Transactions of the American Fisheries Society

ISSN: 0002-8487 (Print) 1548-8659 (Online) Journal homepage: http://www.tandfonline.com/loi/utaf20

Shortnose Sturgeon in the Gulf of Maine: Use of Spawning Habitat in the Kennebec System and Response to Dam Removal

Gail S. Wippelhauser, Gayle B. Zydlewski, Micah Kieffer, James Sulikowski & Michael T. Kinnison

To cite this article: Gail S. Wippelhauser, Gayle B. Zydlewski, Micah Kieffer, James Sulikowski & Michael T. Kinnison (2015) Shortnose Sturgeon in the Gulf of Maine: Use of Spawning Habitat in the Kennebec System and Response to Dam Removal, Transactions of the American Fisheries Society, 144:4, 742-752, DOI: 10.1080/00028487.2015.1037931

To link to this article: https://doi.org/10.1080/00028487.2015.1037931

Transactions of the American Fisheries Society 144:742–752, 2015

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2015.1037931

ARTICLE

Shortnose Sturgeon in the Gulf of Maine: Use of Spawning Habitat in the Kennebec System and Response to Dam Removal

Gail S. Wippelhauser*
Maine Department of Marine Resources, State House Station 172, Augusta, Maine 04333, USA

Gayle B. Zydlewski
School of Marine Sciences, University of Maine, 5741 Libby Hall, Orono, Maine 04469-5741, USA

Micah Kieffer
U.S. Geological Survey, Conte Anadromous Fish Research Center, One Migratory Way, Box 796, Turners Falls, Massachusetts 01376, USA

James Sulikowski
Marine Science and Education Center, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005, USA

Michael T. Kinnison
School of Biology and Ecology, University of Maine, Murray Hall, Orono, Maine 04469, USA

Abstract
Evidence has become available in this century indicating that populations of the endangered Shortnose Sturgeon *Acipenser brevirostrum* migrate outside their natal river systems, but the full extent and functional basis of these migrations are not well understood. Between 2007 and 2013, 40 Shortnose Sturgeon captured and tagged in four Gulf of Maine river systems migrated long distances in coastal waters to reach the Kennebec System where their movements were logged by an acoustic receiver array. Twenty-one (20%) of 104 Shortnose Sturgeon tagged in the Penobscot River, two (50%) of four tagged in the Kennebec System, one (50%) of two tagged in the Saco River, and 16 (37%) of 43 tagged in the Merrimack River moved to a previously identified spawning site or historical spawning habitat in the Kennebec System in spring. Most (65%) moved in early spring from the tagging location directly to a spawning site in the Kennebec System, whereas the rest moved primarily in the fall from the tagging location to a wintering site in that system and moved to a spawning site the following spring. Spawning was inferred from the location, behavior, and sexual status of the fish and from season, water temperature, and discharge, and was confirmed by the capture of larvae in some years. Tagged fish went to a known spawning area in the upper Kennebec Estuary (16 events) or the Androscoggin Estuary (14 events), an historical spawning habitat in the restored Kennebec River (8 events), or two spawning areas in a single year (7 events). We have provided the first evidence indicating that Shortnose Sturgeon spawn in the restored Kennebec River in an historical habitat that became accessible in 1999 when Edwards Dam was removed, 162 years after it was constructed. These results highlight the importance of the Kennebec System to Shortnose Sturgeon throughout the Gulf of Maine.

*Corresponding author: gail.wippelhauser@maine.gov
Received October 10, 2014; accepted March 30, 2015

Shortnose Sturgeon *Acipenser brevirostrum* historically inhabited large coastal river systems from the Saint John River in New Brunswick to the St. Johns River in Florida (Vladykov and Greeley 1963). Many of these populations were reduced or extirpated by the construction of dams, overfishing, and poor water quality. As a result, the Shortnose Sturgeon was listed as endangered throughout its range in 1973 under the federal U.S. Endangered Species Act (ESA). More than 20 years later, the final recovery plan for the species recognized 19 distinct population segments, including four in the Gulf of Maine: the Kennebec System (Kennebec, Androscoggin, and Sheepscot rivers) in Maine, the Penobscot River in Maine, the Merrimack River in Massachusetts, and the Saint John River in New Brunswick (NMFS 1998). In a recent biological assessment, the Shortnose Sturgeon Status Review Team (SSRT) concluded, on the basis of life history characteristics, migration patterns, and results of a range-wide genetic analysis, that Shortnose Sturgeon populations formed five regional clusters (SSRT 2010). Although three of the regional clusters, including the Gulf of Maine group, appeared to be functioning as a metapopulation, the SSRT recommended that each riverine population be considered a distinct unit for management and recovery (SSRT 2010).

Identifying extant populations and locating important habitat are necessary steps in the protection and recovery of Shortnose Sturgeon (SSRT 2010). In the Gulf of Maine, important habitat has been described for four major river systems. In the Kennebec System, Wippelhauser and Squiers (2015) identified a 1-km-long spawning area in the Androscoggin Estuary immediately below Brunswick Dam, a spawning area in the upper Kennebec Estuary below Edwards Dam (river kilometer [rkm] 58–74), a wintering area in Merrymeeting Bay (rkm 42), and a potential foraging area (rkm 17–20) in the lower Kennebec Estuary (Figure 1). McCleave et al. (1977) also identified the Back and Sasanoa rivers (Figure 1) as potential foraging areas, and foraging has been documented in Sagadahoc Bay (Fire et al. 2012), a small embayment adjacent to the mouth of the lower Kennebec Estuary (Figure 1). In the estuarine portion of the Merrimack River, a spawning site (rkm 30–32), three wintering sites (rkm 16–23), and foraging habitat (rkm 7–12) have been identified (Kieffer and Kynard 1993, 1996; SSRT 2010). Telemetry studies in the Penobscot River led to the identification of a wintering area in the upper estuary (rkm 37– 42: Lachapelle 2013) and potential foraging areas in the lower and middle estuary (rkm 10–25: Fernandes et al. 2010; Dionne et al. 2013). Although many late-stage prespawning females were captured and tagged in the Penobscot Estuary, no spawning activity has been detected (Fernandes et al. 2010; Wegener 2012; Dionne et al. 2013). In the Saint John Estuary, one spawning site (COSEWIC 2005) and eight wintering sites have been identified (Dadswell 1979; Li et al. 2007).

Restoring habitat or access to habitat is an equally important step in the recovery of Shortnose Sturgeon populations. The presence of dams, some originally constructed during the period of industrial growth in the late 1800s and early 1900s, may affect Shortnose Sturgeon by restricting access to habitat, altering flows, or altering temperature (NMFS 1998). Atkins (1887) wrote that the spawning grounds of sturgeon in the Kennebec River were believed to be mainly between the municipalities of Augusta and Waterville, because the number of sturgeon greatly decreased after the construction of Edwards Dam in Augusta. Thus, Edwards Dam, located at rkm 74, prevented sturgeon from accessing spawning habitat that probably extended to Taconic Falls at rkm 103 in Waterville (Figure 1). In the early 1990s, the Federal Energy Regulatory Commission (FERC) was considering applications for the relicensing of 11 hydropower projects in the Kennebec River watershed including the Edwards Project. On November 25, 1997, FERC issued an order denying the application for a new license for the Edwards Project and required the licensee to file within 1 year a plan to retire the project and remove the dam. The order stated that Shortnose Sturgeon and Atlantic Sturgeon *A. oxyrinchus* historically ascended the river as far upstream as Waterville, inhabited the waters below Edwards Dam in 1997, and did not use fishways, and so providing access for them was only possible through dam removal. Edwards Dam was removed in the summer and fall of 1999 (Crane 2009), but no funding was provided for postremoval assessment.

Recent acoustic telemetry studies have demonstrated that some Shortnose Sturgeon make lengthy coastal migrations between river systems in the Gulf of Maine, often using rivers where they previously had not been documented. Over 70% of Shortnose Sturgeon caught in the Penobscot River and tagged with an acoustic transmitter left the basin, and the majority was subsequently detected in the Kennebec System (Fernandes et al. 2010; Dionne et al. 2013). Interestingly, 52% of these coastal migrants also entered small coastal rivers where their presence had not been documented previously, often moving more than 10 km upstream (Zydlewski et al. 2011). Between 2010 and 2011, six individuals, which had been caught in the Merrimack River and tagged with acoustic transmitters, were detected by an acoustic receiver array in the estuarine portion of the Saco River, the first documented occurrence of the species in this river system (Little et al. 2012). In addition, four Shortnose Sturgeon were captured in the Saco River of which two were acoustically tagged before being released (Little et al. 2012).

Our primary objectives were to determine the origins of Shortnose Sturgeon migrating into the Kennebec System and their behavior and distribution within the Kennebec System. Of particular interest was whether Shortnose Sturgeon were using historical spawning habitat that became accessible after the removal of Edwards Dam in 1999.

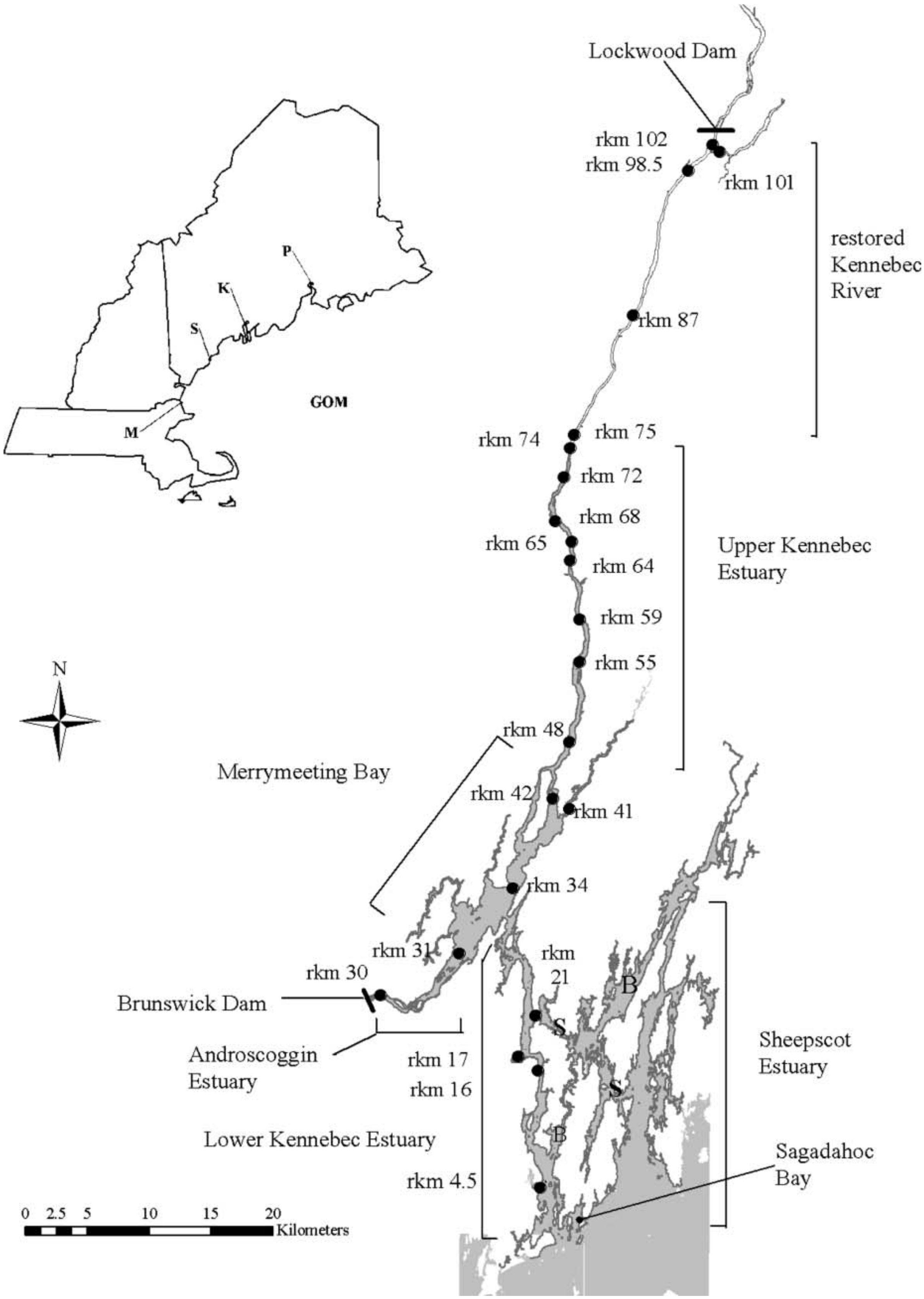

FIGURE 1. Location of the receiver array (solid circles), major ecological zones, Sasanoa River (S), Back River (B), Sagadahoc Bay, and dams (solid bars) in the Kennebec System in Maine. Inset shows where the Kennebec System (K) and Penobscot (P), Merrimack (M), and Saco (S) rivers enter the Gulf of Maine (GOM).

STUDY AREA

Shortnose Sturgeon caught and tagged with acoustic transmitters in the Penobscot, Saco, and Merrimack rivers and the Kennebec System were tracked in the primary study area of the Kennebec System, which encompasses a portion of the Kennebec River and the estuaries of the Kennebec, Androscoggin, and Sheepscot rivers (Figure 1). The free-flowing Kennebec River extends from Taconic Falls at rkm 103 to the head of tide at rkm 74. Salinity in the upper Kennebec Estuary (rkm 74–45), Merrymeeting Bay (rkm 45–30), and the 8.4-km-long Androscoggin Estuary rarely exceeds 0‰. Salinity in the lower Kennebec Estuary (rkm 30–0) ranges from 0‰ to 32‰ depending on location and freshwater discharge. The lower Kennebec Estuary and the more saline Sheepscot Estuary are connected by two passages, the Sasanoa River and Back River. Historically, the upstream limits of Shortnose Sturgeon in the Kennebec System likely were Pejepscot Falls, the current location of the Brunswick Dam, at the head of tide on the Androscoggin River, and Taconic Falls, the current location of the Lockwood Dam. The Kennebec River was inaccessible to sturgeon from 1837 to 1999 due to the presence of Edwards Dam. Hereafter, we refer to the reach between rkm 74 and rkm 103 as the restored Kennebec River.

METHODS

Acoustic receiver array.—An array of 18–20 stationary acoustic receivers (Vemco VR2 in 2007, Vemco VR2W from 2008 to 2012) was deployed at 16–22 sites in the Kennebec System (Figure 1). In most instances, the receivers were anchored in narrow reaches of the channel where a single receiver was able to monitor the entire width of the channel for tagged fish. Maximum detection distance for a VR2W receiver tested in the Kennebec System was 900–1,000 m. Most receiver locations were identified by distance (rkm) relative to the estuary mouth (Figure 1). However, receivers in the Androscoggin Estuary were arbitrarily denoted rkm 30 and rkm 31 and do not reflect distance from the ocean. Receivers typically were deployed in April and retrieved between October and November, but not all receivers were deployed or successfully recovered in each year of the study. For example, the receiver at rkm 59 was lost during the summer of 2007 and not replaced until the spring of 2009. Beginning in 2009, we also used a portable receiver (Vemco 100) and a Vemco directional hydrophone to determine the presence of tagged fish at wintering areas after the receiver array had been removed. The wintering area near rkm 42 was scanned for tagged fish in 2009 (February 11), 2010 (February 23), 2011 (January 6 and February 24), and 2012 (February 16), and a newly identified area near rkm 65 was scanned in 2012 (February 16) and 2013 (March 4).

Capture and tagging.—Capture, handling, and tagging protocols were similar, but not identical, among the four river systems, which differed in the amount and type of accessible habitat, distribution of fish, and length of sampling season. However, the differences in methods were minor and did not bias the study. Capture, handling, and tagging of Shortnose Sturgeon complied with National Marine Fisheries Service (NMFS) protocols for sturgeons (Kahn and Mohead 2010) and researchers' ESA Section 10(a)(1)(A) permit conditions (permits 1549, 1578, 1595, and 16306). Shortnose Sturgeon primarily were captured during targeted sampling with bottom-set gill nets in the estuarine portion of the four river systems, but a few were captured in a large-mesh gill net used to sample Atlantic Sturgeon in the Penobscot River (Table 1). A major difference among rivers was winter sampling in the Merrimack River that required special handing protocols. In each system, captured Shortnose Sturgeon were removed from the gill net and placed in a floating net-pen prior to processing. During this process, an individual was transferred to a small, on-board holding tank where TL (cm), FL (cm), and weight (kg) were measured. The fish also was scanned for the presence of a PIT tag with an AVID Power Tracker II, V, or VII reader. If none were found, a 23-mm Biomark (Merrimack River) or 14-mm AVID PIT tag was injected into the musculature of the fish along the right-side base of the dorsal fin. To ensure tag retention in the fish from the Merrimack River in winter, the injection site was closed with a suture. In addition, an external tag with a unique identification number was attached to each Shortnose Sturgeon captured in the Penobscot (Carlin dangler or plastic-tip dart tag) and Saco (T-bar tag) rivers. A small fin clip was taken from all newly captured fish in the Penobscot, Saco, and Merrimack river systems and stored in ethanol prior to transfer to the NMFS genetic archive.

TABLE 1. Details of gill-net sampling in four Gulf of Maine river systems to capture Shortnose Sturgeon. Nets were constructed of a single mesh size, except in the Kennebec System, which had panels of 15.2-, 17.8-, and 20.3-cm mesh (all mesh is stretch measure).

River system	Area sampled (rkm)	Soak time (h)	Months	Year	Net dimensions		
					Mesh (cm)	Length (m)	Height (m)
Penobscot	7–46	0.2–23.8	May–Nov	2006–2012	16.2, 30.5	45, 90	2.4
Kennebec	4–42	0.7–5.0	Sep–Nov	2011	15.2–20.3	90	2.4
Saco	0–2	0.5	May–Nov	2009–2011	15.2	100	2.0
Merrimack	5–33	0.1–26.0	Jan–Dec	2008–2013	15.2, 20.3	100	2.4

TABLE 2. Details of 153 Shortnose Sturgeon captured in four Gulf of Maine river systems and tagged with acoustic transmitters (one Merrimack River fish was tagged twice).

River system	Number tagged	Weight (kg)	TL (cm)	Tag attachment technique	Tag life (years)
Penobscot	104	2.0–11.0	77.4–125.4	Internal	2.0, 5.0, 10.0
Kennebec	4	2.9–4.9	88.0–96.4	Internal	5.0
Saco	2	2.9–3.2	75.0–105.0	Internal	5.0
Merrimack	24	3.4–10.7	91.1–114.2	Internal	3.2, 10.0
Merrimack	20	6.6–9.6	90.0–115.0	External	0.8–1.1, 3.2

A subset totaling 134 of the Shortnose Sturgeon captured in these rivers was surgically implanted with Vemco acoustic transmitters, the specifications of which varied among river systems and years, that broadcast a coded or noncoded signal over a range of drifting transmission intervals (10–130 s) for 0.8–10.0 years and weighed approximately 5–20 g in air (Table 2). In the Penobscot and Merrimack rivers, an endoscopic examination with a borescope (Kynard and Kieffer 2002) was performed to identify prespawning females for tagging. An individual's maturation status was characterized as unknown, male (observed releasing sperm), female with immature eggs, or female with mature eggs. In the Kennebec System and Saco River, only fish >55 cm TL and assumed to be adults (Bain 1997) were selected for tagging. Surgery was only performed on fish that appeared to be in excellent health and when water temperature was between 8°C and 25°C. Fish were anesthetized with buffered MS-222 (tricaine methanesulfonate), a transmitter was inserted into the body cavity through a 3-cm incision on the ventral body wall, and the incision was closed with internal and external or just external sutures. Tags were treated with a disinfectant prior to insertion, and in the Merrimack River tags were coated with a biologically inert elastomer to prevent internal tissue irritation (Kieffer and Kynard 2012a). In all river systems, tags weighed less than 2% of the fish body weight in air. Tagged fish were allowed to recover in the floating net-pen for at least 15 min and released only after they showed clear signs of recovery by displaying proper orientation and normal swimming ability.

In the Merrimack River, a subset of 20 prespawning females captured in winter aggregations was tagged with an externally mounted Vemco transmitter (Table 2), which allowed gravid females to be tagged without invasive surgery during cold winter temperatures that slow a sturgeon's ability to heal. Small, 1-year tags (8.0 g in air) were used, because they were less likely to detach prematurely or ensnare a derelict fishing line as has been observed for larger multiyear tags. A harness made of 100-lb test monofilament was attached to the tag and secured with copper crimps and a coating of resilient plastic encasing compound. Harness ends were threaded through two perforations at the base of the dorsal fin created with a hypodermic needle and were secured externally with padded plastic disks and crimped copper–aluminum sleeves designed to eventually corrode and detach as described by Kieffer and Kynard (2012a).

Approved tagging methods for sturgeon have been refined over decades to reduce mortality and improve postsurgery recovery. They are considered to have minimal impact on fish behavior or health as was observed for Shortnose Sturgeon carrying internal and external tags in multiple years in the Merrimack and Connecticut rivers (Kieffer and Kynard 2012a). Similarly, Miller et al. (2014) found no difference in growth or critical swimming velocity among juvenile Green Sturgeon *A. medirostris* that underwent surgery with or without tag implantation or were handled and anesthetized but did not undergo surgery.

Analysis of telemetry data.—Receivers in the Kennebec System were downloaded two to four times throughout the deployment periods and for a final time when they were retrieved for the year. Data were sorted by transmitter number and date, and spurious codes were culled. Fish position (rkm) was plotted against date for each tagged fish and for groups of fish, and positions were visually inspected to determine overall movement patterns.

Spawning activity in the Androscoggin Estuary was inferred from detections of tagged late-stage females during the known spawning season in areas previously confirmed as spawning sites by the capture of hundreds of adult Shortnose Sturgeon including ripe males and Shortnose Sturgeon eggs and larvae (Wippelhauser and Squiers 2015). The amount of time a Shortnose Sturgeon spent at the spawning site was defined as the elapsed time between the first and last detection of the individual by the receiver at rkm 30.

Because the spawning area in the upper Kennebec Estuary was imprecisely known and undocumented in the restored Kennebec River, spawning activity in these areas was identified by the detection of tagged late-stage females during the known spawning season when water temperature and discharge were suitable for spawning (Dadswell et al. 1984; SSRT 2010; Kieffer and Kynard 2012b) and by the capture of early life stages. In most cases, the amount of time a Shortnose Sturgeon spent at the spawning site was defined as the elapsed time between the first and last detection of the individual by the receiver at rkm 59 or an adjacent one if receiver at rkm 59 was lost or did not detect a tagged fish. The receiver at rkm 59 was used because most tagged sturgeon passed it just twice, i.e., at the beginning and end of the spawning season. However, for 11 fish that made multiple trips past this receiver during the spawning season, the 0.9–5.0 d spent downstream from rkm 59 was not considered as time spent at the spawning area. Identified late-stage females detected by receivers between rkm 59 and rkm 74 were assumed to be spawning in contemporary habitat in the upper Kennebec Estuary while those detected by receivers at rkm 87 or rkm 102 were assumed to be within the range of historical spawning habitat in the restored Kennebec River.

Tagged Shortnose Sturgeon were considered to winter in the Kennebec System if they moved to a known or suspected wintering site in late fall, remained at the site until the acoustic array was removed, or were detected at or near the site in spring when the array was redeployed. We identified the year a Shortnose Sturgeon wintered as the year the winter began. For example, the winter of 2007 includes the period from late fall 2007 to early spring 2008.

Ichthyoplankton sampling.—To confirm spawning in the upper Kennebec Estuary and restored Kennebec River, we attempted to capture Shortnose Sturgeon eggs and larvae from 2009 to 2011 with a modified plankton net (or a D-net). The D-net was constructed of 800- or 1,600-μm mesh, had a 1-m-diameter opening, and was 4.3 m long. The mouth of the net was attached to a half-circle stainless steel frame 1 m across and 0.5 m high, and the net was set on the river bottom facing into the current. Sampling events were limited and solely intended to verify the presence of viable eggs or larvae (Table 3). Organisms were rinsed from the nets, and dead or moribund individuals and eggs were immediately preserved in 5% formalin. Preserved samples were sorted in the laboratory under a dissecting microscope, and eggs and larvae were transferred to 75% ethanol for subsequent identification according to Jones et al. (1978) and Gilbert (1989). Live sturgeon larvae, however, were transported in water to the laboratory, examined and photographed under a dissecting microscope, and returned to the river.

Environmental data.—Mean daily discharge for the Androscoggin River was obtained for U.S. Geological Survey (USGS) gauge 01059000, located approximately 27 km above the Brunswick Dam. Similar data for the Kennebec River were obtained for USGS gauge 01049265, located at rkm 87. The data were not adjusted for freshwater entering below the gauge. Beginning in 2009, water temperature was recorded every 8 h at rkm 30, rkm 42, rkm 67, and rkm 102 by a data logger (HOBO U10-001) in a waterproof housing. The temperature logger was attached approximately 1 m from the bottom to a line between a receiver and its anchor. Mean daily temperature was calculated for each data logger site. In 2011, the temperature logger and receiver at rkm 68 were lost during high water, and data recorded at rkm 102 and rkm 42 were used as a proxy for temperatures at rkm 68. In 2012, the temperature logger and receiver at rkm 102 and receiver at rkm 87 were lost during a flood, and data recorded in the Androscoggin Estuary were used as a proxy for temperatures in the upper Kennebec Estuary. Mean water temperatures in the Androscoggin Estuary were 0.6–0.8°C warmer than in the upper Kennebec Estuary and 1.3–2.1°C warmer than in the Kennebec River between April 1 and June 15 with the greatest differences occurring after May 30.

RESULTS

Spawning Sites

Twenty-one (20%) of 104 Shortnose Sturgeon tagged in the Penobscot River, two (50%) of four tagged in the Kennebec System, one (50%) of two tagged in the Saco River, and 16 (37%) of 43 tagged in the Merrimack River moved to a previously identified spawning area or suspected historical spawning habitat in the Kennebec System in spring. Of the 40 fish, 35 were detected at spawning areas in a single year and five were detected at spawning areas in each of 2 years, resulting in 45 putative spawning events. Most Shortnose Sturgeon went to known spawning areas in the upper Kennebec Estuary (16 events) or the Androscoggin Estuary (14 events), or to historical spawning habitat in the restored Kennebec River (eight events); however, a few went to two spawning areas in a single year (seven events). The 40 prespawning migrants ranged from 82.5 to 120.9 cm TL (mean, 100.74 cm), and most (16 from the Penobscot River, 16 from the Merrimack River, and one from the Kennebec System) were females known to be bearing late-stage eggs. Of the five females detected at spawning areas in the Kennebec System in multiple years, three returned after a 2-year interval and two after a 3-year interval.

Tagged Shortnose Sturgeon displayed two migration strategies in order to reach spawning areas: (1) winter once or twice in the Kennebec System then spawn or (2) enter the system in spring and spawn. Migrants displaying the

TABLE 3. Details of ichthyoplankton net sampling in the Kennebec System to capture early life stages of Shortnose Sturgeon.

Sampling period	Sampling location (rkm)	Number of net sets	Number of larvae caught
May 19–June 15, 2009	64–72	8	23
May 17–May 19, 2010	102	4	2
May 12, 2011	102	2	0
May 3–June 6, 2011	67–73	4	7

first strategy included 11 fish tagged in the Penobscot River that emigrated from that system between summer and fall, wintered in the Kennebec System, and then moved to a spawning area the following spring. A single fish from the Saco River also emigrated in the fall, but spent two winters in the Kennebec System before moving to a spawning area. In addition, two fish tagged in the Kennebec System wintered in the system once or twice before moving to a spawning area in the spring. Migrants displaying the second strategy included 10 fish tagged in the Penobscot River and 16 tagged in the Merrimack River that emigrated from those systems in early spring and migrated to a spawning area in the Kennebec System the same year.

Shortnose Sturgeon were detected at the spawning areas from April 7 to June 6 throughout all study years when water temperature was increasing and discharge was decreasing (Figure 2). Tagged fish were in the Androscoggin Estuary when bottom temperatures ranged from 8.8°C to 16.4°C, in the Upper Kennebec Estuary from 7.0°C to 17.6°C, and in the restored Kennebec River from 5.8°C to 16.2°C. Discharge when Shortnose Sturgeon were at the spawning areas was typically ≤558 m^3/s, although in some years fish experienced discharge as high as 1,487 m^3/s (Figure 2).

The amount of time an individual spent at a spawning site ranged from 0.1 to 26.7 d. Fish spent the least amount of time in the Androscoggin Estuary (mean, 4.0 d; range, 0.1–7.8 d); three were at the site for less than 1 d (2.4–12.0 h). Shortnose Sturgeon spent the most time in the restored Kennebec River (mean, 12.5 d; range, 6.1–21.8 d), followed by those that visited two sites (mean, 11.2 d; range, 3.8–26.7 d) and those that went to the upper Kennebec Estuary (mean, 9.9 d; range, 1.6–15.2 d). Most Shortnose Sturgeon that went to the upper Kennebec Estuary or restored Kennebec River remained above rkm 59, but 11 fish made one to five trips downstream during the spawning season, traveling as far as the receiver at rkm 41. The mean amount of time required for these trips was 1.8 d (range, 0.9–5.0 d). Shortnose sturgeon made these trips less often from 2008 to 2011 (four fish) than from 2012 to 2013 (seven fish).

Spawning was documented for the first time in historical habitat of the restored Kennebec River and was confirmed in the upper Kennebec Estuary. In 2009, 23 Shortnose Sturgeon larvae were caught from May 20 to June 9 in the upper Kennebec Estuary between rkm 67 and rkm 72 when the bottom water temperature was 14.2–18.4°C (Figure 2B). Two Shortnose Sturgeon larvae were captured on May 17, 2010, in the restored Kennebec River just downstream from the Lockwood Project Dam when the water temperature was 13.0°C (Figure 2C). In 2011, seven Shortnose Sturgeon larvae were caught on June 6 in the upper Kennebec Estuary between rkm 67 and rkm 73 when bottom water temperature was 16.2–16.7°C (Figure 2D). No eggs were collecting during the sampling.

DISCUSSION

In the Gulf of Maine, Shortnose Sturgeon that were tagged in estuarine portions of the Penobscot, Merrimack, and Saco rivers migrated long distances in coastal waters to reach spawning habitat in the Kennebec System. Fish tagged in the Penobscot River migrated approximately 150 km in late fall or early spring, and one fish tagged in the Saco River migrated 100–150 km, depending on the route, in late fall to reach the Kennebec System. Shortnose Sturgeon from the Merrimack River traveled the longest distance, an estimated 200–250 km, to reach the Kennebec System. These migration distances, estimated as a direct path, are conservative. Mean transit time to the Kennebec System from the Penobscot River was 11.4 d (range, 8.0–16.2 d) in the spring and 12.4 d (range, 5.9–25.6 d) in the fall (Dionne et al. 2013), and from the Merrimack River was 12.1 d (range, 6.8–22.1 d) in the spring (M. Kieffer, unpublished data). These data suggest that Shortnose Sturgeon are likely capable of reaching the Kennebec System from any other river in the region in 1 to 4 weeks. The timing and extent of these movements indicate that a substantial number of Shortnose Sturgeon in the Penobscot, Merrimack, and Saco rivers made highly directed movements to the Kennebec System, despite the existence of known spawning activity in the Merrimack River.

These findings suggest that the Kennebec System is targeted for spawning and staging for spawning (use of wintering habitat) by many Shortnose Sturgeon inhabiting other Gulf of Maine river systems, and thus plays an important role in the life cycles and production of Shortnose Sturgeon at a large regional scale as well as a local scale. The more-saline lower Kennebec Estuary primarily was used as a migratory corridor, and just three of the Shortnose Sturgeon tagged in other river systems spent an extended period of time (48–136 d) in this area after leaving a spawning or wintering area. Movements and redistribution of fish between other rivers and the Kennebec System is consistent with recent nuclear DNA analysis that found modest or no detectable genetic divergence between adult Shortnose Sturgeon from the Kennebec System and those from other Gulf of Maine rivers (SSRT 2010). This pattern is potentially consistent with either a true metapopulation (sensu Hanski and Simberloff 1997) consisting of interconnected demes with reproduction occurring in each, or with a core Kennebec System population that ranges widely to make use of feeding and wintering habitats in additional rivers. Further data are required to address these alternatives, since the function of each patch (river) within the system has not been fully elucidated. The reality may be somewhere in between these two possibilities given that reproduction is known to occur in the Merrimack River (Kieffer and Kynard 1996) but has not yet been detected in the Penobscot River in more than 7 years of larval sampling.

The Kennebec System clearly has suitable environmental conditions for spawning and growth of young of year fish, but only the restored Kennebec River has been studied in detail.

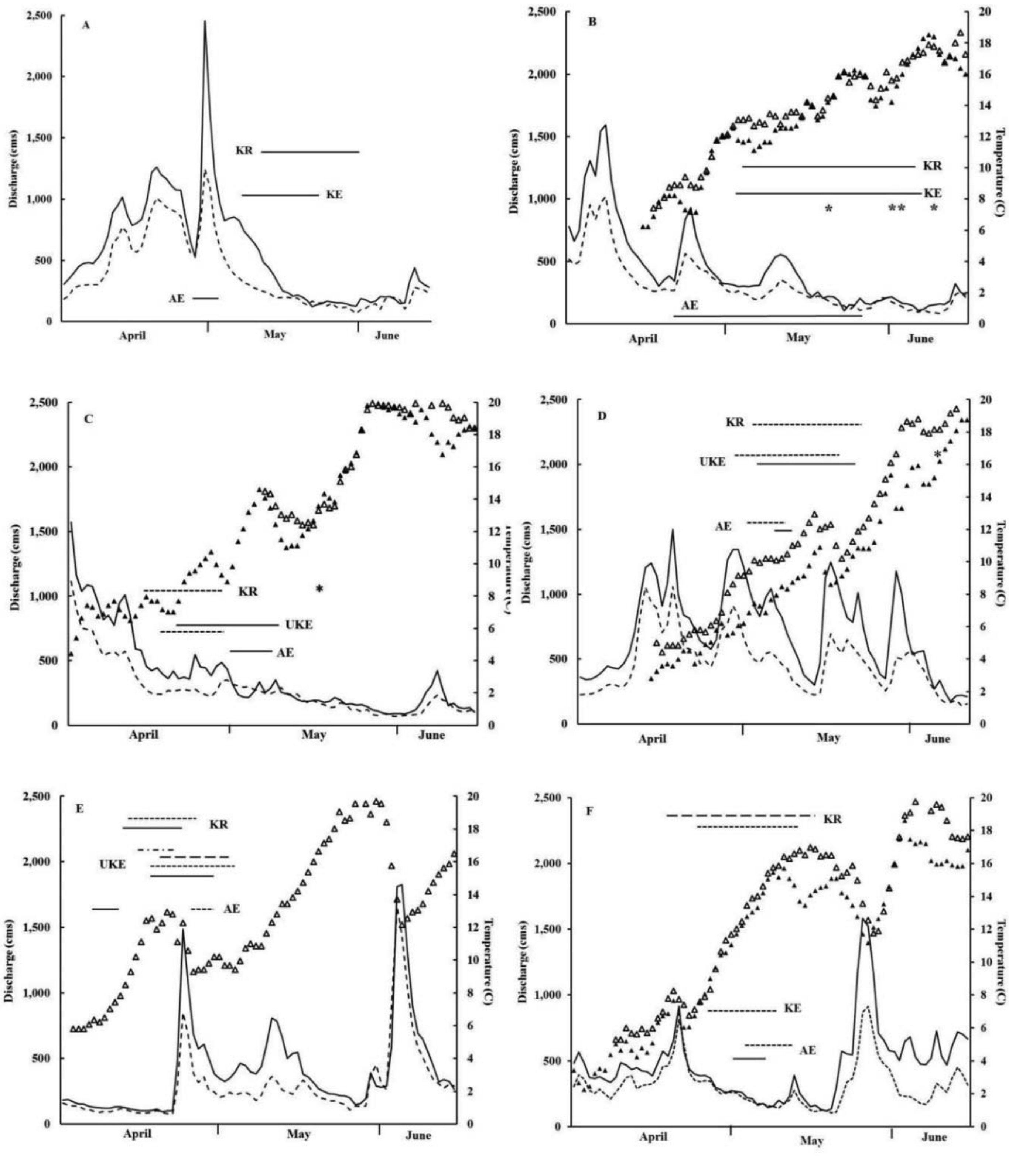

FIGURE 2. Shortnose Sturgeon occupation of spawning sites in the Kennebec System relative to freshwater discharge in the Kennebec (solid line) and Androscoggin (dotted line) rivers, and bottom water temperature in the Kennebec River and Estuary (solid triangles) and Androscoggin Estuary (open triangles) in (**A**) 2008, (**B**) 2009, (**C**) 2010, (**D**) 2011, (**E**) 2012, and (**F**) 2013. Horizontal lines indicate when Shortnose Sturgeon tagged in the Penobscot (solid line), Kennebec (long-dashed line), Saco (dotted line) and Merrimack (dashed dotted line) river systems were at a spawning site in the Androscoggin Estuary (AE), upper Kennebec Estuary (UKE), and Kennebec River (KR). Stars indicate when larvae were captured.

Yoder et al. (2006) reported that dissolved oxygen was mostly 8–9 mg/L in July and August. Stone and Webster Environmental Technology and Services (1995) surveyed the entire Edwards Dam impoundment, and found the most common sediment types were coarse sands, gravel, and mixtures of gravel with cobble. A survey of the lower Edwards Dam impoundment (rkm 75–87) found approximately 90% of the area consisted of rock, sand, and gravel or combinations of these substrates (Dudley 1999). Productivity in this reach also appears to be high. Casper et al. (2006) reported that the abundance of zoobenthos increased by 190% at a site closest to the former dam (about 4 km upstream) and by 31% at two sites farther upstream (14 and 24 km). While areas of suitable spawning habitat have been found in the Penobscot River (Wegener 2012), the use of this habitat for spawning has not been documented. Although spawning is known to occur in the Merrimack River (Kieffer and Kynard 1996), our findings suggest that 45% of adults from the Merrimack River still go to the Kennebec System to spawn. Again, this calls into question the relative roles of these populations in the larger regional context.

Two prespawning migration patterns were observed in this study, a two-step migration consisting of a long fall migration to a wintering area followed by a short migration in spring and a long one-step migration in late winter–early spring. These migrations are analogous to patterns seen within other river systems (Dadswell et al. 1984; Kynard 1997), but differ in the type of habitat transited. Fish migrated through ocean waters between river systems in the Gulf of Maine (Zydlewski et al. 2011; Dionne et al. 2013), rather than within a river system (Kynard 1997). Migration distance in the Gulf of Maine often exceeded the 140-km maximum reported within other river systems in the Northeast (Kynard 1997), even when the additional distance fish covered when exploring coastal rivers was not considered.

Recent evidence clearly shows that Shortnose Sturgeon travel long distances in coastal waters. In the Gulf of Maine, tagged individuals moved an estimated 100–250 km between river systems (Fernandes et al. 2010; Zydlewski et al. 2011; Little et al. 2012; Dionne et al. 2013; the present study). Dadswell et al. (2014) reported the capture of a Shortnose Sturgeon in an intertidal fish weir in the Minas Basin, Nova Scotia, a presumed foraging area located approximately 165 km from the mouth of the Saint John River. Two Shortnose Sturgeon tagged in the Hudson River were recaptured in the Connecticut River, a minimum straight line distance of more than 100 km (Savoy 2004). In Georgia, Shortnose Sturgeon tagged as juveniles in the Altamaha River were caught in the Ogeechee River, a distance of more than 65 km from river mouth to river mouth (Peterson and Farrae 2011). In a multistate telemetry study, one tagged Shortnose Sturgeon traveled more than 423 km from the Cape Fear River in North Carolina to the Altamaha River in Georgia (J. Facendola, North Carolina Department of Environmental and Natural Resources, personal communication), and three fish migrated more than 212 km in consecutive years between the Waccamaw River (Winyah Bay System) in South Carolina and the Savannah River that borders South Carolina and Georgia (B. Post, South Carolina Department of Natural Resources, personal communication).

Critical habitat never has been designated for Shortnose Sturgeon as it has been for Gulf sturgeon and the Southern Distinct Population Segment of Green Sturgeon. Nonetheless, it is important for state and federal fisheries agencies to know the location of habitat that is essential to the life cycle and conservation of Shortnose Sturgeon when reviewing proposed construction and dredging projects or consulting during the federal licensing process for hydropower facilities. Since 2006, five tidal power projects, one dredging project, a new bridge, and armoring of a gas line have been proposed in the Kennebec System. Protecting limited spawning and wintering habitat and protecting Shortnose Sturgeon when they are concentrated in these areas are especially important and perhaps all the more so given a potentially important role of the Kennebec System for Shortnose Sturgeon throughout the Gulf of Maine. In the Gulf of Maine, just five spawning sites have been identified: three in the Kennebec System (Wippelhauser and Squiers 2015; the present study), one in the Merrimack River (Kieffer and Kynard 1996), and one in the Saint John River (COSEWIC 2005). Wintering sites are more numerous: eight have been identified in the Saint John River (Dadswell 1979; Li et al. 2007), three in the Merrimack River (M.K., unpublished data), two in the Kennebec System (Wippelhauser and Squiers 2015; the present study), and one in the Penobscot River (Fernandes et al. 2010; Dionne et al. 2013).

Importantly, we have provided the first evidence that Shortnose Sturgeon access and spawn in historical habitat that became accessible when Edwards Dam was removed in 1999 and that use of this site is not trivial. In less than a decade, nearly one-third of the putative spawning events included the restored Kennebec River; i.e., Shortnose Sturgeon went to this spawning area exclusively or went to two sites including the restored Kennebec River in a single year, and spawning was confirmed by the capture of two larvae. The fact that Shortnose Sturgeon continued to use spawning habitat in the Androscoggin Estuary and upper Kennebec Estuary while uisng newly available habitat in the restored Kennebec River may indicate the population is expanding and offers hope for the possible recovery of spawning populations in other Gulf of Maine rivers where historical habitat has been made accessible by dam removal, such as the 2013 removal of the Veazie Dam in the Penobscot River. However, full use of the restored Kennebec River and other Gulf of Maine rivers for spawning may require additional time, given the late maturation age of this species, and could be limited by additional factors, such as predation, food resources, and climate variability that disrupts successful spawning in some years. Even if Shortnose Sturgeon successfully spawned in the restored reach of the Kennebec River within a year of dam removal, the resulting offspring would have only matured within the last few years. Regardless, the results of this study emphasize the need to consider Shortnose Sturgeon population biology and critical habitat at scales spanning much of the coastal Gulf of Maine as well as coordinated and concerted monitoring of known, suspected, and potentially restored habitats to better understand the risks and benefits of complex population structure (e.g., metapopulations or dispersed core populations) for sturgeon recovery in this region.

ACKNOWLEDGMENTS

This research was funded by NMFS grants NA07NMF4720053 and NA10NMF4720023. G. Zydlewski and M. Kinnison also were supported by the Maine Agricultural and Forest Experiment Station (contribution number 3298). All methods were conducted under NOAA ESA Section 10(a)(1)(A) Permit Numbers 1549, 1578, 1595, and 16306 for take of protected species for scientific purposes. We thank Matthew Altenritter, Megan Altenritter, Jason Bartlett, Gregory Beadle, James Beaudry, Toby Bonney, Edith Carson, Michael Counts, Phillip Dionne, Matthew Dzaugis, Claire Enterline, Stephen Fernandes, Cory Gardner, Nathaniel Gray, Craig King, Kevin Lachapelle, Josh Noll, Mark Pasterczyk, George Zink, and Joseph Zydlewski for assistance in the field. Any use of trade, product, or firm names is for descriptive purposes only and does imply endorsement by the U.S. Government.

REFERENCES

Atkins, C. G. 1887. The river fisheries of Maine. Pages 673–728 *in* G. B. Goode, editor. The fisheries and fishing industries of the United States, section V, volume 1. Government Printing Office, Washington, D.C.

Bain, M. B. 1997. Atlantic and Shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48:237–247.

Casper, A. F., J. H. Thorp, S. P. Davies, and D. L. Courtemanch. 2006. Ecological responses of zoobenthos to dam removal on the Kennebec River, Maine, USA. Archiv für Hydrobiologie Supplement 158:541–555.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2005. Assessment and update status report on the Shortnose Sturgeon *Acipenser brevirostrum* in Canada. COSEWIC, Ottawa.

Crane, J. 2009. "Setting the river free": the removal of the Edwards dam and the restoration of the Kennebec River. Water History 1:131–148.

Dadswell, M. J. 1979. Biology and population characteristics of the Shortnose Sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichthyes: Acipenseridae), in the Saint John River Estuary, New Brunswick, Canada. Canadian Journal of Zoology 57:2186–2210.

Dadswell, M. J., G. Nau, and M. J. W. Stokesbury. 2014. First verified record for Shortnose Sturgeon, *Acipenser brevirostrum* LeSueur, 1818, in Minas Basin, Bay of Fundy, Nova Scotia, Canada. Proceedings of the Nova Scotia Institute of Science 47:273–279.

Dadswell, M. J., B. D. Taubert, T. S. Squiers, D. Marchette, and J. Buckley. 1984. Synopsis of biological data on Shortnose Sturgeon, *Acipenser brevirostrum* LeSueur 1818. NOAA Technical Report NMFS 14.

Dionne, P. E., G. B. Zydlewski, M. T. Kinnison, J. Zydlewski, and G. S. Wippelhauser. 2013. Reconsidering residency: characterization and conservation implications of complex migratory patterns of Shortnose Sturgeon (*Acipenser brevirostrum*). Canadian Journal of Fisheries and Aquatic Sciences 70:119–127.

Dudley, R. W. 1999. Riverbed-sediment mapping in the Edwards Dam impoundment on the Kennebec River, Maine by use of geophysical techniques. U.S. Geological Survey, Open-File Report 99-200, Reston, Virginia.

Fernandes, S. J., G. B. Zydlewski, J. D. Zydlewski, G. S. Wippelhauser, and M. T. Kinnison. 2010. Seasonal distribution and movements of Shortnose Sturgeon and Atlantic Sturgeon in the Penobscot River estuary, Maine. Transactions of the American Fisheries Society 139:1436–1449.

Fire, S. E., J. Pruden, D. Couture, Z. Wang, M.-Y. Dechraoui Bottein, B. L. Haynes, T. Knott, D. Bouchard, A. Lichtenwalner, and G. Wippelhauser. 2012. Saxitoxin exposure in an endangered fish: association of a Shortnose Sturgeon mortality event with a harmful algal bloom. Marine Ecology Progress Series 460:145–153.

Gilbert, C. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight)–Atlantic and Shortnose sturgeons. U.S. Fish and Wildlife Service Biological Report 82(11.122).

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York.

Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the Mid-Atlantic Bight: an atlas of eggs, larval, and juvenile stages, volume 1. Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service FWS/OBS-78/12.

Kahn, J., and M. Mohead. 2010. A protocol for use of Shortnose, Atlantic, Gulf, and Green sturgeons. NOAA Technical Memorandum NMFS-OPR-45.

Kieffer, M. C., and B. Kynard. 1993. Annual movements of Shortnose and Atlantic sturgeon in the lower Merrimack River, Massachusetts. Transactions of the American Fisheries Society 122:378–386.

Kieffer, M. C., and B. Kynard. 1996. Spawning of Shortnose Sturgeon in the Merrimack River, Massachusetts. Transactions of the American Fisheries Society 125:179–186.

Kieffer, M., and B. Kynard. 2012a. Long-term evaluation of telemetry tagging on Shortnose Sturgeon. Pages 297–320 *in* B. Kynard, P. Bronzi, and H. Rosenthal, editors. Life history and behaviour of Connecticut River shortnose and other sturgeons. World Sturgeon Conservation Society, Special Publication 4, Neu Wulmstorf, Germany.

Kieffer, M., and B. Kynard. 2012b. Spawning and non-spawning migrations, spawning, and the effect of river regulation on spawning success of Connecticut River Shortnose Sturgeon. Pages 73–113 *in* B. Kynard, P. Bronzi, and H. Rosenthal, editors. Life history and behaviour of Connecticut River shortnose and other sturgeons. World Sturgeon Conservation Society, Special Publication 4, Neu Wulmstorf, Germany.

Kynard, B. 1997. Life history, latitudinal patterns, and status of the Shortnose Sturgeon, *Acipenser brevirostrum*. Environmental Biology of Fishes 48:319–334

Kynard, B., and M. C. Kieffer. 2002. Use of a borescope to determine the sex and egg maturity stage of sturgeons and the effect of borescope use on reproductive structures. Journal of Applied Ichthyology 18:505–508.

Lachapelle, K. T. 2013. Wintering Shortnose Sturgeon (*Acipenser brevirostrum*) and their habitat in the Penobscot River, Maine. Master's thesis. University of Maine, Orono.

Li, X., M. K. Litvak, and J. E. H. Clark. 2007. Overwintering habitat use of Shortnose Sturgeon (*Acipenser brevirostrum*): defining critical habitat using a novel underwater video survey and modeling approach. Canadian Journal of Fisheries and Aquatic Sciences 64:1248–1257.

Little, C. E., M. Kieffer, G. Wippelhauser, G. Zydlewski, M. Kinnison, and J. A. Sulikowski. 2012. First documented occurrences of the Shortnose Sturgeon (*Acipenser brevirostrum*, Lesueur, 1818) in the Saco River, Maine, USA. Journal of Applied Ichthyology 29:709–712.

McCleave, J. D., S. M. Fried, and A. K. Towt. 1977. Daily movements of Shortnose Sturgeon, *Acipenser brevirostrum*, in a Maine estuary. Copeia 1977:149–157.

Miller, E. A., H. E. Froehlich, D. E. Cocherell, M. J. Thomas, and J. J. Cech. 2014. Effects of acoustic tagging on juvenile Green Sturgeon, incision healing, swimming performance, and growth. Environmental Biology of Fishes 97:647–658.

NMFS (National Marine Fisheries Service). 1998. Recovery plan for the Shortnose Sturgeon (*Acipenser brevirostrum*). Prepared by the Shortnose Sturgeon Recovery Team for the NMFS, Silver Spring, Maryland.

Peterson, D. L., and D. J. Farrae. 2011. Evidence of metapopulation dynamics in Shortnose Sturgeon in the southern part of their range. Transactions of the American Fisheries Society 140:1540–1546.

Savoy, T. F. 2004. Population estimate and utilization of the lower Connecticut River by Shortnose Sturgeon. Pages 345–352 *in* P. M. Jacobson, D. A. Dixon, W. C. Leggett, B. C. Marcy Jr., and R. R. Massengill, editors. The Connecticut River ecological study (1965–1973) revisited: ecology of the lower Connecticut River 1973–2003. American Fisheries Society, Monograph 9, Bethesda, Maryland.

SSRT (Shortnose Sturgeon Status Review Team). 2010. A biological assessment of Shortnose Sturgeon (*Acipenser brevirostrum*). Report to the National Marine Fisheries Service, Northeast Regional Office, Gloucester, Massachusetts.

Stone and Webster Environmental Technology and Services. 1995. Edwards Dam removal evaluation–physical and biological study results. Prepared for the Federal Energy Regulatory Commission, Washington, D.C.

Vladykov, V. D., and J. R. Greeley. 1963. Order Acipenseroidei. Pages 24–60 *in* H. B. Bigelow, editor. Fishes of the western North Atlantic, part 3. Soft-rayed bony fishes. Memoirs of the Sears Foundation for Marine Research, Yale University, New Haven, Connecticut.

Wegener, M. T. 2012. Reproduction of Shortnose Sturgeon in the Gulf of Maine: a modeling and acoustic telemetry assessment. Master's thesis. University of Maine, Orono.

Wippelhauser, G. S., and T. S. Squiers Jr. 2015. Shortnose Sturgeon and Atlantic Sturgeon in the Kennebec River system, Maine: a 1977–2001 retrospective of abundance and important habitat. Transactions of the American Fisheries Society 144:591–601.

Yoder, C. O., B. H. Kulik, J. M. Audet, and J. D. Bagley. 2006. The spatial and relative abundance characteristics of the fish assemblages in three Maine rivers: Kennebec River Bingham, ME to Merrymeeting Bay (2002–3), Androscoggin River Errol, NH to Merrymeeting Bay (2003), Sebasticook River Pittsfield, ME to Winslow Me (2003). Center for Applied Bioassessment and Biocriteria, Midwest Biodiversity Institute, Technical Report MBI/12-05-1, Columbus, Ohio.

Zydlewski, G., P. E. Dionne, M. T. Kinnison, J. Zydlewski, and G. S. Wippelhauser. 2011. Shortnose Sturgeon use small coastal rivers: the importance of habitat connectivity. Journal of Applied Ichthyology 47(Supplement 2): 41–44.