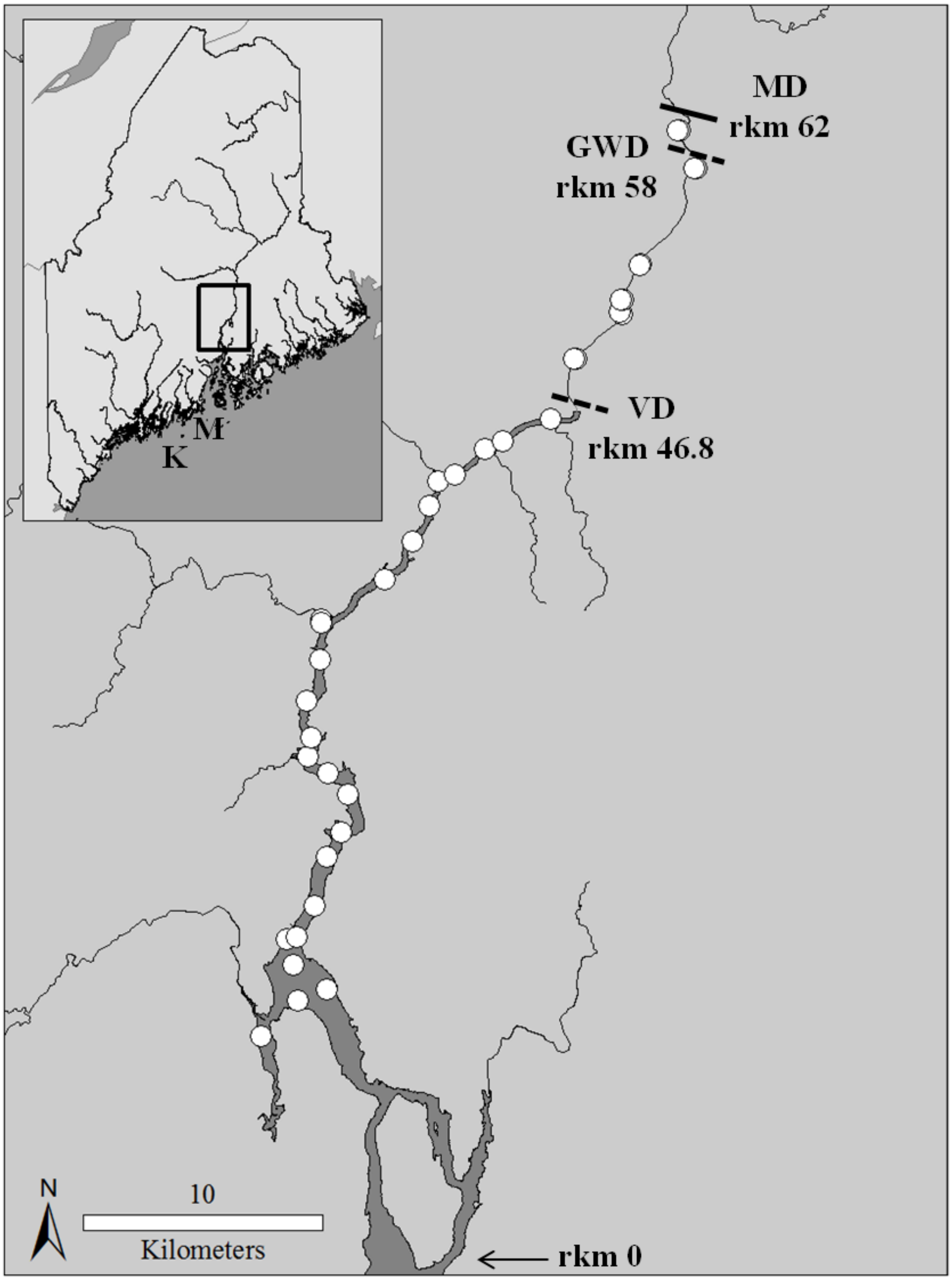

Figure 1.1. Map of the Penobscot River from the southern tip of Verona Island (rkm 0) to Milford Dam (MD, rkm 62). Map inset shows the state of Maine with the rectangle surrounding the enlarged study area. The Kennebec River (K) is located 140 km to the south and the Medomak River (M) is located approximately 100 km to the south. Removed dams are represented by dashed lines. GWD is Great Works Dam, removed in 2012. VD is Veazie Dam, removed in 2013. Points on the map indicate locations of acoustic receivers deployed for the full season (approximately early April through early December in each year from 2013 to 2015). The array is cooperatively maintained by the University of Maine and the USGS Maine Cooperative Fish and Wildlife Research Unit.

Since 2007, shortnose sturgeon have been documented frequently moving from the Penobscot River, through the Gulf of Maine, to other coastal Maine rivers including the Kennebec, Merrimack, and Saco (Dionne et al. 2013; Fernandes et al. 2010; Zydlewski et al. 2011). Tagged individuals, identified as females carrying late-stage eggs while in the Penobscot River, were tracked moving to the Kennebec complex (including the Sheepscot, Kennebec, and Androscoggin Rivers), where they were detected on known spawning grounds during the spring (Wippelhauser et al. 2015). This high degree of connectivity within the Gulf of Maine and the lack of documented reproduction in the Penobscot River (Fernandes et al. 2010; Wegener 2012) suggest that shortnose sturgeon inhabiting various rivers in the region exist as a metapopulation, rather than as isolated populations (Altenritter 2015). Genetic analyses of individuals captured within the Penobscot River indicated similarity to individuals captured in the Kennebec complex (Wirgin et al. 2010) and structure analysis is indicative of a metapopulation (King et al. 2010), underlining the connectivity of the systems.

Harden Jones (1968) described three primary habitat uses for migratory species: foraging, refuge, and spawning. Rather than completing all three activities within the Penobscot River, shortnose sturgeon have been documented using spawning habitat in other Gulf of Maine rivers (Wippelhauser et al. 2015). However, with the increased access to freshwater habitat facilitated by the PRRP dam removals, an important question is whether shortnose sturgeon will continue to move to the Kennebec complex to spawn, or if they will begin reproducing in the Penobscot River, completing the triangle of habitat use described by Harden Jones (1968). The 14 km of habitat now available is non-tidal fresh water and represents a significant increase in availability of this critical habitat, important for both shortnose sturgeon spawning and growth (Bemis & Kynard 1997). 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 around age one (Jenkins et al. 1993). Freshwater reaches are also utilized by shortnose sturgeon as overwintering habitat, which has been considered as a staging area for individuals before they move upstream to spawning habitat in the spring (Buckley & Kynard 1985; Fernandes et al. 2010; Lachapelle 2013). Thus, the dam removals increased the amount of available freshwater habitat for multiple life stages during multiple seasons. In doing so, the dam removals satisfied one objective, “restore access to habitats”, of the shortnose sturgeon recovery (National Marine Fisheries Service (NMFS) 1998). Our research aimed to determine whether individuals in the Penobscot River actually used that newly accessible habitat, and if so, how and when.

The primary goal of this study was to describe shortnose sturgeon movement patterns and seasonal distribution in the Penobscot River and Gulf of Maine during the first two years following the PRRP dam removals. Specific objectives of this study included (1) comparing movement patterns, both within the Penobscot River and to other Gulf of Maine rivers, pre- and post-dam removal, (2) describing shortnose sturgeon seasonal distribution in the Penobscot River to infer habitat use, and (3) confirming the presence of spawning activity by sampling for eggs and larvae. The use of both acoustic telemetry and early life stage sampling provided information to answer the important question of whether spawning by shortnose sturgeon commenced within the Penobscot River following the dam removals. We hypothesized that, if spawning activity began, the proportion of individuals remaining within the river for the entire year, rather than emigrating to other coastal rivers for certain seasons, would increase. In addition, the use of upstream freshwater habitat during the spring could indicate spawning activity, and the collection of eggs or larvae could confirm this new habitat use in the Penobscot River. By examining shortnose sturgeon movement patterns and seasonal distribution following dam removals, this research offers insight into the initial response of this endangered species to restoration efforts, which has implications for the status of this metapopulation in the Gulf of Maine.

Methods

Capture and tagging

Adult shortnose sturgeon were captured in the Penobscot River using gill nets fished between rkm 20 and 46. Gill netting occurred during the months of June through October from 2010 to 2015. Gill nets (16.2 or 30.5 cm stretch mesh, 2.44 m high and 45 or 90 m long) were fished on the river bottom and netting followed the rules of ESA Permit Number 16306. Once shortnose sturgeon were captured, processing of individuals followed the protocol described by Dionne et al. (2013). Briefly, all individuals were kept in a floating net pen until processing, which occurred in an aerated trough of water. Measurements, including mass and fork length, were taken for each individual and all (not previously) captured individuals received PIT and floy tags. Using a borescope, reproductive condition was evaluated; this method allowed for identification of females carrying eggs. Individuals were characterized as “unknown” when the borescope could not be inserted or no eggs were visible.

Individuals chosen for acoustic tagging were placed in an aerated trough of river water with buffered MS-222 (tricaine methane sulfonate). The tagging procedure also followed the methods of Dionne et al (2013). Transmitters were VEMCO model V16TP-4X (16 mm by 71 mm, 26 g weight in air) or V16-4X (16 mm by 68 mm, 24 g weight in air) (VEMCO, Halifax, Nova Scotia, Canada). The maximum transmitter battery life was 5, 6.7, or 10 years. To maximize the likelihood of documenting spawning migrations, most individuals in 2014 and 2015 selected for acoustic tagging were those identified as females by the presence of early or late stage eggs. As gill netting occurred in the late summer and fall, females carrying late stage eggs were expected to spawn the following spring and tagging these individuals could allow tracking of their movements to spawning grounds, within or outside of the Penobscot River.

Acoustic telemetry

Our study period extended from the fall of 2013, when the Veazie Dam was removed, until the end of the winter 2015-2016 season (1 September 2013 - 29 February 2016). A network of acoustic receivers (Figure 1.1) allowed continuous collection of data on tagged shortnose sturgeon movements in the Penobscot River. Each year an array, consisting of 37 VEMCO VR2W receivers, was deployed for the duration of the year when ice was not present in the river (Table 1.1). The full receiver array was deployed between Verona Island (rkm 0) and upstream of the Great Works Dam remnants (rkm 60). A smaller array (consisting of 3 to 9 receivers) was deployed each winter to monitor shortnose sturgeon at wintering sites. Receiver placement allowed approximately 1 km reach resolution of fish presence throughout the river. Acoustic receiver arrays maintained by the Maine Department of Marine Resources and NOAA were deployed yearly in the Kennebec complex and other coastal Maine rivers (Damariscotta, Medomak, and Passagassawakeag) (G. Goulette personal communication, Wippelhauser et al. 2015). Detection data from those arrays were provided for the individuals included in this study.

Table 1.1. Summary of acoustic receiver array and tags present in shortnose sturgeon considered for analysis by season.

Array type	Deployment period	Receivers	Season	Time period	Active tags
full	10 Apr - 6 Dec 2013	37	fall 2013	1 Sep - 6 Nov 2013	12
winter	6 Dec 2013 - 16 May 2014	3	winter 13-14	7 Nov 2013 - 28 Feb 2014	13
full	14 Apr - 23 Nov 2014	37	spring 2014	1 Mar - 25 May 2014	13
			summer 2014	26 May - 31 Aug 2014	13
			fall 2014	1 Sept - 1 Nov 2014	14
winter	17 Nov 2014 - 12 June 2015	3	winter 14-15	2 Nov 2014 - 28 Feb 2015	19
full	22 Apr - 11 Dec 2015	37	spring 2015	1 Mar - 25 May 2015	17
			summer 2015	26 May - 31 Aug 2015	15
			fall 2015	1 Sept - 25 Oct 2015	25
winter	23 Nov 2015 - 1 Apr 2016	9	winter 15-16	26 Oct 2015 - 29 Feb 2016	30

Mobile acoustic tracking occurred frequently to supplement the stationary receiver array. A VR100 (VEMCO) was used from motorboat, canoe, and shore to monitor for tags present in the river. In spring of 2014 and 2015, mobile tracking was performed weekly to monitor for any upstream movements of tagged individuals, with tracking both upstream and downstream of the removed dam sites. Mobile tracking was essential during the spring in the upper portion of the river (approximately rkm 42 and higher) because increased acoustic noise associated with high flows could cause decreased tag detectability. Stich (2014) found that tag detection decreased with increasing discharge in the Stillwater branch of the Penobscot River for smaller VEMCO model tag types, with detection probability ranging from 0.028 to 0.81. The larger sized tags deployed in sturgeon are expected to have better detection probability.

Acoustic data analysis

Acoustic receiver data were examined using the program Vue (VEMCO). Detections were compiled by year and by season (spring, summer, fall, and winter - Table 1.1). Only positive detections were used to describe movements and seasonal distribution (no extrapolation or interpolation methods were used). The individuals included in this study were all tagged in the Penobscot River, with the exception of one individual tagged in the Merrimack River on 14 October 2010 (M. Kieffer, personal communication). This individual spent multiple seasons in the Penobscot River and was also detected in the Kennebec complex, the Damariscotta River, and the Passagassawakeag River. At the start of the study period (Fall 2013), 12 individuals carried active acoustic tags (implanted earlier in the year or during previous years; Table 1.1). During the study period, additional tags were deployed: one in 2013, six in 2014, and 19 in 2015. When an individual was tagged, it was not considered as part of the cohort for that season; its first inclusion in the detection dataset was for the first season during which its tag was active for the entire duration of the season. For example, if an individual was tagged on 10 September 2014, that individual was first included in the winter 14-15 cohort.

To describe seasonal movement patterns and spatial distribution within the Penobscot River by season, time frames for each season were determined following the methods of Dionne et al. (2013) and Lachapelle (2013). The spring season was characterized as beginning on March 1 and extending until the last day considered suitable for spawning (the day water temperatures reached above 15° C). Summers extended from that day until August 31 (following Dionne et al. 2013). The distinction between fall and winter was made following Lachapelle (2013); "winter" began on the day when 90% of the tagged wintering individuals were present at the wintering site (based on tag detections at the nearest receiver).

Movement patterns

To compare the movement patterns of shortnose sturgeon in the first years following dam removal to pre-dam removal patterns, we referenced the work of Dionne et al. (2013). That study established the proportion of tagged individuals in the Penobscot River that behaved as residents (never leaving the river during the four year study period), or as emigrants (making movements out of the river either during spring, summer, or fall) pre-dam removal. From 2006 - 2009, 28% of individuals were river residents and 72% emigrated to other coastal Maine rivers (Dionne et al. 2013). Spring emigrants composed 24% of the individuals included, 15% were summer emigrants, and

33% were fall emigrants. Of the 46 individuals included in the study, mean mass was 5.6 ± 0.3 kg, mean fork length was 85.9 ± 1.7 cm, and six were confirmed females (Dionne et al. 2013).

Following the methods of Dionne et al. (2013) we characterized movement patterns exhibited by tagged individuals post-dam removal (fall 2013 through winter 15-16). We only included those individuals carrying active tags for a full year or more. As such, acoustic data from the spring and summer of 2013 were included for some individuals to allow for accurate characterization of movement patterns (n = 6). Occupants were those individuals that remained in the Penobscot River for the duration of the time their tag was active during the study period. It should be noted that Dionne et al. (2013) used the term "resident" for this behavior but we call these "occupants" instead of "residents" to avoid associating those individuals with their river of capture in a way that would suggest they originated there. Emigrants were those that left the Penobscot River and the date of emigration was the final date when an individual was detected in the Penobscot River during the season that it emigrated. Similarly to Dionne et al. (2013), spring, summer, and fall emigrants were defined based on the season during which they left the river.

The detection datasets from receivers deployed in the other coastal rivers were checked for the presence of emigrants. Immigration frequently followed emigration, and date of immigration was the first day when an individual was detected in the Penobscot River following its absence after emigration. Our determination of an expired transmitter also followed the methods used by Dionne et al. (2013). Single detections were excluded from the dataset because they likely indicated false detection. Detection data for each individual were exported from Vue as a .csv file for further analysis within Microsoft Excel and ArcMap (ArcGIS for Desktop 10.2.2, Environmental Systems Research Institute, Redlands, CA).

Seasonal distributions

To quantify river use by season, detection data for each tagged individual was grouped by season for each year (Table 1.1). A metric, “detection days”, was calculated as the number of different tags detected on each day of the season for each receiver. For example, if four different individuals were detected at some point in the day on 12 September 2015 at the receiver at rkm 36.5, then the value associated with that date for that receiver would be 4. The sum of detection days for the receiver at rkm 36.5 for the entire season was therefore used to represent the sturgeon occupancy of the approximately 1 km reach associated with that receiver. Because this final value was dependent on the number of active tags within the river during the season, the total detection days (number of individuals detected on a receiver on each day of the season) was divided by the number of active tags present within the Penobscot River during each season. This standardized value was used in ArcMap to visualize seasonal distribution at each receiver (~1 km river reach) during each season by showing the percent of total detection days contributed at each receiver location.

The detection datasets for each season (as previously defined in the section “Acoustic data analysis”) were used to provide median rkm utilized by tagged individuals during each season and all other rkm values describing seasonal distribution. Detection data for all individuals present within the Penobscot River during the season were used, whether those individuals were present for the entire duration of the season or for only a portion of the season (i.e. emigrants and immigrants were included).

Early life stage sampling

Ichthyoplankton nets and egg mats were deployed to collect early life stage shortnose sturgeon in spring 2014 and 2015. Sampling with D-shaped ichthyoplankton nets (5.0 m length, tapered width from 1.0 to 0.3 m from mouth to cod end, 1000 µm Nytex mesh) occurred between rkm 36.5 and 42 based on expected suitable spawning habitat determined by Wegener (2012). Ichthyoplankton nets were fished at night for two consecutive 3 hour periods. The contents of the sampling container were retrieved and sorted. The targeted date range for ichthyoplankton sampling was from the time when river temperatures became suitable to support spawning (9° C) until temperatures reached 25° C, or July 1 to capture the larval development window (Kynard 1997).

Sampling for the presence of shortnose sturgeon eggs was completed using circular mats with high surface area (30 cm in diameter) attached to circular cement blocks deployed on the river bottom, a method used with success by other researchers (Duncan et al. 2004; Fox et al. 2000). These egg mats were deployed in areas based on suitable spawning habitat predictions by Wegener (2012). The targeted date range for egg mat deployment was the duration of time that the river exhibited temperatures suitable for spawning (9°-15° C) (Dadswell 1979; Kynard 1997). Egg mats were checked at least twice per week to detect if any fish eggs had adhered to the surface.

Results

A total of 37 shortnose sturgeon were included in this study, with between 12 and 30 active tags considered during each season (Table 1.1). Thirty-one (84%) were identified as females during their initial capture or subsequent recaptures. The sex of the remaining 6 individuals could not be identified. For the 37 individuals, mean (± SD) fork length was 87.0 ± 6.9 cm and the mean mass was 6.2 ± 1.6 kg.

Movement patterns: emigrants

Eighteen of the 37 individuals carried tags that were active for at least one full year during the study period and the movement patterns of these individuals were categorized. Mean (± SD) fork length of these 18 individuals was 84.0 ± 7.4 cm and the mean mass was 5.5 ± 1.5 kg. We observed that 78% of tagged individuals emigrated from the river during the study period, with 71% of these individuals being detected at spawning grounds in the Kennebec complex during the spring.

Ten of the 18 (56%) individuals were classified as spring emigrants and eight of these were confirmed females. During spring of 2013, six of these individuals emigrated from the river between 14 April and 4 May; all six were confirmed females, with five of them carrying eggs the previous fall. All six were detected by receivers in coastal rivers and five of the six were detected on spawning grounds in the Kennebec complex (G. Wippelhauser, personal communication). During spring 2014, one tagged female emigrated from the river on 3 May (when the water temperature was 6.3°C). This individual was not detected on the Kennebec complex receiver array (G. Wippelhauser, unpublished data). During spring 2015, four tagged individuals moved out of the

Penobscot River (between 4 May and the 20 May). Two out of the four emigrants were confirmed females and three out of the four emigrants were detected on receiver arrays in other Maine rivers after they left the Penobscot River. Two emigrants were detected on Kennebec complex receivers within 9 days of leaving the Penobscot River. A third emigrant left the Penobscot River on 20 May, 2015 and was detected by receivers in the Medomak River, approximately 100 km from Penobscot River, on 10 June. With the exception of two individuals who did not return to the river during the study period, spring emigrants returned to the Penobscot River during the summer (between 25 May and 21 July) of the same year they had emigrated.

Four (22%) individuals were classified as fall emigrants, with one of the four confirmed as female. Two tagged individuals left the river during the fall of 2013; one on 28 September and the other on 1 November. One of these individuals was confirmed in the Kennebec complex the following spring. In 2014, three tags left the system during the fall (between 16 and 22 October), with one of the three emigrants having previously departed during fall of 2013. Two of the three 2014 fall emigrants were detected on the Kennebec complex array within 12 days of departure from the Penobscot River. In the spring of 2015, no individuals were detected on receivers in the Kennebec complex. In 2015, three individuals emigrated from the Penobscot River during the fall (between 18 September and 13 October). One of these emigrants, which had also emigrated in fall of 2014, was detected in the Medomak River 4 days after departure from the Penobscot River and then in the Kennebec complex 9 days after departure from the Penobscot River. This individual was also confirmed to overwinter in a tributary of the Kennebec River (J. Bartlett, personal communication). Two of the fall emigrants also made short trips out of the Penobscot River during the summer seasons in 2014 and 2015, returning after 20 to 39 days from departing. One of these individuals had also emigrated from the river in the summer of 2013. Individuals returned to the Penobscot River either during the following spring or summer after emigrating the previous fall; dates of immigration for fall emigrants ranged from 15 May to 2 June.

Movement patterns: occupants

Four (22%) of the 18 individuals were classified as occupants, remaining within the Penobscot River for the entire time that their tags were active during the study period. Three of these occupants were confirmed to be egg-carrying females. Occupants exhibited a consistent seasonal movement pattern within the Penobscot River, and when emigrants were present in the river, they conformed to these general movements as well. During the spring (Mar – May), individuals in the Penobscot River moved from freshwater overwintering areas downstream to the estuary in the summer (Jun – Aug), then gradually moved upstream in the fall (Sep – Nov) before settling in overwintering areas around rkm 43 (Nov – Feb).

Comparison of pre- and post-dam removal movement patterns

The proportions of occupants and emigrants observed post-dam removal were not significantly different than those observed by Dionne et al. (2013) pre-dam removal (Pearson's Chi-squared test $p=0.86$). Prior to the dam removals, Dionne et al. (2013) observed that 72% of individuals tagged in the Penobscot River emigrated, and 55% of these emigrants were detected on spawning grounds in the Kennebec complex during the spring. Post-dam removal, 78% of individuals emigrated from the river and 71% of those individuals were detected on Kennebec complex spawning grounds during the spring. Within the emigrant movement pattern categories (spring, summer, and fall), some change in the season of emigration was suggested post-dam removal by the Pearson's Chi-squared test (p=0.03), likely caused by the decrease in summer emigrants and increase in spring emigrants.

Penobscot River spring movements

During spring 2014, the first following the Veazie Dam removal, the water temperature range over which sturgeon are expected to move upstream and spawn, 9° to 15° C, occurred from 8 May until 25 May 2014 (Figure 1.2a). During this time period, no tagged individuals moved upstream from the wintering site. Of the 13 individuals with active tags during that season, eight (62%) were present within the Penobscot River for the duration of the spring. The farthest upstream any tagged individuals moved during spring 2014 was rkm 36.5 (Figure 1.3a).

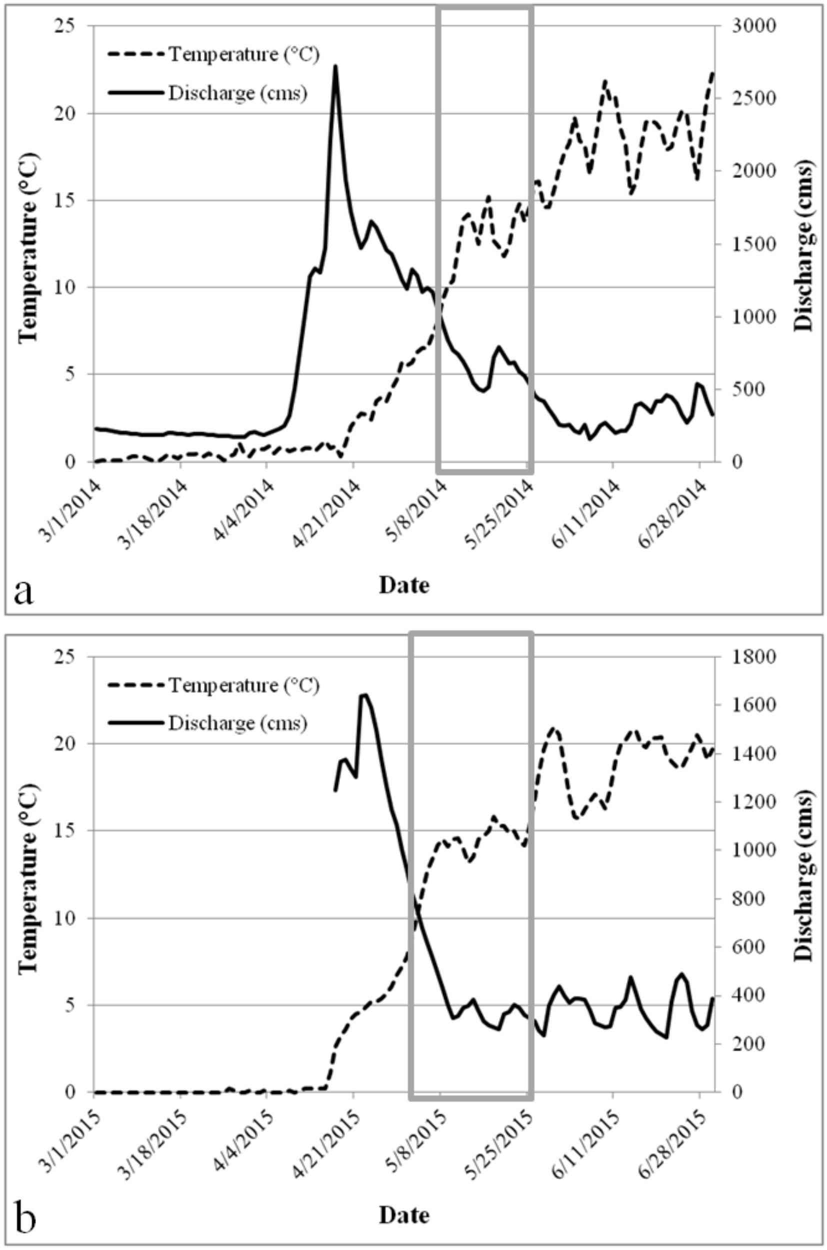

Figure 1.2. Water temperature and discharge during spring 2014 (a) and 2015 (b). Discharge data were not available during the early spring in 2015 due to a malfunction of the USGS gauge. The boxes highlight the time period during which water temperature ranged from 9° to 15° C, suitable temperatures for spawning.

In 2015, suitable water temperatures for spawning occurred between 3 May and 25 May (Figure 1.2b). Of the 17 active acoustic tags present in shortnose sturgeon during that season, ten of the tagged individuals (59%) were present within the Penobscot River for the duration of the spring season. The farthest upstream any tagged individuals were detected was rkm 36.5 (Figure 1.3b).

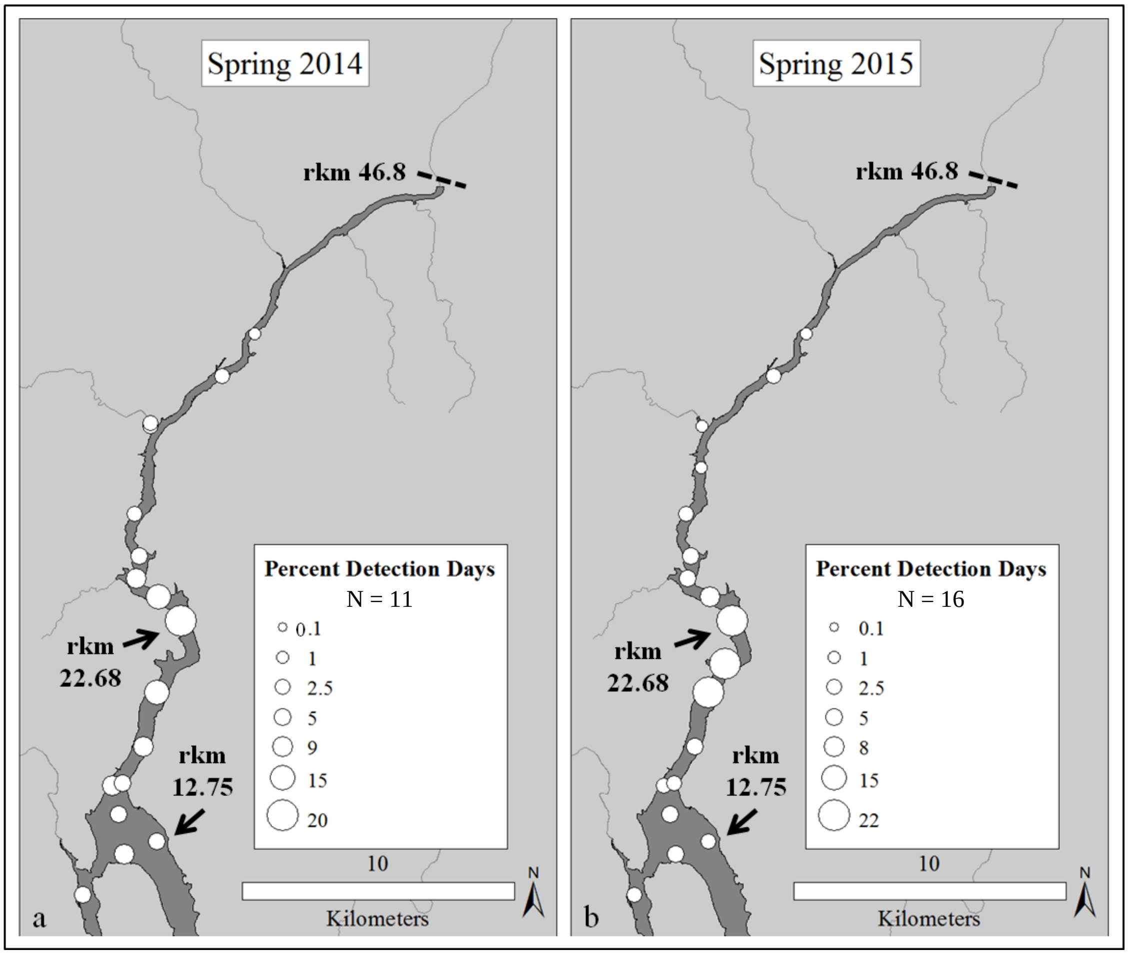

Figure 1.3. Distribution of tagged individuals during spring 2014 (a) and 2015 (b). Circle sizes correspond to the percent of total detection days during the season that occurred at that receiver location and N is the number of active tags present.

Penobscot River seasonal distribution

During the spring of 2014 and 2015, shortnose sturgeon in the Penobscot River primarily occupied a reach in the lower river (from approximately rkm 19.39 to 24.15) (Figure 1.3). In spring of 2014, the reach used most (containing the 25th through 75th percentiles of detections) was 8.5 km in length and in 2015 the most used reach was 4.8

km in length (Figure 1.4). The median rkm utilized during the spring of 2014 was rkm 22.68 and in 2015 was rkm 20.59. The shift in median rkm occupied between the start and end of the spring in 2014 was from rkm 22.68 to 24.15. In 2015, the median rkm utilized at the start of the spring was rkm 24.15 and at the end of the season was rkm 22.68.

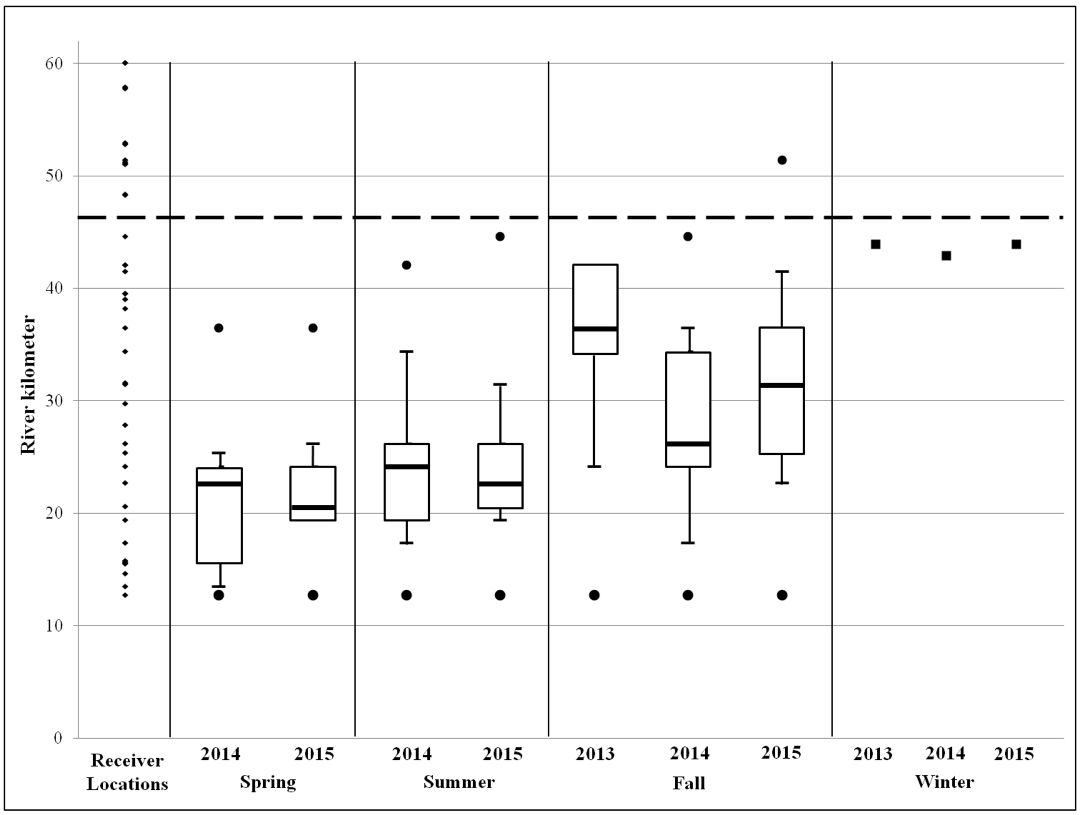

Figure 1.4. Box plots of river kilometer locations of tagged shortnose sturgeon by season (box ends = 25th and 75th percentiles of tag detections; line within the box = median; whisker = 10th and 90th percentiles; dots = outliers). The dashed line represents the former Veazie Dam (rkm 46.8). The far left panel shows the locations of receivers. The far right panel shows the location of the wintering site.

During the study period, summer distribution in the Penobscot River was primarily in the lower river between rkm 20.5 and 26.2 (Figure 1.5). Shortnose sturgeon were most frequently detected on receivers in a 6.8 km reach during the summer of 2014 and in 2015 were most frequently detected in a 5.6 km reach (Figure 1.4). The median rkm of summer 2014 detections was rkm 24.15 and in 2015 was rkm 22.68. The most upstream location where tagged shortnose sturgeon moved during the summer of 2014 was rkm 42.08 and in 2015 individuals moved as far as rkm 44.6 (Figure 1.5). The shift in median rkm occupied between the start and end of the summer in 2014 was from rkm 24.15 to 26.2. In 2015, the median rkm utilized at the start of the spring was rkm 20.6 and at the end of the season was rkm 26.2.

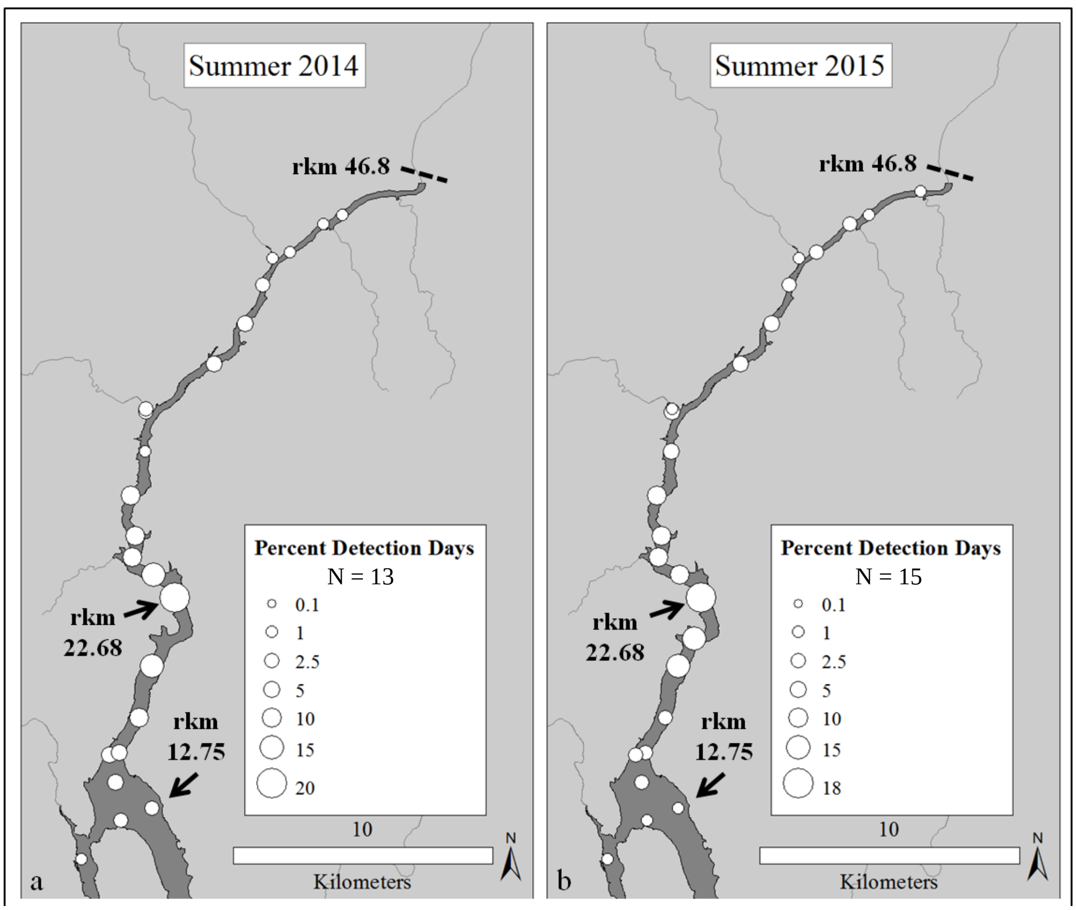

Figure 1.5. Distribution of tagged individuals during summer 2014 (a) and 2015 (b). Circle sizes correspond to the percent of total detection days during the season that occurred at that receiver location and N is the number of active tags present.

Each fall, the distribution of shortnose sturgeon shifted upstream and individuals were most frequently detected by receivers between rkm 24 and 36 (Figure 1.6). Tagged individuals were more widely dispersed within the river during the fall season than in the spring or summer and the length of the most utilized reach was 7.7 km in 2013, 10.2 km in 2014, and 11.1 km in 2015 (Figure 1.4). The median location of detections during the fall was rkm 36.5, rkm 26.2, and rkm 31.4 for 2013, 2014, and 2015, respectively. The farthest upstream that tagged individuals moved during the fall of 2013 was rkm 42.08 and in 2014 was rkm 44.6 (Figure 1.6).

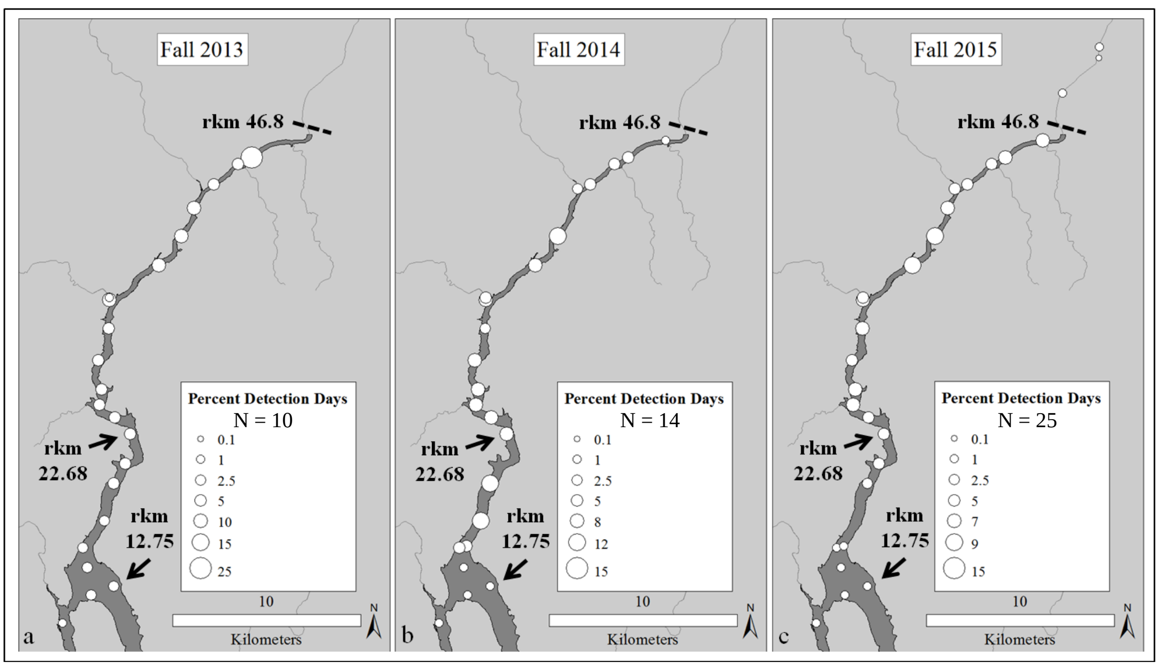

Figure 1.6. Distribution of tagged individuals during fall 2013 (a), 2014 (b), and 2015 (c). Circle sizes correspond to the percent of total detection days during the season that occurred at that receiver location and N is the number of active tags present.

In 2015, from 11 - 12 October, three tagged individuals made an upstream movement as far as rkm 51.39 before returning downstream of the former Veazie Dam site (Figure 1.7). All three individuals were confirmed females and the average time spent upstream of the former Veazie Dam site was 17.6 h.

During the fall of each year, a shift from lower river habitat to upstream freshwater habitat occurred. In 2013, the median rkm occupied at the start of the fall was rkm 34.38 and at the end of the season was 39.5. In 2014, the shift in median rkm utilized was from rkm 25.4 to rkm 39.5 and in 2015, the shift was from rkm 27.8 to 42.1.

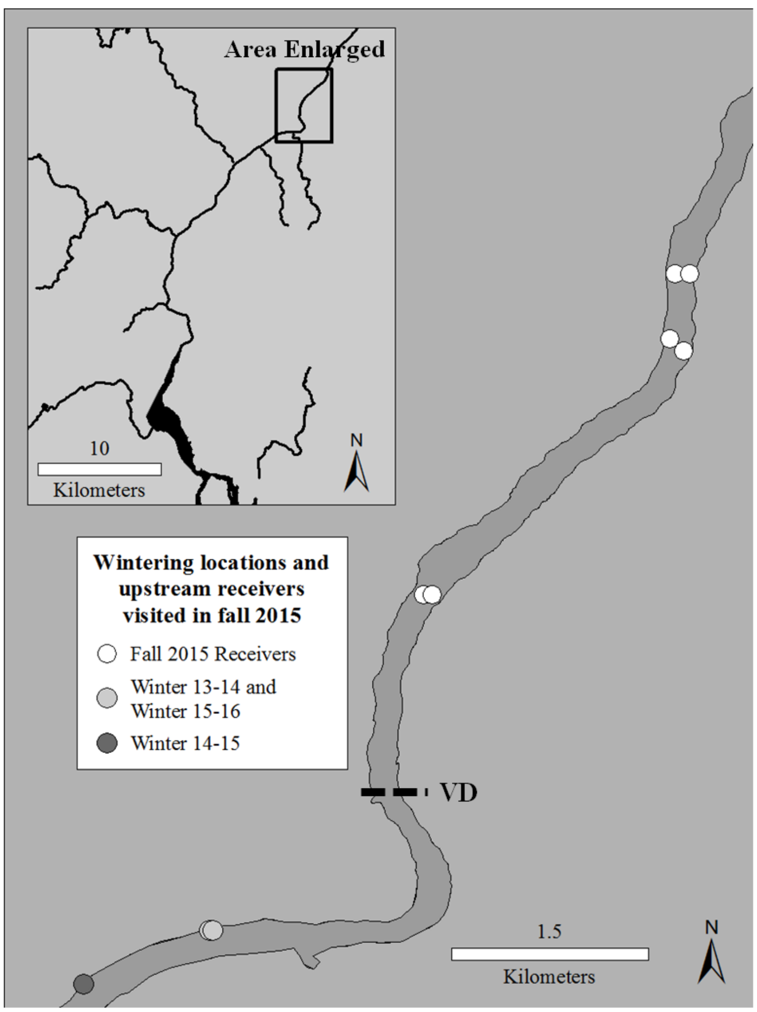

Figure 1.7. Map of Penobscot River from approximately rkm 42 to 43. Wintering sites are depicted for 2013-2014, 2014-2015, and 2015-2016. Receiver locations upstream of the former Veazie Dam (VD) are displayed, showing the locations where shortnose sturgeon were detected in October 2015.

During each winter, tagged individuals settled at a single upstream location between rkm 42.9 and 43.9 during the late fall (Figure 1.4). Based on mobile tracking of these individuals, a small array of receivers was deployed to bracket the wintering site. With only one exception, all tagged individuals present in the Penobscot River for the start of the winter seasons settled at a single wintering site, with individuals arriving between 7 September and 13 November. At the start of the winter season in 2014, one individual was present at rkm 36.5 and was never detected by receivers bracketing the wintering site. This individual was detected by receivers around rkm 20 when the full array was deployed in spring 2015. Tagged individuals that emigrated earlier in the year were assumed to have wintered in other coastal Maine rivers.

In 2013, the wintering site was on the west shore of the river at rkm 43.9, 2.9 km downstream of the former Veazie Dam site (Figure 1.7). Nine of the potential 13 active tags were detected at this wintering site or by receivers in close proximity (approximately 1 km upstream and downstream) to the wintering site prior to the winter season. All wintering individuals moved downstream from the wintering site (and out of the detection range of the winter receivers) on the 14^{th} or 15^{th} of December, after which time no tagged individuals were detected in the river until the full receiver array was deployed in April 2014. The median date on which individuals departed the wintering site was 15 December 2013.

The wintering site in 2014 was identified as a deep hole on the west shore where Meadow Brook enters the river, at rkm 42.9 (Figure 1.7). Fourteen of 18 active tags were present at the wintering site at the start of the season. Most individuals departed from the wintering site over the month of December 2014, with one individual being detected until

5 January 2015. All of these individuals moved downstream of the winter receiver array and were not detected again until the full array was deployed in spring 2015. The median date for departure from the wintering site in 2014 was 11 December 2014.

In 2015, wintering occurred at rkm 43.9, where individuals had aggregated in the winter of 2013-2014 (Figure 1.7). Twenty six of the 30 active tags were present at the wintering site. The earliest departure from the wintering site occurred on 1 January 2016 and the latest occurred on 7 March. The median date on which individuals left the wintering site was 1 February 2016. All individuals moved downstream when they departed from the reach monitored by winter receivers.

Early life stage sampling

Early life stage sampling occurred between 21 May and 22 Jun 2014, and 8 May and 6 July 2015. In 2014, egg mats were deployed continuously from 21 May to 2 June when water temperature ranged from 13.5°C to 20.3°C. In 2015, egg mats were deployed from 8 May to 6 July when water temperatures ranged from 14.3°C to 22.2°C. Egg mats were deployed at approximately rkm 54.5, 43 and 40. No sturgeon eggs were collected.

In 2014, ichthyoplankton sampling occurred over 8 nights (a total of 168 hours of fishing) and was divided between two locations, the former Bangor Dam head pond (rkm 42) and downstream of the former Bangor Dam (rkm 40) (Table 1.2). Water temperatures ranged between 15.7°C and 21.6°C. In 2015, ichthyoplankton sampling was conducted over 13 nights when water temperature ranged from 15.2°C to 21.0°C. Overall, nets were fished for 286 hours at three locations between rkm 36.5 and 42 (Table 1.2). No early life stage sturgeon were captured. However, eggs and larvae of other species were captured in both years.

Table 1.2. Ichthyoplankton sampling overview for 2014 and 2015.

2014 Sampling Overview			
Sampling Location (rkm)	Number of Sampling Nights	Water Temperature Range (°C)	Fishing Time (h)
42	5	15.7-21.6	123
40	3	19.2-20.1	45
Total	*8*	*15.7 - 21.6*	*168*
2015 Sampling Overview			
Sampling Location (rkm)	Number of Sampling Nights	Water Temperature Range (°C)	Fishing Time (h)
42	9	15.2-19.4	214
40	3	16.5-20.4	55
36.5	1	21	17
Total	*13*	*15.2 - 21.0*	*286*

Discussion

Shortnose sturgeon movement patterns and seasonal distributions following the recent dam removals indicate that the Penobscot River continues to offer important habitat for the species in the Gulf of Maine. However, spawning was not documented. The continued high degree of connectivity with other coastal rivers in the Gulf of Maine, along with the lack of spawning activity, suggests that shortnose sturgeon captured in the river remain dependent on spawning in the Kennebec complex. For all individuals occupying the Penobscot River (occupants and emigrants), seasonal distributions within the river were consistent among years and similar to those observed prior to the dam removals (Dionne et al. 2013), with upstream/freshwater river use predominating in fall and winter and estuarine/downriver use dominating in spring and summer. The movement of three individuals upstream of the former Veazie Dam site in October 2015 marked the first time shortnose sturgeon were confirmed upstream of rkm 46.8 since the construction of the dam in the early 1900's. Though access to this newly available habitat did not occur during the spring spawning season, the upstream exploration in fall represents an important first step towards use of the freshwater habitat made available by the Penobscot River dam removals.

The movement patterns observed during our study indicate that a high degree of connectivity still exists between the Penobscot River and other coastal Maine rivers. The proportion of emigrants, 78%, is similar to that reported prior to dam removal, 72% (Dionne et al. 2013). Dionne et al. (2013) reported that known females were 19.6 times more likely to emigrate from the Penobscot River within the first year of capture than individuals of unknown sex, suggesting differential migration. In this study, females carrying eggs were targeted when implanting acoustic tags to maximize the chance of following individuals to spawning areas, so we could not compare female emigration rates to the rates of individuals of unknown sex. However, the results of this study are consistent with the hypothesis that differential migration occurs from the Penobscot River. The timing of movements out of and back to the Penobscot River also indicated that migration through the Gulf of Maine is related to spawning activity. Spring emigrants departed during the time period when spawning would occur based on suitable river conditions and always returned after water temperatures exceeded the suitable spawning range. When fall emigrants returned while temperatures were still suitable for spawning, they immediately settled in the vicinity of other tagged individuals present within the lower river need rkm 20, which has been identified as the primary foraging area (Dzaugis 2013; Fernandes et al. 2010). In addition, over 70% of Penobscot River emigrants were detected on receivers close to spawning grounds in the Kennebec complex during the spawning season (G. Wippelhauser, unpublished data; Wippelhauser et al. 2015). The lack of spawning activity documented by early life stage sampling and telemetry during the spring served as another indication that shortnose sturgeon captured in the Penobscot River likely spawn elsewhere.

These findings lend support to the theory proposed by Altenritter (2015), that the Kennebec complex represents the core spawning population maintaining a metapopulation of shortnose sturgeon in the Gulf of Maine. Altenritter (2015) suggested that increases in abundance of shortnose sturgeon in the Kennebec complex from the late 1990's to 2013 could have prompted some individuals to arrive in the Penobscot River while searching for less competitive conditions. In this proposed scenario describing the dynamics of shortnose sturgeon in the Gulf of Maine the Penobscot River serves as an outpost for feeding and wintering (Fernandes et al 2010). Seasonal distributions of shortnose sturgeon in the Penobscot River and frequent movements to the Kennebec complex observed during our study are consistent with this scenario.

An alternative scenario describing shortnose sturgeon in the Penobscot River is that the river does support a spawning population that exhibits significant exchange with the Kennebec complex population (Fernandes et al. 2010), and monitoring has failed to document the reproduction. We may have failed to document early life stages because spawning occurred in different areas than were sampled or only a few individuals spawned. If only a small number of individuals spawned, this would increase the odds that no tagged individuals would be among that group, and thus acoustic telemetry would be of limited power in revealing upstream spring movements and aggregation of individuals at a spawning site. It is also possible that gill netting efforts unknowingly targeted only a part of the population, for example, the individuals that did not move upstream in the spring to spawn. An interesting observation of the individuals we identified as occupants during this post-dam removal study hints that spawning could have begun in the river. Three of the four occupants were confirmed to be egg-carrying females in the fall of 2014 and the following spring, these individuals did not leave the river as would be expected based on their reproductive status and the findings of past studies (Dionne et al. 2013; Fernandes et al. 2010; Billard & Lecointre 2000). While additional explanations exist, perhaps these individuals remained in the Penobscot River during the spring of 2015 and we failed to document the spawning activity. This highlights the importance of continued monitoring for spawning activity in the Penobscot River.

Two of the three primary habitat uses for migratory species (foraging, refuge, and spawning; Jones 1968) have been documented in the Penobscot River (Dzaugis 2013; Fernandes et al. 2010; Lachapelle 2013), underlining the important role of Penobscot River habitat in supporting shortnose sturgeon. We observed that the distribution of individuals within the Penobscot River shifted by season, following the pattern expected of individuals using foraging and wintering habitat (Billard & Lecointre 2000; Kynard 1997). During the spring and early summer, individuals were concentrated within the lower river in an 8 km reach confirmed as important foraging habitat (Dzaugis 2013). In the late summer and fall, individuals moved upstream and eventually aggregated in wintering habitat between rkm 42.9 and 43.9.

With increased access to freshwater habitat in the Penobscot River, the system has the potential to play an even greater role in supporting shortnose sturgeon in the Gulf of Maine. For example, the significant difference between the proportions of emigrants leaving during each season, post-dam removal, suggests that the use of habitat during summer and fall could be increasing compared to pre-dam removal. Dionne et al. (2013) observed 48% of tagged individuals left the river during the summer or fall, indicating their use of other rivers for foraging and wintering habitat. In contrast, less than a quarter of post-dam removal individuals emigrated during the summer or fall. This means a high proportion of individuals remained in the Penobscot River to forage and spend the winter. If individuals spend a greater proportion of the year in the Penobscot River while they forage and winter, this could increase the likelihood that the third habitat use described by Harden Jones (1968), spawning, might begin in the river.

In the first 5 km made accessible by the PRRP dam removals, habitat suitability modeling predicted that suitable spawning habitat is available to shortnose sturgeon at any discharge likely to occur during the spring (Chapter 2). This river reach was accessed by three tagged females over a two-day period in the fall of 2015, which marked the first time shortnose sturgeon were confirmed to utilize habitat made available by the dam removals. With this documented upstream exploration, we can confirm that, at least at the discharge present in the river on 11 October 2015, some individuals are capable of swimming over the rapids located at the former Veazie Dam site. After their brief movement as far as rkm 52, they moved back downstream of the former Veazie Dam site and joined the wintering aggregation at rkm 43.9, where they remained until mid-winter when all wintering individuals moved downstream. It is important to note that only a small proportion (approximately 3%) of the total number of shortnose sturgeon present in the Penobscot River carry acoustic tags. With 30 active tags deployed during fall of 2015, and a conservative abundance estimate of 1000 individuals (Dionne 2010), the three explorers could represent about 100 shortnose sturgeon that moved into the reach made available by the Veazie Dam removal.

Behaviors like the brief exploration of habitat upstream of the former Veazie Dam site could be precursors of greater future use of this habitat by shortnose sturgeon. The tendency of some individuals within a population to be highly exploratory can drive the colonization of new sites (Conrad et al. 2011; Sih et al. 2004). Besides the upstream exploration documented in the fall of 2015, other tagged individuals also exhibited movement patterns that suggest changing behaviors post-dam removal. For example, the only individual included in this study not tagged within the Penobscot was a female shortnose sturgeon acoustically tagged on 14 October 2010 in the Merrimack River. This individual moved extensively within the Gulf of Maine between 2010 and 2014, and then began exhibiting movement patterns consistent with other fall emigrants in the Penobscot River, suggesting that it has begun to primarily use the Penobscot River (Kieffer, Wippelhauser, unpublished data). If, in the Penobscot River, the recent variability of some individuals' movement patterns represents exploration or "straying", then the continuation of these behaviors could lead to the commencement of spawning in the river because individuals will become more familiar with the newly available habitat and consider returning.

Additional movement patterns and changing seasonal distributions point to the potential for spawning to begin within the Penobscot River. In other rivers supporting shortnose sturgeon, wintering habitat, often in close proximity to spawning habitat, is considered to be a staging area for shortnose sturgeon prior to their movement upstream in the spring to spawn (Buckley & Kynard 1985; Dadswell 1979; Wippelhauser et al. 2015). In the Kennebec complex, shortnose sturgeon winter in habitat as close as 2 km downstream of spawning habitat, and are therefore able to make a brief movement upstream to spawn when water temperatures warm (Wippelhauser et al. 2015). Kynard (1997) characterized this kind of migration as a "short one-step" movement to spawning areas. Since the PRRP dam removals, wintering in the Penobscot River has occurred between rkm 43 and 44, locations placing individuals within a few kilometers of freshwater habitat that has been confirmed to offer suitable spawning conditions (Chapter 2). Despite the proximity to suitable habitat, individuals left the system during the springs following dam removal just as they had done prior to the restoration (Dionne et al. 2013; Fernandes et al. 2010; Wippelhauser et al. 2015). This could also be considered a "short one-step" migration, though the Penobscot River emigrants perform this migration between river systems rather than within one system (Dionne et al. 2013; Kynard 1997). If spawning were to commence in the Penobscot River, the "short one-step" migration from wintering to spawning habitat within the river would be more energetically favorable than the longer migration that involves traveling approximately 140 km through the Gulf of Maine.

The initiation of shortnose sturgeon reproduction (or continuation, if undocumented spawning already occurs) in the Penobscot River would have important implications for the species within the Gulf of Maine. Reproduction by individuals in the Penobscot River would suggest that shortnose sturgeon populations are expanding in the Gulf of Maine. The successful reproduction of individuals in the Penobscot River would promote increased resilience for Gulf of Maine shortnose sturgeon. Currently, if recruitment in the Kennebec complex were low in a given year, this would represent a high proportion of total recruitment for Gulf of Maine shortnose sturgeon because, while spawning has been confirmed in the Merrimack River, total abundance is relatively low (Kieffer & Kynard 1996). If individuals began to spawn in the Penobscot River, this would have the potential to contribute significantly to the abundance of shortnose sturgeon in the Gulf of Maine; Altenritter (2015) predicted that even levels of successful reproduction in the Penobscot River as low as 1 or 5% would result in increased abundance of shortnose sturgeon in the Gulf of Maine by about 7%.

The results of this study indicate that shortnose sturgeon in the Penobscot River continued to exhibit movement patterns and seasonal distributions similar to those reported pre-dam removal, though some divergent patterns were shown. Signs of change suggested by this study include the exploration of habitat upstream of the former Veazie Dam and the shift in seasonal emigration rates toward more spring emigrants. In future years, with more time elapsed following the Penobscot River restoration efforts, changes in shortnose sturgeon movement patterns and seasonal distribution may become more evident. This study encompassed the initial years post-dam removal, but, when dealing with a long-lived species, significant change, such as spawning in newly available habitat, may not be realistic over such a short time frame (Doyle et al. 2005; National Marine Fisheries Service (NMFS) 1998; Strayer et al. 2014). The factors driving reproductive behavior of Gulf of Maine shortnose sturgeon are complex and continued research is needed to establish what drives the persistent use of the Kennebec complex to spawn. Continued collection of data on how shortnose sturgeon use the Penobscot River and other coastal Maine rivers is essential to build a complete understanding of how the Penobscot River Restoration Project will affect this endangered species in the Gulf of Maine.

CHAPTER 2:

RIVER REACH RESTORED BY DAM REMOVAL OFFERS SUITABLE SPAWNING HABITAT FOR ENDANGERED SHORTNOSE STURGEON

Abstract

The lowermost dam on the Penobscot River, Maine, was removed in 2013, making new habitat available for eleven species of diadromous fish. Endangered shortnose sturgeon (*Acipenser brevirostrum*) have never been documented spawning in the Penobscot River, but the dam removal facilitated access to fresh water essential for spawning. Spawning success also depends on the quality of the available habitat. Our project goal was to determine the distribution and amount of suitable spawning habitat based on depths, velocities and bottom substrates in the newly available reach upstream of the removed dam. Previously collected river elevation data and bottom substrate data were used to create two-dimensional hydrodynamic simulations of the reach at various spring discharges using the River2D hydrodynamic modeling program. The simulations were validated and adjusted using depth, velocity, and substrate data collected in 2014 and 2015. Suitable spawning habitat was modeled based on literature-informed suitability curves of depth, velocity, and bottom substrate. Between 41% and 63% of the study area offers usable spawning habitat, depending on river discharge rates. Velocity is the most limiting characteristic for overall suitability at all discharges modeled. At any of the five discharges examined, 51% of the study area is usable spawning habitat. Embeddedness is minimal at sites predicted to offer highly suitable habitat. Based on the habitat

characteristics considered, the newly available reach of the Penobscot River could support shortnose sturgeon spawning, offering critical habitat for this endangered species.

Introduction

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., lamprey, eels, and shad: Liermann et al. 2012). Dams have contributed substantially to declines in shortnose sturgeon (*Acipenser brevirostrum*) populations throughout their range by restricting access to freshwater spawning habitat (Jager et al. 2016; Limburg & Waldman 2009). Recent river restoration activities, including dam removals on the Penobscot River in Maine, have been aimed at restoring access to habitat for diadromous fish populations, including federally endangered shortnose sturgeon. The Penobscot River Restoration Project (PRRP) is a large collaborative effort (Opperman et al. 2011) that resulted in the removal of the two lowermost dams on the river, Great Works Dam (rkm 58) in 2012 and Veazie Dam (rkm 46.8) in 2013 (Figure 2.1). The PRRP also included increases in power generation at existing dams on the river and the installation of a fish elevator and fish bypass structure at two upstream dams. The PRRP dam removals facilitated direct access to 14 km of historic shortnose sturgeon habitat (Opperman et al. 2011). While the dam removals significantly increased access to freshwater habitat, the quality of the newly available habitat for sturgeon-specific needs is largely unknown. Notably, this reach could provide spawning habitat that might benefit shortnose sturgeon recovery in the region, but that outcome would depend on the availability of areas with physical characteristics meeting the specific spawning needs of this species (Kynard 1997).

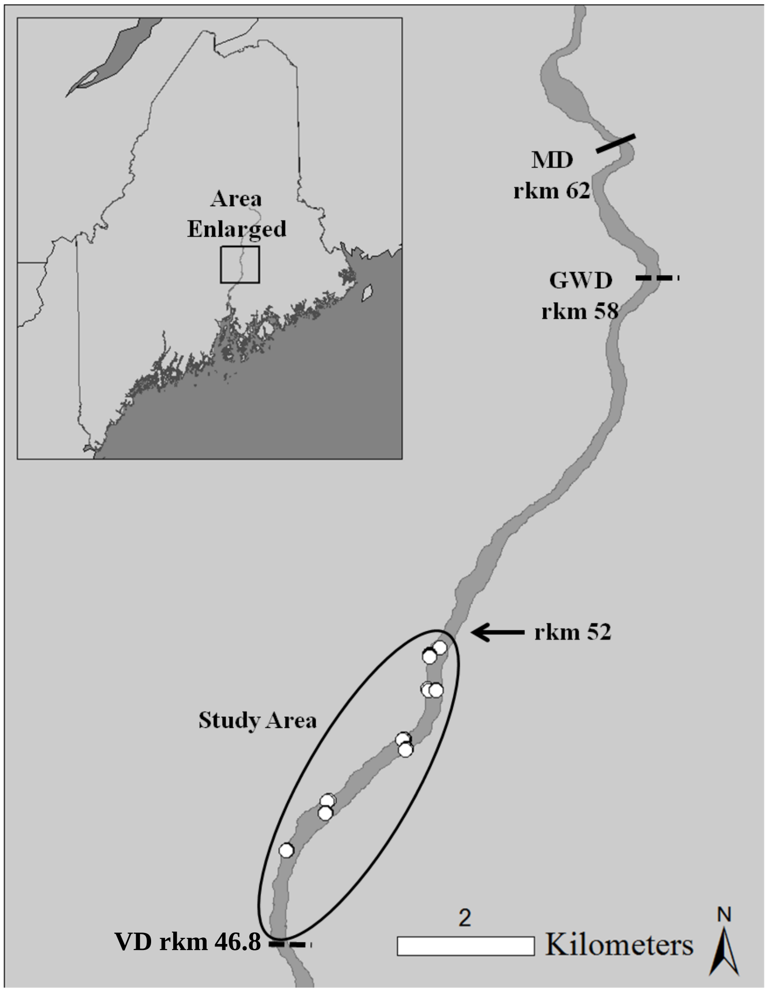

Figure 2.1. The lower Penobscot River, Maine. Removed dams are represented by dashed lines. GWD is Great Works Dam, removed in 2012. VD is Veazie Dam, removed in 2013. MD is Milford Dam, now the lowermost dam on the mainstem Penobscot River. The study area (rkm 47 to 52) is circled. Calibration data collection points are shown in white (multiple sampling points occurred in close proximity at each location shown).

The PRRP dam removals are believed to have restored access to 100% of shortnose sturgeon’s historic range in the Penobscot River, but it is unclear if shortnose sturgeon will spawn in the newly accessible habitat. Females with late stage eggs have been captured in the Penobscot River in summer and fall (Dionne 2010; Fernandes et al.

2010) and, based on the species' behavior in other rivers, might have been expected to remain in-river until spawning the following spring (Buckley & Kynard 1985; Kynard 1997). However, these maturing females were often detected on spawning grounds 140 km away in the Kennebec River during the spring spawning period (Dionne et al. 2013; Fernandes et al. 2010; Wippelhauser et al. 2015; Zydlewski et al. 2011). A central question is whether mature shortnose sturgeon will continue to travel to the Kennebec River to spawn, or begin to use the newly available habitat in the Penobscot River made accessible by the dam removals.

Buckley and Kynard (1985) have suggested that suitable water temperatures and flow conditions must be present to trigger the final maturation of shortnose sturgeon eggs and induce spawning activity. In other river systems, shortnose sturgeon spawn after peak spring flows, when discharge returns to moderate levels (Kynard 1997; Kieffer & Kynard 1996; Buckley & Kynard 1985). Suitable river temperatures range from 9 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 (Dionne 2010; Fernandes et al. 2010; Wegener 2012).

While river discharge and temperature are considered key determinants of the timing of shortnose sturgeon spawning, the location of spawning activity is governed by depth, velocity, and bottom substrate. Spawning typically occurs in the main channel of a river at depths ranging from 1.2 to 10.4 m (Kieffer & Kynard 1996; Richmond & Kynard 1995). Suitable water velocities for spawning range from 0.36 to 1.2 m s^{-1}, based on research conducted in the Connecticut, Merrimack, and Androscoggin Rivers (Buckley & Kynard 1985; Kieffer & Kynard 1996; Squiers et al. 1993). Egg survival is dependent on suitable velocities: at high velocities, eggs might not adhere to substrate and at low velocities eggs could deposit in clumps, inhibiting oxygen uptake and increasing risks of predation and fungal growth (Buckley & Kynard 1985; Crance 1986). Survival of larvae is dependent on velocities of 0.4 to 1.2 m s^{-1}, which allow sufficient downstream drift to rearing habitat (Buckley & Kynard 1981; Richmond & 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 (Cooke & Leach 2004; Kynard 1997). Substrate grain size classes suitable for spawning include boulder, cobble, and gravel (grain sizes ≥ 8 mm) (Buckley & Kynard 1985; Dadswell 1979; Taubert 1980). Highly embedded river bottoms (i.e. bottoms composed of cobble with sand grains interspersed) are not suitable for shortnose sturgeon spawning because the fine sediment fills the crevices that are important for egg and embryo retention and concealment (Richmond and Kynard 1995; NMFS 1998).

The goal of this study was to determine 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 assessments, to address this goal. We focused on the 5 km reach just upstream of the former Veazie Dam site from rkm 47 to 52 (Figure 2.1). 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 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 Area

The Penobscot River watershed is the largest in the state of Maine, draining over 22,000 square km. Its largest tributaries, the East and West Branches, join at Medway, Maine to flow south for approximately 180 km, where the river enters the Gulf of Maine through Penobscot Bay. The study area, rkm 47 - 52, has been characterized as a stretch with small sets of rapids and bedrock outcrops (Dudley & Giffen 1999). The upstream limit of the study area at rkm 52 was chosen for two reasons: (1) it lies just downstream of a set of rapids called Ayer's Rips (FERC 1997), which could pose a velocity barrier to frequent shortnose sturgeon passage and (2) available bathymetry and substrate data were not available upstream of Ayer's Rips. The USGS stream gauge at West Enfield, ME (station number 01034500) is approximately 53 km upstream of the study area and is the closest gauge providing river discharge. The drainage area at the West Enfield station is 17,278 km^2. The mean annual flow there is 345 $m^3 s^{-1}$ for the period of record (1903 to 2015).

Methods

Overview

Hydrodynamic simulations were generated using River2D, a two-dimensional depth averaged finite element model (See Appendix for model details; Steffler & Blackburn 2002; Ghanem et al. 1996; Waddle 2010). Three sub-programs within

River2D (R2D_Bed, R2D_Mesh, and River2D) were used. Data used to create the hydraulic model domain included geo-referenced 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 input 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 for the study area. Additional examination of spawning habitat suitability was accomplished by examining composite suitability and embeddedness data using ArcGIS for Desktop 10.2.2 (Environmental Systems Research Institute, Redlands, CA).

Bathymetry and substrate data collection and validation

Bathymetry and substrate data used in the River2D simulations were collected in 2007 (CR Environmental 2008) using a SyQwest, Inc Hydrobox precision echosounder (SyQwest, Inc, Cranston, RI) and a Trimble DGPS (Trimble, Sunnyvale, CA) to collect bathymetry. A side scan sonar (Edgetech, Inc Model 560, Edgetech, West Wareham, MA), sediment sampling, and video surveys were used to generate a bottom substrate map (CR Environmental 2008). Substrate data for the Penobscot River are limited and were only available from the pre-dam removal study conducted in 2007. Because our interest was in the post-dam removal conditions of 2014 and 2015, we assessed the validity of using the pre-dam removal data to simulate post-dam removal conditions by estimating the conditions necessary for incipient motion of the river bottom sediment

(Wilcock et al. 2009). The US Forest Service's bedload assessment for gravel bed streams program (BAGS) was used to calculate bed load transport rates (Pitlick et al. 2009) and estimate the grain sizes most likely to move under the discharge conditions experienced since 2007. While we also used the 2007 bed elevation data, we assumed that only water surface elevations relative to the river bottom would change as a result of dam removal.

Bed load transport capacities were calculated for four discharge scenarios representing hydrologic conditions observed between 2007 and 2015. Incipient motion and transport rates were calculated with the surface-based equation of Wilcock and Crowe (2003) in BAGS (Pitlick et al. 2009). Three discharge rates and a continuous discharge time series were considered: i) annual average discharge (402 $m^3 s^{-1}$), ii) 2-year flood (2002 $m^3 s^{-1}$), iii) 10-year flood (3253 $m^3 s^{-1}$), and iv) the recorded discharge record since the removal of the Veazie Dam (from December 1, 2013 to December 31, 2015). The study area was divided into two segments (upper and lower) and cross sections at the half-way point in each segment were examined using BAGS. Grain size distribution data were extrapolated from 2007 survey data. Water surface elevation measurements for pre- and post-dam removal scenarios were obtained from Kleinschmidt Associates' HEC-RAS modeling results for the study area (Milone & MacBroom 2008). BAGS calculations with both default and calculated Manning's *n* were compared for two discharges where HEC-RAS data were readily available (784 $m^3 s^{-1}$ and 4729 $m^3 s^{-1}$; Wilcock et al. 2009). Because calculations did not vary between estimated and default Manning's *n* (paired t-test, $p = 0.24$), default values were used for the remaining calculations.

Pebble counts were conducted in areas defined by the 2007 survey as cobble facies (distinct patches dominated by cobble; Buffington & Montgomery 1999a) to provide finer scale quantification of bottom substrate grain sizes. We wanted to account for the smaller grains also likely to be present in the 34% of the total study area reported to be cobble facies in 2007. Pebble counts were conducted along the river shore during late summer and early fall in 2014 following the protocols of Bevenger and King (1995) and Wolman (1954) to determine the proportion of smaller grains present in cobble areas. In addition to the availability of more fine grains for transport, the presence of small grains can promote increased transport through smaller intergranular friction angles (Buffington & Montgomery 1999b).

After validating applicability of the 2007 survey data to post-dam removal modeling, the 2007 survey map delineating substrate facies was georeferenced in ArcMap 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 in ArcMap of the substrate data to the bed elevation dataset. The substrate data were incorporated into 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.

Spring river discharge

Inflow discharge rates for the simulations were chosen to characterize suitable habitat availability under a range of conditions realistic for spring in the Penobscot River. Discharge data were collected for spring dates on which water temperature was suitable for shortnose sturgeon spawning (9° to 15° C). Daily mean river discharge data from

2006 to 2015 from the USGS West Enfield, ME gauge (01034500) website (U.S. Geological Survey 2016a) were considered. Water temperature data came from the Eddington, ME USGS gauge (01036390) for the same time period, except for 2014, when the Eddington gauge did not collect temperature data. For this year, water temperature at the Piscataquis gauge (USGS 01031500) was used. This was the closest gauge that collected water temperature and the spawning period dates used for spring of 2014 (from the Piscataquis gauge) were similar to the those used for other years (from the Eddington gauge). In comparing the water temperature records for March 1 to July 1 2015 collected at the Eddington and Piscataquis gauges, the correlation coefficient (R^2) was 0.987.

Five discharge conditions associated with the 5th, 25th, 50th, 75th, and 95th percentiles were determined using USGS gauge data to represent variable discharge conditions shortnose sturgeon would encounter if spawning in the study area. Because the discharge data were collected at West Enfield, approximately 53 rkm upstream of the upper boundary of the study area, StreamStats Version 3.0 (U.S. Geological Survey 2016b) was used to estimate mean monthly flows for both West Enfield, the location of the gauge that provided the spring discharge rates, and the upper boundary of the study area at rkm 52. Streamstats has an approximate error rate for mean monthly discharge of 10 to 28% in unregulated streams (Dudley 2004). The difference between the mean monthly discharges estimated for the rkm 52 and West Enfield sites were plotted versus discharge at West Enfield. A regression of the two was used to determine the additional discharge entering the Penobscot River from tributaries upstream of the study area ($y = 0.14x + 7.60$, $R^2 = 0.97$, $p < 0.001$). This additional discharge amount was added to each West Enfield spring discharge rate to provide estimates of discharge for the study area.

Model calibration and validation

Depth and velocity data for calibrating and validating River2D simulations of the study area were collected on March 16, 2016. Velocity data were collected using a Model 2000 Flow-Mate (Marsh-McBirney Inc., Frederick, MD) deployed from a boat. At each collection site (Figure 2.1), measurements were recorded for three points in the water column (~ 18 cm up from the bottom, mid-depth, and ~ 30 cm from the water surface). Water depth was measured at each location using a Humminbird 386ci GPS Fishfinder (Johnson Outdoors Marine Electronics, Eufaula, AL). The calculated discharge at the upstream boundary of the study area on this date was 678 $m^3 s^{-1}$. This discharge was used during a simulation run with an outflow elevation of 7 m (based on observed depths at the outflow boundary). Once the simulation was run to convergence, the simulated x and y coordinates of all mesh points, along with predicted depth and depth-averaged velocity values were output. Data were imported into ArcMap and a spatial join was performed to link each calibration data point to its closest simulated mesh node (the average distance of a calibration point to its closest simulation node was 1.76 ± 0.55 meters). A paired t-test was used to determine if the difference between the measured and simulated depths was significant ($n = 25$). If so (p-value < 0.05), the mean of the differences was added to the outflow elevation and the simulation was re-run to convergence. The simulated depths at 678 $m^3 s^{-1}$ corresponded closely with the measured depths (p-value > 0.05) and no further calibration was necessary. The same process was performed to link velocity measurements to corresponding simulated velocities for paired t-test validation ($n = 25$, significant p-value < 0.05).

Specific inflow and outflow elevation values were required as input parameters to model each spring discharge and were acquired using USGS gauge data to adjust the calibrated inflow and outflow elevations for the 678 $m^3 s^{-1}$ simulations to reflect elevations for the five spring discharges. To acquire depth measurements for the five spring discharge simulations for use in calibration, a similar adjustment approach was taken with the field-measured depths from March 16, 2016. Calibration of depth for each spring discharge simulation was completed following the process used for the 678 $m^3 s^{-1}$ simulation. Velocity could not be validated for the five spring discharges because field collection of velocity measurements was not completed for those specific discharges.

Habitat suitability indices

Habitat suitability index (HSI) curves were used for calculating habitat suitability in River2D (Figure 2.2). HSI curves designate habitat characteristics on a scale from 0 to 1; we considered HSI values for 0.7 to 1 to be highly suitable, HSI values from 0.4 to 0.69 to be moderately suitable, and HSI values from 0 to 0.39 to indicate low suitability. HSI curves for depth, velocity, and channel index (the metric used to represent bottom substrate) were created based on Wegener (2012), Crance (1986), and Squiers et al. (1993). Three velocity curves were used during analyses. The narrow velocity curve closely followed velocity preferences reported by Squiers et al. (1993) while the broad curve was based on Wegener (2012). The adjusted velocity curve was created by applying the measured versus simulated velocity regression equation (Figure 2.3b inset) to the velocity values used to create the broad curve (see Results).

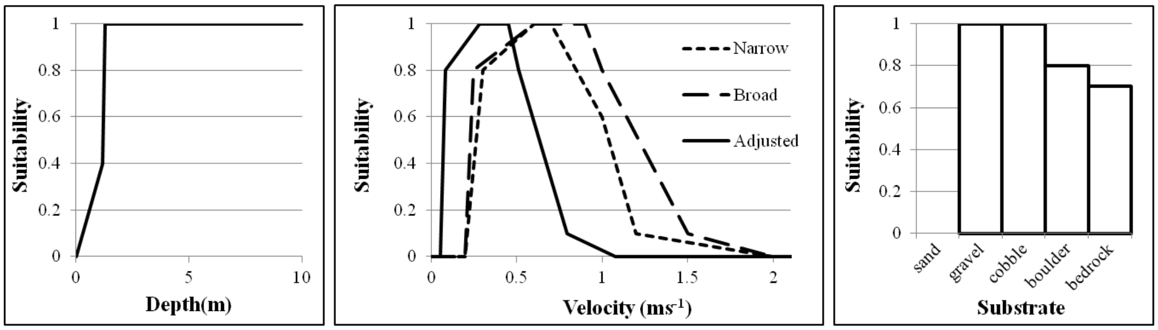

Figure 2.2. Shortnose sturgeon spawning habitat suitability index curves for depth, velocity, and bottom substrate.

Predicting habitat suitability

After model creation and calibration, habitat suitability at each spring discharge was determined using the PHABISM Weighted Usable Area approach in River2D (Bovee 1982). 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 (for each node of the mesh, the minimum value for the three separate suitability indices) was used to determine combined suitability. Weighted Usable Area (WUA) was calculated by multiplying the combined suitability value at each node by the area associated with the node and summing WUA for all nodes. Percent WUA is the WUA relative to the total area of the wetted study reach.

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

For each spring discharge simulation, the suitability results files (including combined suitability values at each simulation node) were imported to ArcMap for additional analysis. The combined suitability value of each simulation node was used to assign cell values to an output raster using the mean value option when more than one node fell within each cell. Raster cell size was kept as the default allowed by the Point to Raster tool (10.4 by 10.4 m). Rasters were averaged to create a composite map of habitat suitability for all spring discharges simulated.

Raster-based WUA was calculated by multiplying the cell's suitability value by the cell area, and summarizing the entire study. Total area was calculated by summing the area of polygons created from the raster. To confirm that this method corresponded closely to the approach used in River2D to calculate WUA, the process was repeated using each spring discharge habitat suitability raster and the percent WUA determined by each method was compared. The mean difference between percent WUA values calculated from the rasters versus River2D was less than 1% (0.5%). To test for a relationship between the distance upstream of the former Veazie Dam and composite suitability, the Locate Features Along Routes tool was used to determine the distance of each of the simulation nodes upstream of the dam. A Pearson Product Moment Correlation was used to test this relationship.

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 success following habitat selection, we separately mapped embeddedness throughout the study reach for joint consideration alongside the aforementioned HSI predictions. Embeddedness measurements were taken along the river shore during the late summer of

2015, when river discharge was at its minimum, exposing habitat that would be covered during the spring spawning season. Quantifying embeddedness followed the system described by Platts et al. (1983). A tape measure was extended perpendicular to the river along the shoreline from the vegetation line down to 1 m into the river. At each meter along the tape measure, a meter stick was laid parallel to the river, alternating in the upstream or downstream direction, and at every 10 cm along the meter stick, the piece of substrate immediately adjacent to the 10 cm mark was examined to determine its amount of embeddedness with sand. The percent coverage by fine sediment was summarized using a rating system from 1 to 5; 75% to 100% coverage with fine grains corresponded to a rating of 1 and <5% coverage by fine grains corresponded to a rating of 5. The overall embeddedness rating at each transect 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 the dataset of composite habitat suitability. Embeddedness survey sites were assigned the composite habitat suitability value of their closest raster cell and the joined attribute table was exported for statistical analysis. In addition, a joint "Embeddedness + HSI index" index was developed to incorporate embeddedness rating with composite habitat suitability. We did not differentially weight HSI or embeddedness in this joint index, but rather scaled the embeddedness ratings for each site to the same 0-1 range as habitat suitability by dividing the embeddedness values by 5. The joint index was calculated by adding the scaled embeddedness rating for each site to the HSI value associated with it from the composite suitability map and dividing by 2.

Results

Substrate data validation

The average bed load transport rate for the upper cross section over the discharge time series was 4.72×10^{-5} kg min^{-1} and 2.69×10^{-4} kg min^{-1} for the lower cross section. Bed load transport rates for the upper cross section of the study area ranged from 2.01×10^{-11} kg min^{-1} to 1.61×10^{-6} kg min^{-1} for pre-dam removal and 1.25×10^{-7} kg min^{-1} to 9.10×10^{-3} kg min^{-1} for post-dam removal. For the lower cross section of the river, the calculated pre-dam removal bed load transport rates ranged from 6.30×10^{-14} kg min^{-1} to 5.04×10^{-9} kg min^{-1} and for post-dam removal values ranged from 7.12×10^{-7} kg min^{-1} to 0.057 kg min^{-1}.

There was no difference in the pre- and post-dam removal geometric mean grain size for the upper or lower reach cross sections. The geometric mean grain size 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 data collection in 2007 would be limited to the movement of very coarse gravel and smaller grains. As only 4% of the total study area was reported to be covered by gravel and sand (CR Environmental 2008), the assumption of limited changes to the area was supported and 2007 survey data were therefore used for the River2D modeling of suitable spawning habitat for this study.

Small grain sizes (< 45.3 mm) composed 39.8% of the pebble counts we conducted in 2014 in areas defined as cobble facies in 2007. The estimated prevalence of small grains within cobble-dominated areas and the determination that 34% of the entire study area was dominated by cobble in 2007 suggests that an additional 13.6% of the study area bottom is susceptible to transport under the evaluated discharge rates.

Model calibration and validation

The five discharges used to represent spring river conditions were 310, 422, 667, 972, and 1480 $m^3 s^{-1}$ (Table 2.1). All spring discharge simulations were calibrated to predict depths comparable to field-measured depths (Table 2.1; Figure 2.3a). For the calibration day simulation, linear regression confirmed a significant correspondence between measured and simulated depths (Figure 2.3a inset, $y = 0.80x + 0.51$, $R^2 = 0.60$, $p < 0.001$). The slope of the regression line was not significantly different than 1, indicating a lack of skew ($p = 1.84$).

Velocity predictions from the simulation could not be fully validated with field data. Simulated velocity values were significantly different from measured depth averaged velocities, even after bed roughness values and eddy viscosity coefficients were adjusted in River2D (Steffler & Blackburn 2002), with the simulation consistently predicting lower values (Figure 2.3b, paired t-test, $p < 0.001$). When the velocity validation results were considered along with bottom substrate type, mean differences between measured and simulated velocities ranged from 0.43 $m s^{-1}$ to 0.59 $m s^{-1}$ (see Appendix). When only bottom velocity (rather than depth averaged) measurements were compared to simulated values, they were still significantly different and had a mean difference of 0.25 $m s^{-1}$ (Appendix, paired t-test, $p < 0.001$). Measured (depth averaged) and simulated velocities were linearly related, $R^2 = 0.50$ with a difference of 0.49 $m s^{-1}$ (Figure 2.3b inset, $y = 0.57x – 0.06$, p-value < 0.001). The slope of the regression line was not significantly different than 1, indicating a lack of skew (p = 2.0). The standard deviations of measured and simulated velocities were 0.27 and 0.21 m s^{-1}, respectively. As such, velocities predicted by the five spring discharge simulations were assumed to be under predicted.

Table 2.1. Depth calibration paired t-test results. Mean difference is between simulated and measured depths. After one or more iterations, simulations were all successfully calibrated (paired t-test values > 0.05). The simulations represented in this table were the final depth-calibrated simulations (and were subsequently used to obtain habitat suitability).

Percentiles	**Discharge (m^3 s^{-1})**	**Mean difference (m)**	**95% Confidence Interval**	**p-value**
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	1480	0.34	-0.06, 0.74	0.09

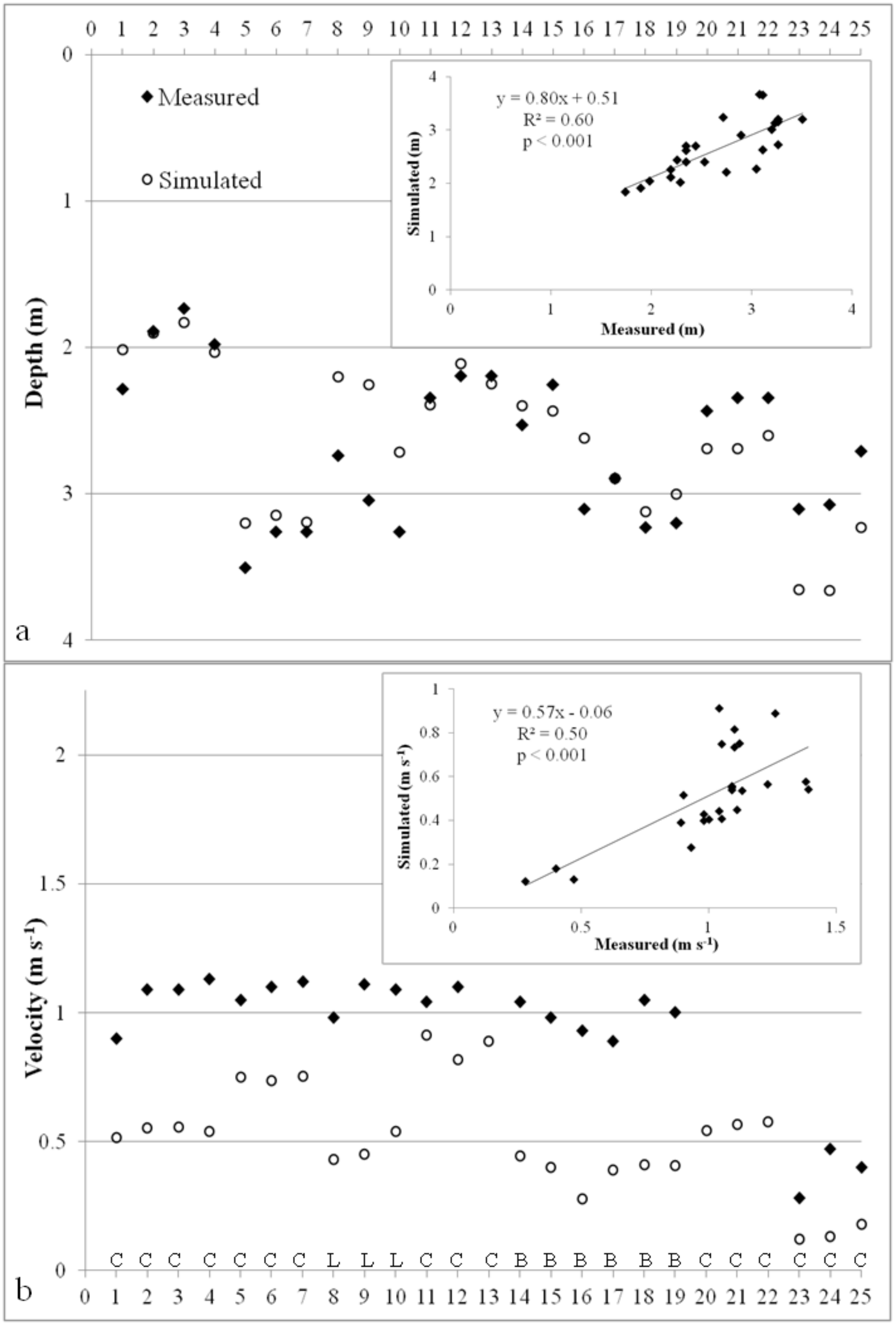

Figure 2.3. Measured and simulated depths (a) and velocities (b) at 25 sites within the study reach of the Penobscot River for a discharge of 678 $m^3 s^{-1}$. The inset graphs are linear regressions of measured versus simulated depths (a) and velocities (b). Letters associated with each site indicate bottom substrate type: cobble (C), bedrock (B), or boulder (L).

Three velocity HSI curves were used to evaluate combined suitability at the five spring discharges. An adjusted velocity HSI curve (Figure 2.2) was created by applying the measured versus simulated velocity regression equation (Figure 2.3b inset) to the broad curve to account for the model's under prediction of velocity. WUA was used to assess differences when applying each of the three velocity HSI curves. The broad velocity HSI curve resulted in the greatest percent usable area for all discharge rates (Figure 2.4). The narrow and adjusted velocity HSI curves yielded lower percent WUA values. The adjusted velocity HSI curve resulted in the lowest percent WUA at all discharge rates and the mean difference between percent WUA at each discharge using the broad and adjusted velocity curves was 18.15 ± 5.39. With the adjusted velocity HSI curve, the correlation between percent WUA and discharge produced a correlation coefficient (R^2) of 0.77, indicating that discharge rate is a useful predictor of habitat suitability. Because the adjusted velocity HSI curve was most reflective 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

All following results reflect the adjusted velocity HSI curve. Habitat suitable for shortnose sturgeon spawning was present throughout the length of the study reach at all discharges considered (Figure 2.4) and generally increased with increasing discharge. Percent WUA was least for the 5^{th} and 10^{th} percentile discharge simulations with 41% of the study area being usable. Percent WUA was greatest for the 75^{th} 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 49 (Figure 2.5). Combined 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.

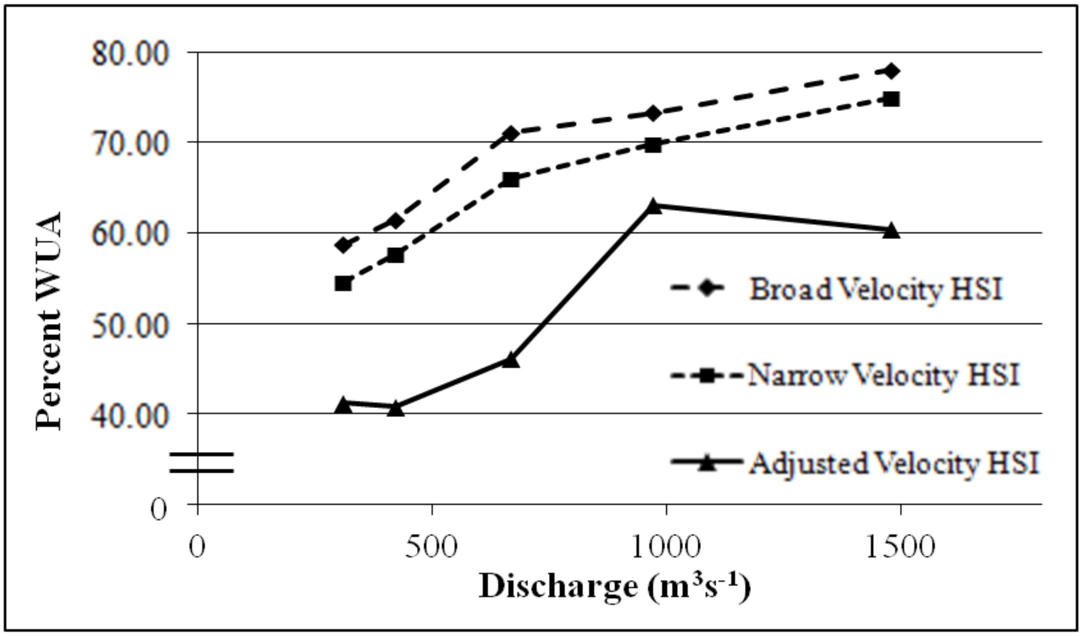

Figure 2.4. Percent WUA at five spring discharges. Three velocity HSI curves (Figure 2.3) were included to examine how combined suitability varies with differing suitable velocity ranges (broad, narrow, and adjusted).

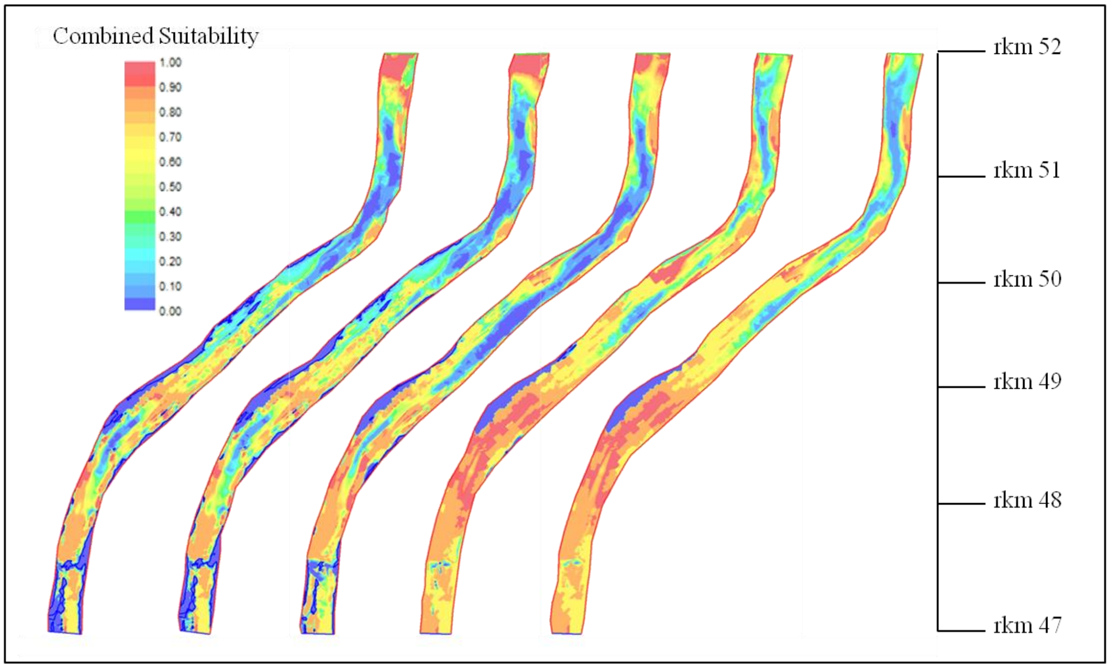

Figure 2.5. Spawning habitat suitability maps for the five spring discharges (using adjusted velocity HSI curve). Areas with the highest combined (depth, velocity, and channel index) suitability are shown by the by warmest colors. The far left simulation is for 310 $m^3 s^{-1}$ and each progressive map represents simulations with increasing discharge (422 $m^3 s^{-1}$, 667 $m^3 s^{-1}$, 972 $m^3 s^{-1}$, and 1480 $m^3 s^{-1}$ on the far right).

At all spring discharges, velocity was the most limiting characteristic for suitable spawning habitat in the study area (Table 2.2). 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%.

Table 2.2. Percent WUA by habitat characteristic for each spring discharge using the adjusted velocity HSI curve. Highlighted values are the lowest percent WUA for that spring discharge rate and represent the habitat characteristic that is most limiting to combined suitability.

		Spring Discharge ($m^3 s^{-1}$)				
		310	422	667	972	1480
Characteristic	Depth	75	77	91	97	100
	Velocity	58	56	55	77	74
	Bottom Substrate	82	82	83	82	82

The composite suitability map of the five spring discharges suggested 51% of the study area offers usable habitat for spawning (Figure 2.6). Two regions in the study reach provide the highest suitability at all flows, the most upstream portion of the study area (around rkm 52) and some mid-channel habitat between rkm 47.5 and 49.

There was a significant but weak relationship between distance upstream of the former Veazie Dam and composite suitability. The Pearson Product Moment Correlation between distance and composite suitability was significant (p-value < 0.001) with a coefficient of -0.1.

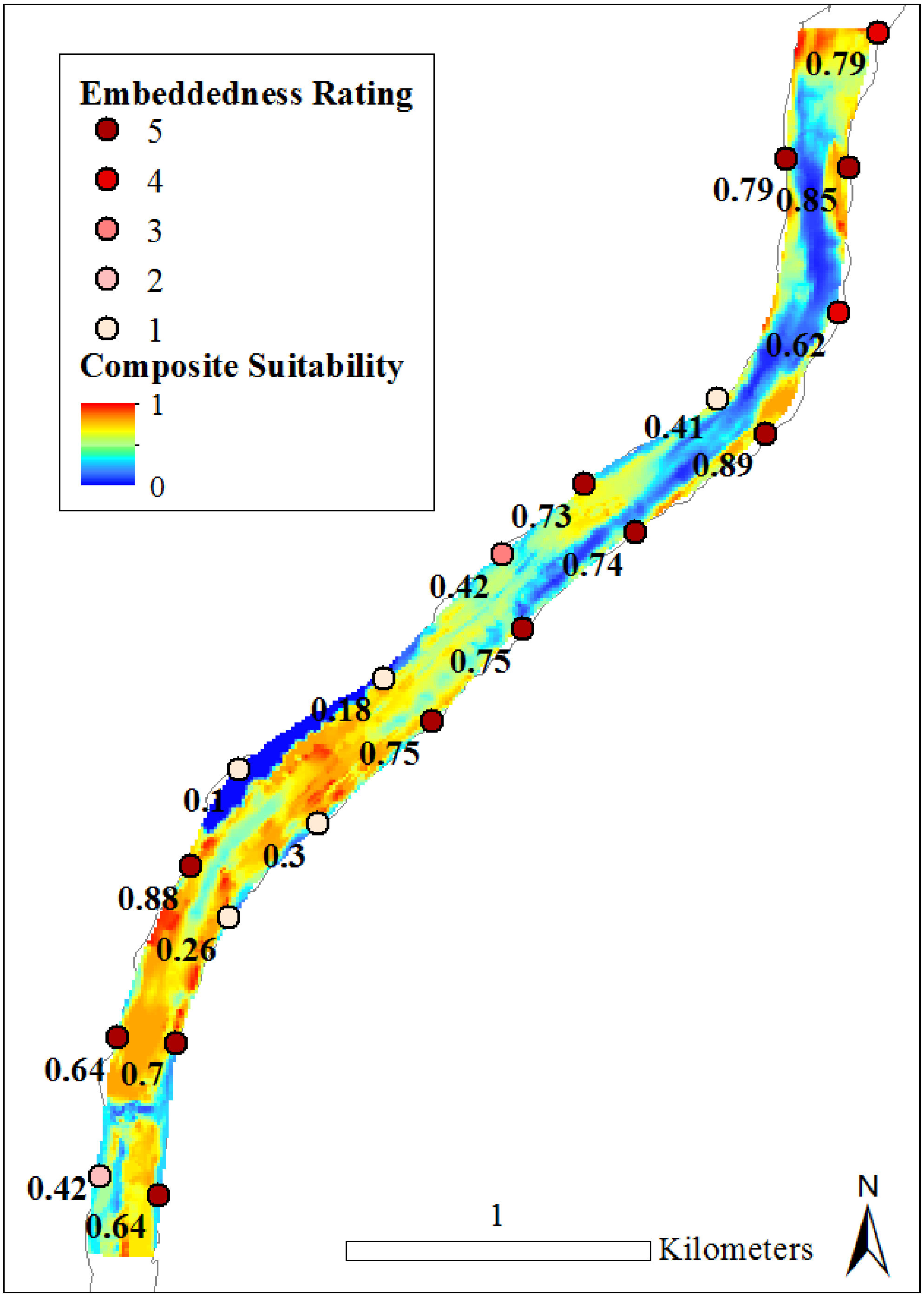

Figure 2.6. Composite map of habitat suitability within the study area at all spring discharge rates. Areas with the warmest color are predicted to offer highly suitable habitat at all five spring discharge rates. Areas with the coolest colors do not offer suitable spawning habitat at any spring discharge rates. 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) and light pink is highly embedded with fine sediment (not suitable). Values associated with each embeddedness point are Embeddedness + HSI index values.

Embeddedness

Sites with suitable levels of embeddedness were distributed throughout the study area on both shores of the river (Figure 2.6). East shore sites had a median embeddedness rating of 4.1 while the west shore sites were 3.1. The mode for all sites was 5 and the average was 3.5 (n = 20). Locations where embeddedness data were collected that were within areas of high (0.7 to 1) composite suitability exhibited low levels of embeddedness (ratings of either 4 or 5) (Figure 2.6). In areas with moderate (0.4 to 0.69) composite suitability, 70% had low embeddedness and in areas with low composite suitability (0 to 0.39), 33% of the sites had low embeddedness. Embeddedness decreased as the composite suitability value for an embeddedness site increased (coefficient = 0.47; p = 0.037). Overall, ten of the 20 embeddedness sites had joint Embeddedness + HSI index values of 0.7 or greater, indicating of 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 never been documented in the Penobscot River (Dionne et al. 2013; Fernandes et al. 2010; Wegener 2012), but with an increase in available freshwater habitat, and the presence of suitable spawning habitat, spawning might commence. In the Kennebec River, shortnose sturgeon spawning in habitat made accessible by dam removal began within 10 years of the Edwards Dam removal in 1999 (Wippelhauser et al. 2015). Shortnose sturgeon in the Penobscot River were first confirmed to access the newly available habitat as far upstream as rkm 52 in the fall of 2015 (Chapter 1).

However, in the spring, when we expect spawning to occur, individuals have not been documented moving upstream of the former Veazie Dam since its removal in 2013. By focusing on the study area from rkm 47 to 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.

In other rivers, shortnose sturgeon have been described using 1 or 2 km long reaches for spawning (Kieffer & Kynard 1996; Wippelhauser & Squiers 2015). The 14 km reach made accessible by the Veazie and Great Works Dam removals represents a substantial increase in the amount of critical freshwater habitat for shortnose sturgeon in the Penobscot River. While this research focused on the first 5 km of this newly available habitat, future research on the reach from rkm 52 to the Milford Dam (rkm 62) would enhance understanding of the quality of habitat made available by the PRRP dam removals. However, the 5 km study area may represent the reach most likely to support spawning because the rapids at rkm 53 may 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 area for shortnose sturgeon spawning. This encouraging conclusion is magnified when considering that the dam removal also increased the amount of freshwater habitat downstream of spawning grounds, which is vital for survival of larval and juvenile shortnose sturgeon (Kynard 1997). Larval sturgeon are not hatched with salinity tolerance and have been reported to travel between 15 and 25 km from spawning grounds to downstream rearing habitat (Bath et al. 1981; Taubert 1980). In the Penobscot River, salt water has been reported to reach rkm 20 or 30 during the spring, while in dryer summer months salt water can reach rkm 32 or 42 (Haefner 1967;

Stich et al. 2016). Prior to the PRRP dam removals, freshwater spawning and rearing habitat was limited to, at the most, 16 km. If spawning commenced within the study area, between 10 and 32 km would be available to larval and juvenile fish as rearing habitat, depending on the intrusion of salt water.

Shortnose sturgeon are predicted to 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 and 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, thought to be the most important habitat characteristic determining spawning habitat suitability for shortnose sturgeon (Kieffer & Kynard 1996; Kynard 1997), was the most limiting characteristic for all spring discharge simulations. The importance of velocity in influencing spawning habitat choice has been related to the requirements of eggs and larvae for appropriate water velocities to support their survival (Kynard 1997; Kieffer & Kynard 1996). Particularly at the three lowest discharges, water velocities were too great within the main channel from approximately rkm 51.5 downstream to rkm 49.5. 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, in the upper portion of the study area, suitable spawning habitat is not found within the main channel due to high velocities.

Spawning shortnose sturgeon in other rivers prefer bottoms composed of gravel, cobble, boulder, and ledge (Crance 1986; Kieffer & Kynard 1996; Squiers et al. 1993). In addition, spawning habitat is expected to contain low levels of embeddedness because the presence of fine grains within interstitial spaces of the bottom substrate limits survival of eggs (Richmond & 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; the glacial history of the area created a system with a limited supply of fine sediment (Borns et al. 2004). Dudley and Giffen (1999) reported that the study area falls within a zone characterized by rapids and bedrock outcrops, with bluffs of unconsolidated material along the banks. Limited amounts of fine sediment settle and embed the river bottom because of persistent flows throughout the year, thus promoting suitable levels of embeddedness (CR Environmental 2008).

Habitat suitability predictions from hydrodynamic simulations were based on calibrated and field-validated data. Field-collected measurements were used to successfully calibrate all spring discharge simulations for depth. The River2D model underestimated velocities, a feature that has been reported by other researchers working with the program. Wegener (2012) also found River2D under predicted velocity by 0.11 $m\ s^{-1}$ to 0.31 $m\ s^{-1}$ within a reach in the Penobscot River. During a study evaluating the depth and velocity predictions of River2D in areas around large boulders, Waddle (2010) showed a tendency for River2D to under predict velocities by approximately 0.6 m s^{-1}. We addressed this underestimation by adjusting the HSI curve used to predict velocity suitability.

Following a dam removal, physical changes such as increased water surface slope and altered water depths could drive alterations in habitat characteristics that affect shortnose sturgeon spawning (see Appendix). With steeper water surface slopes, flow velocities could increase enough to transport larger grain sizes, altering bottom conditions. However, in the study area, the transport capacity did not substantially change, despite the increase in slope post-dam removal. Our calculations using BAGS indicated that the use of the 2007 substrate data to represent the river bottom was reasonable. Still, current-day substrate and higher resolution embeddedness data should be collected to decrease the uncertainty of using pre-dam removal data (Chapter 3).

Spawning shortnose sturgeon will respond to a suite of habitat characteristics when they select spawning habitat. Therefore, the treatment of depth, velocity, and bottom substrate as independent or equally important features of the environment by River2D is not biologically realistic. 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. Water velocity has been suggested as the most important habitat characteristic determining where shortnose sturgeon spawn (Buckley & Kynard 1985; Kynard 1997). We speculate that if velocity had been given higher weight, predicted WUA would decrease for moderate discharges because velocity was the most limiting characteristic for the 50th percentile discharge simulation. In calculating the Embeddedness + HSI index values, we also did not attempt to differentially weight the variables. Better documentation of the physical conditions at spawning locations is necessary to inform more accurate HSI curves for shortnose sturgeon spawning. It would be particularly informative to acquire more information on the physical conditions present at spawning habitat used by shortnose sturgeon in the Gulf of Maine (i.e. in the Kennebec complex and the Merrimack River (Kieffer & Kynard 1996; Wippelhauser et al. 2015)).

The methods used in this study allow us to synthesize information concerning four habitat characteristics that influence shortnose sturgeon spawning habitat suitability. Using River2D, we obtained suitability predictions based on depth, velocity, and bottom substrate over a range of discharges likely to occur during the spring spawning season. By importing the River2D habitat suitability results into ArcMap and converting them to raster format, many additional analysis steps were possible. A composite suitability map was created that provides information on where suitable spawning habitat was present no matter the spring discharge. With the embeddedness point data in ArcMap, suitability predictions for all four characteristics were considered. Although the spatial resolution of these Embeddedness + HSI index locations was limited to 20 data points along the shore of the river, these methods can easily be applied to a larger embeddedness dataset to provide finer scale details on overall spawning habitat suitability. While researchers have employed River2D to model spawning habitat for shortnose sturgeon (Wegener 2012) and other species previously (Hatten et al. 2013; Yi et al. 2010), our additional analysis methods using ArcMap could be useful in other systems to further refine River2D habitat suitability predictions for multiple fish species.

With the confirmation that shortnose sturgeon visited the area upstream of the former Veazie Dam during fall of 2015 (Chapter 1), this study offers timely information on the suitability of the habitat for spawning. Shortnose sturgeon in other northern rivers, such as the Merrimack River, MA, overwinter in areas close to spawning grounds and when water temperatures warm in the spring, individuals move from these staging areas a short distance upstream to spawn (Buckley & Kynard 1985). In the Kennebec River, shortnose sturgeon overwinter in habitat as close as 2 km downstream of spawning habitat (Wippelhauser et al. 2015). In recent years, shortnose sturgeon overwintering aggregations have been documented between rkm 43 and 44 (Lachapelle 2013; Chapter 1). The close proximity of overwintering habitat to suitable spawning habitat within the study area conforms to the trend observed in other rivers that support sturgeon spawning (Buckley & Kynard 1985; Kynard 1997). The confirmation that shortnose sturgeon can swim upstream of the rapids at the former Veazie Dam offers additional encouragement that spawning by shortnose sturgeon could begin to occur in the Penobscot River. Increased monitoring efforts during the spring for upstream movements of tagged adults and for eggs and larvae will continue to determine whether fish make use of the newly available habitat. The habitat suitability maps can help to target these monitoring efforts by increasing sampling activity in areas where spawning is more likely to occur. While the results of this study are encouraging, the true confirmation of the quality of the habitat will be realized when early life stage sturgeon are documented in the Penobscot River. If spawning begins, it would not only have great implications for the future of shortnose sturgeon in the Gulf of Maine, but would also present a great opportunity to expand our understanding of the habitat that shortnose sturgeon require for spawning.

CHAPTER 3:

CONSIDERING THE FUTURE FOR SHORTNOSE STURGEON IN THE PENOBSCOT RIVER, MAINE

Abstract

Diadromous fish species, including shortnose sturgeon (*Acipenser brevirostrum*), face numerous threats, many directly caused by humans. Conservation efforts in recent decades have been implemented to counteract the negative impacts of dams, pollution, and overfishing. For example, recent dam removals from the Penobscot River, Maine facilitated access to additional freshwater habitat important for shortnose sturgeon to complete their life history. Recent research found the newly available habitat to be suitable for spawning and determined that it was accessed by shortnose sturgeon in the initial years following dam removal. These recent studies provide important and timely information on the response of shortnose sturgeon to river restoration efforts and the potential for spawning to commence in the Penobscot River, which would promote the species' continued recovery. It is important for research on movements and habitat suitability to continue to inform efforts to effectively manage this endangered species. Additional threats to shortnose sturgeon exist and managers have limited information on the extent to which the recovery of this species might be affected by each threat independently as well as cumulatively. For example, climate change will affect shortnose sturgeon in numerous ways, including through changes to habitat features such as salinity and temperature. The goal of this chapter was to summarize the results of recent studies of shortnose sturgeon movement patterns and habitat suitability in the Penobscot River

and to suggest future directions of research that build on previous studies while highlighting emerging issues related to climate change.

Introduction

Efforts to promote the recovery of endangered shortnose sturgeon in recent decades include measures to address pollution and decrease fishing pressure (National Marine Fisheries Service (NMFS) 1998). Dam removals offer additional benefits to shortnose sturgeon populations, as access to freshwater habitat is critical for the species to complete important portions of their life history (Dadswell 1979; Kynard 1997). Following the Veazie and Great Works Dam removals from the Penobscot River, Maine in 2012 and 2013, shortnose sturgeon were documented using the newly available river habitat in the first two years post-dam removal (Chapter 1) and the reach upstream of the former Veazie Dam was predicted to offer usable habitat for spawning (Chapter 2). While this research provides important information on the species in the Penobscot River, it is critical that data continue to be collected for use by managers and other researchers. Because of the extensive amount of shortnose sturgeon movement between coastal Maine rivers (Dionne et al. 2013; Fernandes et al. 2010; Wippelhauser et al. 2015), the response of shortnose sturgeon to changes in the Penobscot River has the potential to significantly affect the species within the Gulf of Maine as a whole. In addition, the response of shortnose sturgeon to dam removals in the Penobscot River will be instructive to managers throughout the species' range, where dam removals may be an effective strategy for recovery. However, solutions for one threat to the species must not be examined in a vacuum, as additional threats still exist that might have significant effects on the species. For example, climate change will likely have direct and indirect effects on shortnose sturgeon throughout the species' range. These effects could counteract some of the beneficial changes seen with restoration efforts, such as dam removal, and are therefore important to consider.

Future directions of research

Research concerning movement patterns and seasonal distribution of shortnose sturgeon in the Penobscot River should be continued and improved to better describe how the Penobscot River Restoration Project will affect this endangered species. In the first two years following the dam removals, evidence suggests that shortnose sturgeon continue to spawn outside of the Penobscot River. However, they do use habitat within the river during all times of the year to forage and spend the winter (Chapter 1). To improve the analyses used in Chapter 1, an important next step is to compare calculated rates of emigration and immigration for all individuals carrying acoustic tags pre- and post-dam removal, rather than performing a qualitative comparison to pre-dam removal literature values. This would better elucidate statistical comparisons of how movement patterns have changed post-dam removal. A greater number of active tags and the presence of tags in individuals at various life stages would allow a more complete understanding of shortnose sturgeon use of the Penobscot River. Increasing the number of tags would also provide more detail concerning the types of movements exhibited both within the Penobscot River and among other coastal rivers. Future early life stage sampling could be improved by using habitat suitability maps (Chapter 2) to increase the likelihood of collecting conclusive proof of the start of spawning if it begins in the Penobscot River.

It is important to consider not just the quantity of habitat made available by the Penobscot River Restoration Project, but also how suitable that habitat is to support shortnose sturgeon. The habitat suitability analyses performed using River2D indicated that, at any discharge likely to occur during the spring spawning season, over 50% of the 5 km reach upstream of the former Veazie Dam offers usable spawning habitat (Chapter 2). This study serves as a starting point to perform more analyses of habitat suitability in the 14 km reach made available by the Veazie and Great Works dam removals.

To improve habitat suitability predictions, additional habitat data and model refinements should be made. Current-day substrate data should be collected and additional steps should be taken to improve velocity predictions in the model to better estimate suitability for the entire 14 km reach made available by dam removals, including both the 5 km study area from Chapter 2 and upstream to rkm 62. A greater resolution dataset of embeddedness, for example for the entire width of the river and at a more refined scale (i.e. 10 x 10 m grid), could be collected to inform the quality of habitat based on all characteristics considered important for shortnose sturgeon spawning. Finally, if more data become available concerning shortnose sturgeon spawning habitat preferences in other Gulf of Maine rivers, details of habitat conditions (velocity, depth, and substrate) from those locations could be used to refine habitat suitability index curves and better predict spawning habitats in the Penobscot River. The River2D model and ArcGIS approach could also be used to predict suitable habitat during other seasons and life stages, e.g., foraging and wintering, for shortnose sturgeon and other species.

While the recent increase in available freshwater habitat in the Penobscot River represents a significant step forward for shortnose sturgeon recovery, climate change may present additional challenges for the species. Identified environmental changes resulting from increasing atmospheric CO_2 concentrations include sea level rise, increasing temperatures, and changes in precipitation (Church et al. 2013; Fernandez et al. 2015; Sheffield & Wood 2008). These and other changes will affect shortnose sturgeon in numerous ways, e.g., by changing the availability of essential freshwater habitat. If rising sea levels in the Gulf of Maine cause salt water to intrude farther upstream in the Penobscot estuary, the amount of available freshwater habitat, required by shortnose sturgeon during multiple times of year and at multiple life stages, will be more limited than current-day conditions.

The importance of considering the non-static nature of salinity zones within an estuary was highlighted in the 1998 recovery plan for shortnose sturgeon (National Marine Fisheries Service (NMFS) 1998) because these areas provide essential foraging and refuge habitat. Research has not occurred concerning saltwater intrusion due to sea level rise as a future limiting factor to shortnose sturgeon populations. However a study in the Delaware River suggests that future availability of critical spawning habitat for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) would be limited by sea level rise since the salt front could intrude as far as 11 km upstream of the present-day location (Breece et al. 2013). For shortnose sturgeon in the Penobscot River, saltwater intrusion caused by sea level rise could limit larval and juvenile survival because shortnose sturgeon are not hatched with tolerance to high salinities (Dadswell 1979; Jenkins et al. 1993; Ziegeweid et al. 2008). Future research following the approach of Breece et al.

(2013) could be used to predict the extent of saltwater intrusion under different climate change scenarios to determine whether freshwater habitat availability could limit early life stage shortnose sturgeon survival should spawning commence in the Penobscot River.

Changing precipitation regimes due to climate change will also impact estuarine conditions by altering river discharge rates (Sheffield & Wood 2008). For example, under future drought conditions, the intrusion of salt water caused by sea level rise alone could be exacerbated and result in further intrusion in the estuary. This would further limit larval and juvenile shortnose sturgeon survival. Sea level rise would also change water surface slopes in the estuary, initiating other possible physical changes to shortnose sturgeon habitat such as decreased flow velocities and increased fine sediment deposition.

Water temperature increases associated with climate change will affect shortnose sturgeon both directly and indirectly. Increased temperatures could act in concert with increased salinities to limit survival of shortnose sturgeon at critical life stages (Ziegeweid et al. 2008) and shift the timing of shortnose sturgeon spawning. Warming waters may also alter other species' distributions and could impact shortnose sturgeon by changing their prey availability.

Conclusions

The intent of this chapter was to synthesize results and lessons learned studying shortnose sturgeon movement patterns, seasonal distributions, and habitat suitability and suggest future research paths to build on that new knowledge. I would also like to highlight the necessity of focusing research questions on how climate change could affect shortnose sturgeon in the future. While recent research indicates that suitable spawning habitat exists in the Penobscot River that could contribute to future shortnose sturgeon recovery (Chapter 2), the emerging threat of climate change could drive additional habitat changes that limit the species' success. Researchers should study these potential climate change effects on shortnose sturgeon so that informed decisions can be made to arm against potential negative impacts and increase the likelihood of successful recovery.

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APPENDIX:

MODELING RIVER HYDRODYNAMICS AND SEDIMENT TRANSPORT

This section is intended to accompany Chapter 2 and provides additional information concerning the use of two modeling programs, River2D and BAGS, to examine the study area. The following topics are discussed concerning the two programs: an overview of River2D, some limitations inherent with the program and methods used in Chapter 2, validation of River2D velocity predictions, principles of sediment transport, and the potential for dam removal to drive riverbed changes.

River 2D

Program description

The basic principles underlying River2D are summarized from Steffler & Blackburn (2002):

- River2D is a two-dimensional, depth averaged model based on a conservative form of the St. Venant Equations. Conservation of water mass is used to solve for depth and discharge intensity.
- Three basic assumptions govern River2D: (1) the distributions of horizontal velocities over depth are uniform (2) in the vertical direction, the pressure distribution is hydrostatic and (3) wind forces and Coriolis are negligible.
- Bed sheer stresses are related to the magnitude and direction of the depth averaged velocity and drive the friction slope terms. Bed roughness height, k_s, and

the depth of flow influence the friction slope term via inclusion in the calculation of the Chezy coefficient.

- The depth-averaged transverse turbulent shear stress is modeled with a Boussinesq type eddy viscosity formulation, which includes the eddy viscosity coefficient v_t. This coefficient is composed of three terms: a constant, a bed shear generated term, and a transverse shear generated term.
- When areas within the model mesh are above the water surface, the model uses groundwater flow equations rather than surface flow equations. This approach allows the calculations to continue without any updates to boundary conditions.
- River2D predicts habitat suitability based on the Weighted Usable Area (WUA) approach by Bovee (1982). WUA is calculated as the sum of the product of a suitability index value at each node and the area associated with that node. The depth, velocity, and bottom substrate suitability values for each node are combined into one term to represent the combined suitability index value for that node. This can be accomplished using triple product, harmonic mean, or minimum value (the minimum value approach was used in Chapter 2).
- The Finite Element Method (based on the Streamline Upwind Petrov-Galerkin weighted residual formulation) is used to solve the hydrodynamic equations in River2D. The Newton-Raphson iterative method is used to obtain solutions of unknown values at each time step of the model, which is run until a desired level of convergence is achieved. The discretization of the model is fully conservative, meaning no fluid mass is gained or lost over the study area.

River2D limitations

Using any modeling program to simulate hydrodynamic conditions comes with limitations. Identified limitations of River 2D (from work conducted in Chapter 2) are presented here.

1. River2D assumes that velocities are uniform over depth, an innate assumption of all two-dimensional models (Steffler & Blackburn 2002). This means that three-dimensional effects such as depth varied flows and flows around structures are not included. Thus, the depth averaged velocity values output by River2D cannot provide information on how velocity profiles at each node of the model mesh vary relative to depth and bottom grain size, two important determinants of velocity (Wilcock et al. 2009). Water depth is proportionally related to velocity while bed grain size is inversely related. This is illustrated by the Manning Equation: $U = \frac{\sqrt{SR^{2/3}}}{n}$ where *U* is velocity (m s^{-1}), *S* is bed slope, *R* is hydraulic radius (a ratio of flow area to wetted perimeter), and *n* is Manning's roughness (m). Bed grain size contributes to the roughness term, with larger grains having greater roughness than smaller grains. If three-dimensional velocity data were available for the study area, it would be possible to examine how velocity profiles at locations of different bottom substrate and depth differ. One of the following sections examines Chapter 2 velocity validation results more closely to consider how bottom substrate could have affected the depth averaged velocity predictions by River2D.
2. Because an assumption of River2D is that wind forces and Coriolis are negligible, the accuracy is limited in areas where bed slope changes rapidly or in very large

bodies of water where Coriolis would have an effect. However, the accuracy of simulations of the study area in Chapter 2 is likely not limited by these assumptions because slope does not change rapidly in the study area and it is not large enough for Coriolis forces to play a significant role.

3. In Chapter 2, a range of discharge rates was considered to evaluate shortnose sturgeon spawning habitat in the 5 km study area. The level of uncertainty associated with predicted depth and velocity values in the study area likely varies by discharge, with the results for simulations at higher discharge rates being less certain due to greater depths and therefore potentially greater real-world variability of velocity profiles.
4. Within River2D, bottom substrate is represented by roughness height (k_s). The substrate data available for the Chapter 2 study area was in the form of a map delineating polygons dominated by different substrate types (sand, gravel, cobble, boulder, or bedrock). This information was translated into a form applicable to the River2D input file (k_s values) by determining the median grain size of each substrate type (determined using the size classes defined by the Wentworth Scale; Bevenger & King 1995). In reality, roughness values in areas defined as dominated by a single substrate type, i.e. cobble, will vary because a range of grain sizes comprise each substrate type. It is important to acknowledge the coarse resolution of the substrate data used in Chapter 2, and in the future more detailed grain size information should be collected for use in River2D so that the model can more accurately predict the hydrodynamic conditions of the study area.

Velocity

River2D consistently under predicted velocity values in the study area despite efforts to improve the predictions through various model adjustments suggested by the River2D manual (Steffler & Blackburn 2002). The adjusted velocity HSI curve (Figure 2.2) was created to account for the model's under prediction of velocity, however further examination of the velocity validation results was also performed to better understand what might have caused the discrepancy. Two approaches were performed to consider the under prediction of velocity by River2D: (1) inclusion of bottom texture; (2) use of bottom-velocity rather than depth-averaged velocity.

The mean difference of all field measured velocities versus simulated velocities (n=25) was 0.49 m s^{-1} (Chapter 2). At sites where cobble dominated (n = 16), the mean difference was 0.43 ± 0.21 m s^{-1} (Table A.1). The mean differences between measured and simulated velocities at bedrock and boulder sites were greater (Table A.1). Sample sizes were small when paired velocity values were separated by bottom texture. Future work should increase sample size and examine how changes to the magnitude of bed roughness height k_s (used to represent bottom substrate for each node of the model mesh) affect simulated velocities.

Table A.1. The mean difference of measured versus simulated velocity values when sites are categorized by bottom texture.

substrate	mean difference (ms^{-1})	standard deviation (ms^{-1})	n
cobble	0.43	0.21	16
bedrock	0.59	0.05	6
boulder	0.59	0.06	3

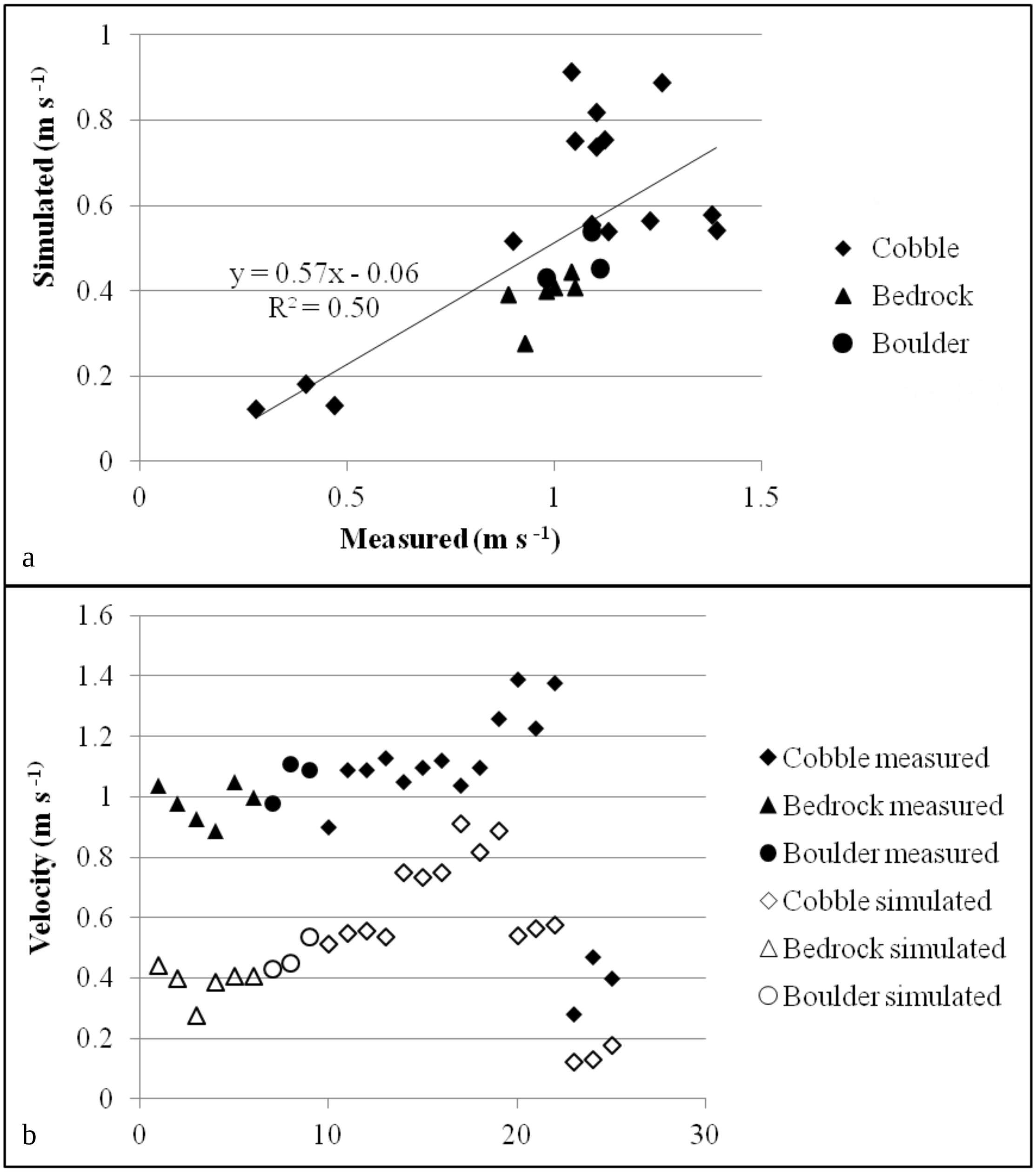

Figure A.1. Linear regression (a) and comparison of values (b) of measured and simulated velocities categorized by bottom texture. The line and regression equation shown in Figure A.1.a represents the linear regression of all sites (see Chapter 2 Figure 2.3).

The program River2D predicts depth averaged velocities. To consider whether River2D velocity predictions more closely matched real-world velocity values at the river bottom, validation methods were repeated using the bottom velocity measurement at each site. Paired t-test results still indicated that the simulated velocities were significantly different from measured bottom velocities ($p < 0.001$), however the mean difference was 0.25 m s^{-1} (Figure A.2). Measured and simulated velocities were linearly related, with $R^2 = 0.65$ (Figure A.3, $y = 0.77x – 0.07$, $p < 0.001$). The slope of the regression line was not significantly different than 1, indicating a lack of skew ($p = 1.94$). These results are consistent with those using depth-averaged measured velocity values, as both indicated under prediction by River2D. However, the decrease in mean difference when bottom velocities were compared to simulated values suggests that River2D predictions may be closer to reality in the lower portion of the water column and the higher velocities present closer to the water surface are less well predicted by the model. More work in the future should address the discrepancy of velocity predictions by River2D so that the program can be accurately used to predict habitat suitability for shortnose sturgeon and other species of interest.

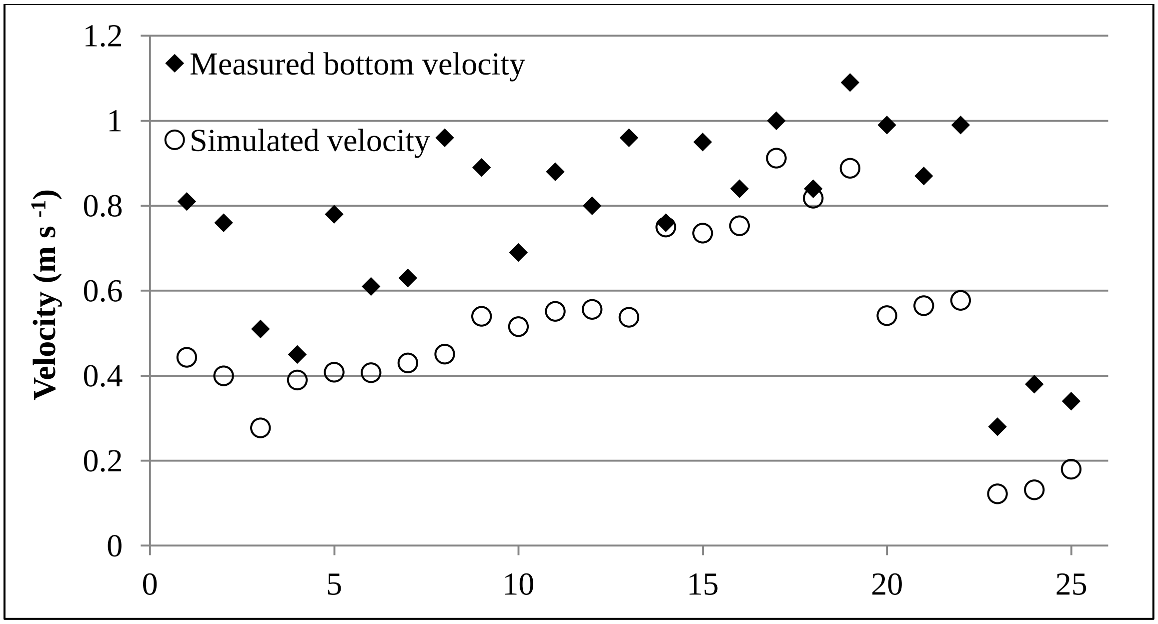

Figure A.2. Measured and simulated velocities at 25 sites within the study reach of the Penobscot River. Measured velocities are those collected closest to the river bottom.

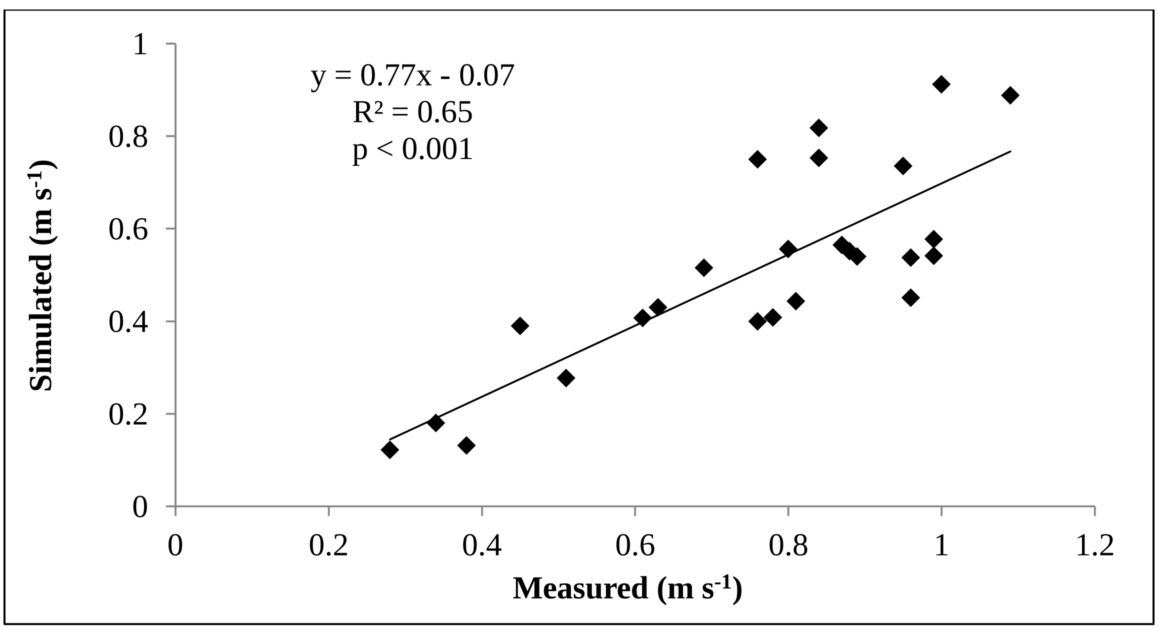

Figure A.3. Linear regression of measured bottom velocities versus simulated velocities.

BAGS

Sediment transport

The supply and rate of transport of sediment in a river reach drives its character; whether deposition or scour occur, its topography, and flow patterns (Wilcock et al. 2009). Lane (1955) described the relationship between slope and the supply of water and sediment to a river reach: $Q_S\, D \sim Q\, S$ where Q_S is sediment supply, D is sediment grain size, Q is discharge, and S is slope. Borland (1960) illustrated this relationship with a well-known schematic diagram representing the relationship as a balance. When a reach is in equilibrium, the four variables will have adjusted so that the amount of sediment supplied to a reach is transported out. If sediment supply increases (or sediment supplied becomes coarser) without increasing discharge or steepening slope, aggradation will occur. Conversely, if slope and/or discharge rate increases without accompanying changes on the other side of the balance, then degradation of the bed will occur.

The removal of dams can influence the variables involved in the Lane/Borland balance relation. For example, a dam removal from a reach can increase the steepness of slope, which would have the potential to drive changes in sediment transport and flow patterns (Wilcock et al. 2009). If slope increases and all other variables remain constant, this could lead to degradation of the bed. Implications of such change would include a decrease in embeddedness; if fine sediment had been present prior to dam removal, then increased sediment transport driven by slope change could remove such fine sediment. As a high level of embedded fine grains in shortnose sturgeon spawning habitat is unsuitable, this change would promote higher suitability.

The program BAGS (Pitlick et al. 2009) was used in Chapter 2 to calculate bed load transport rates and estimate the grain sizes most likely to have moved under the discharge conditions experienced since 2007, when the substrate data used in River2D were collected. With the removal of the Veazie Dam in 2013, the slope of the reach upstream of the dam site (including the 5 km study area) became more steep. This slope change was accounted for in BAGS and no difference between pre- and post-dam removal conditions was indicated by the BAGS calculations results. The lack of change post-dam removal suggests that the study area is sediment supply limited. Despite a steeper slope, the median grain sizes transported did not change. This result supported the use of the 2007 substrate data to represent post-dam removal conditions in the study area, however some amount of change over the time since dam removal has likely occurred. To quantify that change, a finer resolution dataset concerning grain size distributions in the study reach should be collected and examined.

BIOGRAPHY OF THE AUTHOR

Catherine Kelley Johnston was born on March 8, 1990. She was raised in Vassalboro, Maine and graduated from Waterville Senior High School in 2008. She attended Bowdoin College in Brunswick, Maine and graduated in 2012 with a Bachelor's of Arts degree with Honors in Biology. After graduation, Catherine worked as a field research technician in Healy, Alaska studying climate change impacts on the tundra. She contributed to the publication of a paper in 2015 in the *Journal of Geophysical Research: Biogeosciences* concerning this work. She also worked for the Maine Natural Areas Program in Augusta, Maine making maps of the state's protected resources and for the Lake Michigan Biological Station in Zion, Illinois studying fish and zooplankton communities. In May 2014 she moved back to Maine to begin her Master's research. Catherine has been a member of the American Fisheries Society (AFS) since 2015 and served as the secretary of the University of Maine Student Subunit of AFS from May 2015 to May 2016. She is a candidate for the Master of Science in Marine Biology from The University of Maine in August 2016.