

Reconsidering residency: characterization and conservation implications of complex migratory patterns of shortnose sturgeon (*Acipenser brevirostrum*)

Phillip E. Dionne, Gayle B. Zydlewski, Michael T. Kinnison, Joseph Zydlewski, and Gail S. Wippelhauser

Abstract: Efforts to conserve endangered species usually involve attempts to define and manage threats at the appropriate scale of population processes. In some species that scale is localized; in others, dispersal and migration link demic units within larger metapopulations. Current conservation strategies for endangered shortnose sturgeon (*Acipenser brevirostrum*) assume the species is river resident, with little to no movement between rivers. However we have found that shortnose sturgeon travel more than 130 km through coastal waters between the largest rivers in Maine. Indeed, acoustic telemetry shows that shortnose sturgeon enter six out of the seven acoustically monitored rivers we have monitored, with over 70% of tagged individuals undertaking coastal migrations between river systems. Four migration patterns were identified for shortnose sturgeon inhabiting the Penobscot River, Maine: river resident (28%), spring coastal emigrant (24%), fall coastal emigrant (33%), and summer coastal emigrant (15%). No shortnose sturgeon classified as maturing female exhibited a resident pattern, indicating differential migration. Traditional river-specific assessment and management of shortnose sturgeon could be better characterized using a broader metapopulation scale, at least in the Gulf of Maine, that accounts for diverse migratory strategies and the importance of migratory corridors as critical habitat.

Résumé : La conservation d'espèces menacées comprend habituellement des efforts visant à définir et gérer les menaces à l'échelle la plus convenable étant donné les processus affectant les populations concernées. Pour certaines espèces, cette échelle est locale alors que, pour d'autres espèces, la dispersion et la migration relient différentes unités démiques au sein de métapopulations élargies. Les stratégies de conservation actuelles pour l'esturgeon à museau court (*Acipenser brevirostrum*), une espèce en voie de disparition, reposent sur l'hypothèse que les individus sont résidents d'une rivière donnée et ne se déplacent donc pas ou que très peu entre rivières. Nous avons toutefois observé que les esturgeons à museau court se déplacent sur des distances de plus de 130 km dans les eaux côtières entre les plus importantes rivières du Maine. Ainsi, la télémétrie acoustique montre que des esturgeons à museau court entrent dans six des sept rivières ayant fait l'objet d'une surveillance acoustique, 70 % des individus marqués effectuant des migrations côtières entre différents systèmes fluviaux. Quatre patrons de migration ont été cernés pour les esturgeons du fleuve Penobscot (Maine), à savoir les patrons de résident du fleuve (28 %), d'émigrant côtier printanier (24 %), d'émigrant côtier automnal (33 %) et d'émigrant côtier estival (15 %). Le patron de résident ne caractérisait aucun des esturgeons à museau court classés comme étant des femelles arrivant à maturité, ce qui indique une migration différentielle. L'évaluation et la gestion traditionnelles par rivière des esturgeons à museau court pourraient être améliorées, du moins pour le golfe du Maine, si elles étaient plutôt faites à l'échelle d'une métapopulation qui rende compte de la diversité des stratégies migratoires et de l'importance des couloirs de migration comme habitats essentiels. [Traduit par la Rédaction]

Introduction

Species conservation begins with a basic understanding of population abundance and spatial extent. Inappropriate assumptions concerning either of these parameters could negatively impact conservation efforts. In some species, complete population isolation or complete panmixia allow for fairly straightforward assessments of abundance and range. However, many species exist as partially isolated units, or demes, within a larger metapopulation connected via individual dispersal (Hanski 1997; Kritzer and Sale 2004). Such circumstances necessitate a different approach to monitoring and management, one that considers population processes and threats occurring at multiple linked scales. Unfortunately, inferences about population structure can be very dependent on application of appropriate techniques. Improved methods for monitoring the movements of marine and aquatic

species, such as acoustic and radio telemetry, have enabled researchers to document extensive movements of species where traditional capture–recapture methods may not readily detect such movements (Pine et al. 2003; Powell et al. 2000). Importantly, telemetry approaches also allow for characterization of alternate migratory strategies within populations (Jonsson and Jonsson 1993). The expression of different migratory strategies in populations has been identified as an important form of biodiversity to conserve (Wilcove 2007; Robillard et al. 2011), and the prevalence of various migratory strategies may be important in determining the range-wide attributes and risks to metapopulations.

Migration itself is a strategy to cope with the spatial and temporal variation of resource availability and environmental conditions (Gross et al. 1988). Ultimately, migrations evolve where they positively influence fitness relative to resident strategies. Differ-

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P.E. Dionne* and G.B. Zydlewski. University of Maine, School of Marine Sciences, 5741 Libby Hall, Orono, ME 04469-5741, USA.

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

J. Zydlewski. US Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, Orono, ME, USA.

G.S. Wippelhauser. Department of Marine Resources, State House Station, Augusta, ME 04333-0021, USA.

Corresponding author: Gayle Zydlewski (e-mail: gayle.zydlewski@maine.edu).

*Present address: Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501, USA.



ential migration describes variation in migratory strategy, by age or sex, within a population (Dingle and Drake 2007). Examples of differential migration can be found in birds (Cade and Hoffman 1993; Lundberg 1979), insects (Lawrence 1988), mammals (Stewart 1997; White et al. 2007), and fish (Hutchings and Morris 1985; Nordeng 1983; Secor 1999). Such variation is the expectation, given that individuals of different age or sex will often experience different current and residual costs and benefits of migration. In addition to migratory strategy varying by age or sex, alternate migration strategies may result from individual plasticity that allows the organism to alter its movement pattern in response to changes in the environment or changes in resource demands. In this study we characterize movement (or migration) strategies within a metapopulation of an endangered species that historically has been managed as isolated populations.

The range of the shortnose sturgeon (*Acipenser brevirostrum*) once included most major rivers on the east coast of North America from eastern Florida to New Brunswick, Canada. Overharvesting led to the depletion of stocks in the early 20th century, while pollution and the construction of dams have reduced habitat and blocked passage to spawning grounds, further contributing to declines and hampering recovery. Now, under the Endangered Species Act, shortnose sturgeon are managed as distinct population segments, with the largest known population units persisting in the Hudson, Saint John, and Delaware rivers (Kynard 1997). In Maine, shortnose sturgeon have been documented in the Sheepscot–Kennebec–Androscoggin complex (National Marine Fisheries Service 1998), the Penobscot River (Fernandes et al. 2010), and some small coastal rivers (Zydlewski et al. 2011), the only known reproducing population being in the Sheepscot–Kennebec–Androscoggin complex (hereafter referred to as the Kennebec complex).

Although other species of sturgeon (e.g., Atlantic sturgeon (*Acipenser oxyrinchus*)) are known to utilize marine habitat extensively, and adult shortnose sturgeon may enter saltwater environments regularly throughout their lives (Dadswell et al. 1984), shortnose sturgeon were rarely documented far beyond the estuary of their home river and were historically accepted as a river resident species, as reflected under current management (National Marine Fisheries Service 1998). Although coastal movements were never historically considered important for shortnose sturgeon, Dadswell et al. (1984) suggested, on the basis of captures of tagged shortnose sturgeon by fishermen in the Bay of Fundy, that further studies might reveal extensive marine movements. Likewise, exchange of tagged fish between the adjacent Ogeechee and Altamaha rivers in Georgia in the last decade also suggested some limited capacity for intersystem movements at the southern end of their range (D. Peterson, personal communication, 2012, University of Georgia, Warnell School of Forestry and Natural Resources, 180 E Green Street, Athens, GA 30602, USA).

Since 2007, shortnose sturgeon tagged in the Penobscot River were monitored moving to the Kennebec complex, and since 2008 they have been monitored moving between other coastal rivers of the Gulf of Maine (GoM) by an array of acoustic receivers. As much as 40% of fish carrying acoustic tags emigrated from the Penobscot River in 2007 (Fernandes 2008). Analysis of mitochondrial and nuclear DNA variation likewise shows little if any genetic population structuring between fish captured in the Kennebec complex and fish captured in the Penobscot River, further suggesting a high degree of genetic connectivity among these systems (Wirgin et al. 2005, 2009; King et al. 2010). We suggest this high rate of movement and genetic connectivity provides the most compelling data to date in support of a broader “metapopulation” structure over at least part of the shortnose sturgeon range. However, prior tracking and genetic studies have only addressed the scope of connectivity and not the specific migratory patterns that shape it. An understanding of the specific temporal and spatial dynamics of migration is essential to management at a metapopulation

scale because the primary tools to preserve, enhance, or limit connectivity entail monitoring and policy that target the specific pathways and timings of migrations. In this study we used telemetry data to characterize seasonal emigration and immigration patterns of Penobscot River shortnose sturgeon. We also examined movements relative to size and sex to determine the potential for differential migration and to help elucidate the potential proximal and ultimate basis for such movement patterns.

Methods

Study area

The Penobscot River is the largest watershed in the state of Maine, draining an area of roughly 22 300 km². The first impoundment on the river is the Veazie Dam. Constructed in 1910, the Veazie Dam is located near the head of tide and is the current upriver extent of sturgeon movements in the river. The watershed has a long industrial history, including extensive use by the lumber industry for mill operations and the transportation of lumber. These industries impacted the water quality, substrate composition, and hydrography of the river (Haefner 1967; Shorey 1973). Water quality standards have improved, but much of the woody debris and structures associated with the lumber industry remain, and new industrial development continues in the river (e.g., 2008 channel dredging).

Capture and processing

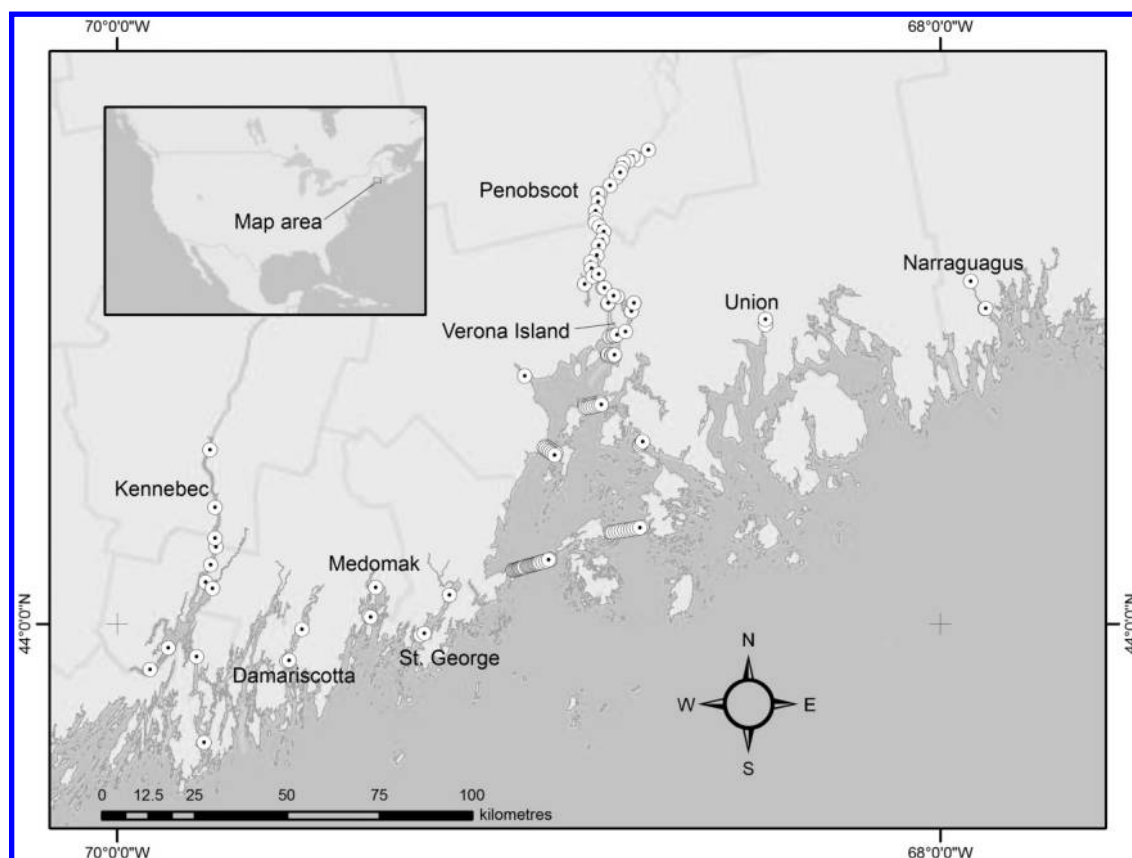
Shortnose sturgeon were captured in the Penobscot River Estuary between the Veazie dam (river kilometre (rkm) 46) and the southern end of Verona Island (rkm 0; Fig. 1). Multifilament gill-nets with 16.2 or 30.5 cm stretch mesh, 2.44 m high, and 45 or 90 m long were fished on the bottom. Nets were fished between rkm 7 and 46 for 0.2 to 23.8 h from May through November in 2006 and 2007 and between rkm 20 and 42 for 0.2 to 3.7 h from May through October in 2008 and 2009.

Once captured, shortnose sturgeon were placed into a floating net pen (1.22 m × 1.22 m × 0.61 m) prior to processing. Measurements were taken, including fork length (cm), total length (cm), and mass (g). Interorbital width (mm) and inner and outer mouth widths (mm) were measured to verify species (from Atlantic sturgeon). An external Carlin dangler tag with an individual identification number was attached just below and forward of the dorsal fin. Every sturgeon was scanned for passive integrated transponder (PIT) tags using an Avid Power Tracker VIII PIT tag reader. If no PIT tag was detected, a 134.2 kHz PIT tag was implanted intramuscularly just forward and below the dorsal fin on the side opposite of the Carlin dangler tag. An endoscopic examination (with a borescope) was performed to assess sex and maturity following the methods of Kynard and Kieffer (2002). This method allowed identification of females with developing eggs only. When eggs were not observed, or if the borescope could not be inserted, the individual was characterized as “unknown” sex. In some cases, the presence of developing eggs was verified during transmitter implantation.

Acoustic telemetry

Acoustic transmitters were implanted in the body cavity of shortnose sturgeon via surgery. Surgery was only performed when fish appeared to be in excellent condition, when water temperatures were between 7 and 25 °C, and dissolved oxygen was 5 ppm or greater. Surgery was not performed on sturgeon that were considered to be in prespawning condition during the spring. Sturgeon were anesthetized with MS-222 (tricaine methanesulfonate), and a number 10 surgical blade was used to make a 3–4 cm incision to one side of the medial ventral line for transmitter insertion. The incision was closed with two sets of sutures. After surgery, the fish were returned to the floating net pen until they showed clear signs of recovery (at least 15 min) and then released at the location of capture.

Fig. 1. Map of coastal Gulf of Maine rivers and acoustic receiver locations. Labeled rivers indicate rivers monitored by acoustic telemetry. White circles indicate acoustic receiver locations. In the Penobscot River, the southern end of Verona Island is considered river kilometre (rkm) 0, and the first dam is at rkm 47.



Sixty-eight shortnose sturgeon were implanted with coded acoustic transmitters (tags) in 2006 (21), 2007 (19), 2008 (17), and 2009 (11). Coded transmitters were Vemco model V9 ($n = 4$) or V13 ($n = 64$). The V9P-2L acoustic transmitters measured 9 mm by 47 mm and weighed 6.4 g in air. The V13TP-1H and V13TP-1L acoustic transmitters measured 13 mm by 45 mm and weighed 12 g in air. The acoustic transmitters were individually coded, providing a means to identify individual sturgeon. The transmitters operated at 69 kHz and had a minimum battery life ranging from 214 to 750 days (actual detection periods were 547 ± 36 days, mean \pm SE); however, early transmitters used in this study did not have preprogrammed end times, so it was not uncommon for transmitters to exceed their minimum tag life.

The Penobscot River–Bay acoustic receiver array (transmitter detection system) deployed for this study consisted of Vemco VR2 and VR2W units (Fig. 1). Maximum detection distance of V9 tags in this system was 500–900 m (J. Hawkes, personal communication, 2012, NOAA–Fisheries, Maine Field Station, 17 Godfrey Drive, Suite 1, Orono, ME 04473, USA). Multiple receivers were deployed at stations where the range of a single receiver would be insufficient to monitor the entire width of the river or bay. The area monitored in the Penobscot River Estuary (rkm 47 to 0) and Bay (rkm 0 to –49) was essentially unchanged from 2006 through 2010, with the exception of lost receivers and station enhancement with additional receivers. Annually, 82 to 122 receivers were deployed to monitor up to 39 stations from about 46 rkm upriver of the southern end of Verona Island (rkm 0) to about 49 rkm downstream of Verona Island, towards the GoM. Receivers were typically in place from April through November.

Since 2007, an acoustic array using the same technology (14 Vemco receivers) was maintained in the Kennebec complex, a

system that is located a minimum of 130 ocean kilometres from the mouth of the Penobscot River. Since 2008, one to three receivers were maintained in each of several coastal Maine rivers between the Penobscot and Kennebec systems: the Damariscotta, Medomak, and St. George rivers, as well as in the Union and Narraguagus rivers to the east of the Penobscot (Fig. 1). One to three receivers were also deployed in proximity to a sturgeon wintering site (rkm 36) in the Penobscot River, during the winters of 2007, 2008, and 2009.

Analysis

Acoustic data processing

All acoustic data reported were from transmitters implanted in shortnose sturgeon captured and released in the Penobscot River. Our tags used locally unique codes, and we did not detect shortnose sturgeon tagged by other researchers.

To characterize movement patterns, we defined emigration and immigration as specific movements relative to the Penobscot River Estuary. Emigrations were movements that took an individual outside of the Penobscot River Estuary. Immigrations are those movements of an individual returning back into the Penobscot River Estuary where they were originally tagged. The date of emigration was the last date an individual was detected upriver of rkm 5 prior to leaving the Penobscot River System. All individuals last detected below rkm 5 were considered potential emigrants, but individuals that were not subsequently detected outside of Penobscot Bay (rkm 0 to –49), or were at large for fewer than 14 days before again being detected above rkm 5, were not considered true emigrants. Immigration date was defined as the date of the first detection of an individual upstream of rkm 5 after it

previously had been designated as a true emigrant. This designation system was conservative with respect to detecting smaller range or shorter duration movements.

Detections consisted of unique identification codes and a date-time recorded at an acoustic receiver station. "Detection events" were consecutive series of detections (of a unique code) at a single location with no other detections recorded at any other receiver station. Any detection event consisting of a single detection greater than 20 rkm from the previous legitimate detection event were considered suspect and filtered out of the data set. Transmitters that were not detected on at least three occasions within 10 rkm and 24 h were also filtered out of the data set. Aside from cases where individuals were clearly detected emigrating from the Penobscot River Estuary, coded acoustic transmitters that were not detected for a minimum of 7 months were excluded from analyses to avoid labeling expired tags as potential emigrants. This time period was chosen because it was near the minimum expected battery life of the shortest-lived coded acoustic transmitters. Coded acoustic transmitters were considered to be shed (from a live or dead fish), and further data removed from analysis, if their movement permanently ceased for a period of greater than 8 weeks between the months of March and November. In the GoM, shortnose sturgeon gather in wintering areas from November through March, during which time their movements are naturally minimal.

Analysis of movement patterns

Individual sturgeon movement patterns were initially divided into two major categories, either "resident" or "migrant" individuals. The migrant category was further subdivided into three migrant subgroups. Individuals were categorized into these movement classes based on the entire period they were detected. Residents were defined as individuals that were never observed leaving the Penobscot River during the life of their acoustic tag. Migrants were individuals documented emigrating from the Penobscot River. Migrant subgroups were subsequently defined by the time that they left the Penobscot River: "spring" emigrants were classified as those individuals emigrating from March through May within the period when water temperature was still suitable for spawning; "summer" emigrants were classified as those emigrating from June through July after suitable spawning water temperatures were exceeded; and "fall" emigrants were those emigrating from September through November, after water temperatures had reached the summer peak. Although primarily defined based on emigration, these movement classes also often involved stereotypic patterns of subsequent immigration (Fig. 2). Average transit times between the Penobscot River and the Kennebec complex for each emigrant subgroup were calculated for periods when receivers were present in both rivers to ensure detection of both departure and arrival.

Movements and fish characteristics

We sought to determine how the size or sex of sturgeon might influence emigration. Because size and sex can be interrelated, we began by comparing the length-mass relationship of known females and individuals of unknown sex using ANCOVA ($\log(\text{mass}) = \text{constant} + \text{sex} + \log(\text{fork length}) + (\text{sex}) \times (\log(\text{fork length}))$) using information on sexual status inferred from borescopic examination. Logistic regression was subsequently used to predict the probability of emigration based on size and sexual characteristics. All fish that emigrated from the Penobscot River within 1 year of their capture, and those that remained in the river for at least 1 year after capture, were used in this analysis. Limiting our analysis to these fish helped ensure that field data on size and sexual status would be reasonably representative of an individual's condition in the period preceding emigration. The best models were selected based on Akaike's information criteria (AIC), and models

with lower AICs were expected to be more parsimonious. The percentage of variation explained by these variables was assessed by Naglekerke's R^2 .

Water data

Water temperature data for the Penobscot River after 16 August 2007 were based on mean water temperatures collected from the same USGS gauging station. Prior to USGS data availability, temperatures were based on values collected from upper estuary fish carrying acoustic transmitters equipped with temperature sensors.

Results

From 2006 to 2009, 454 individual adult (total length > 45 cm) shortnose sturgeon were captured and marked in the Penobscot River. Of these, 68 were implanted with acoustic transmitters. The first acoustic transmitter (tag) was deployed on 14 June 2006, and movement data collected until 1 July 2010 were included in these analyses. Twenty-two of the 68 fish with acoustic tags were removed from our analysis, either because they had not been deployed for at least 7 months at the time of analysis, or they were no longer mobile (detected moving within the arrays or leaving the Penobscot River) for a minimum of 7 months during the study window. With the exception of two cases, we were unable to confirm the reason that a transmitter became immobile. In one case a grey seal (*Halichoerus grypus*) was observed eating an acoustically tagged individual (Fernandes 2008), and in a second case we recaptured an individual that had lost its tag. Other possible explanations for immobile or undetected transmitters include post-tagging or natural mortality or tag malfunction. Of the remaining 46 tags used in these analyses, two were V9 tags, and 44 were V13. The mean detection period of acoustic tags (i.e., the period between the first and last detection of the tag) was 547 days (range 14–1090 days). Mean detection period was not significantly different among movement patterns (ANOVA, $p = 0.900$); only two V9 tags were used in this analysis and detection period for these tags was significantly longer than V13 tags. The movements of the two individuals with V9 tags were characterized as a spring emigrant and a summer emigrant. The mean mass and fork length of individuals with acoustic tags were 5.6 ± 0.3 kg and 85.9 ± 1.7 cm, respectively. Of the 46 individuals with active acoustic tags reported in this study, 16 were identified as females, with the remainder classified as "unknown sex".

Movement patterns

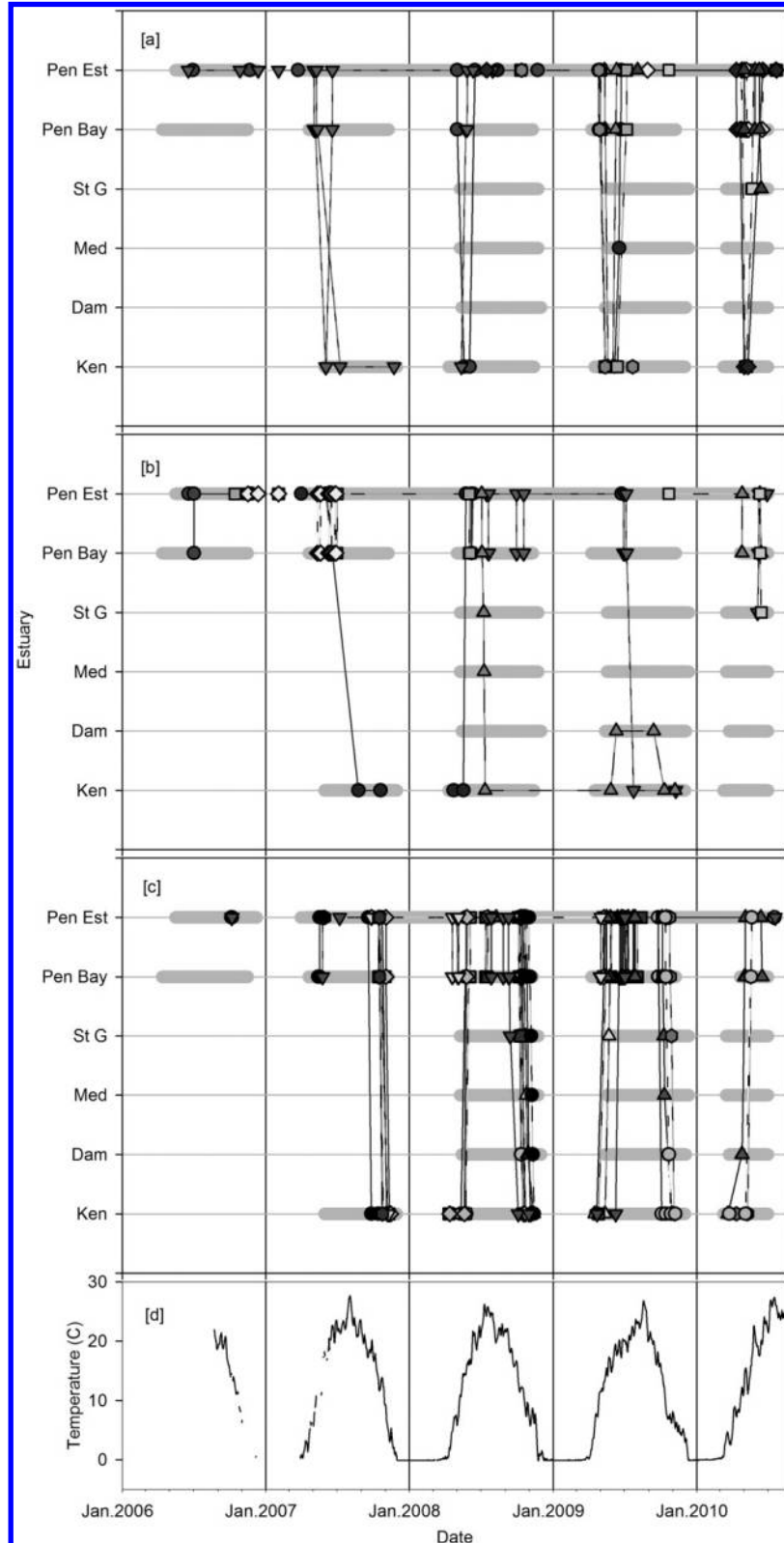
Resident (in-river movements)

Thirteen of the 46 active individuals (28%) with acoustic tags never left the Penobscot River–Estuary–Bay and were classified as Penobscot River "resident". Resident fish followed an in-river movement pattern that involved downriver movement from the wintering area in the spring, followed by gradual upriver movement through the summer prior to returning to the wintering area in the fall (also seen in Fernandes et al. 2010). None of the resident fish were classified as females with developing eggs via the borescope examination. The mean detection period for resident fish was 516 days (239–778 days).

Spring emigrant

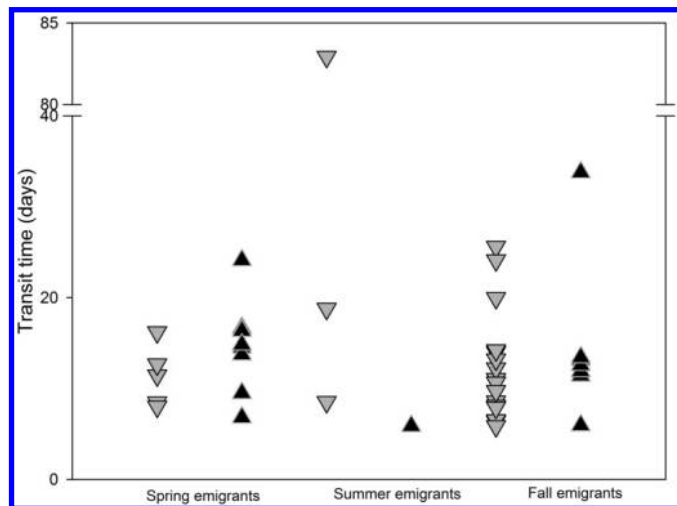
Eleven (of 46, 24%) individuals with acoustic tags were classified as "spring emigrant". Spring emigrants followed an in-river movement pattern similar to resident fish (described above and in Fernandes et al. 2010). However, each individual was documented making a single movement out of the Penobscot River system in the spring, while the resident fish remained in the lower estuary. Spring emigrants were documented leaving the Penobscot River from 12 April to 11 May before water temperatures reached 16 °C (Fig. 2). From 2008 through 2010, when receivers were present in the Kennebec complex during the spring, 78% of the spring emi-

Fig. 2. Coastal movement patterns of shortnose sturgeon monitored in the Penobscot River, Maine: (a) spring emigrant; (b) summer emigrant; (c) fall emigrant; (d) Penobscot River water temperature (°C). The paths of each fish are represented by different symbols and line patterns. The symbols on the lines represent the first and last detection events for each fish in each river or region where it was detected. The thick horizontal gray bars represent the time periods when acoustic receivers were monitoring the Penobscot Estuary (Pen Est), Penobscot Bay (Pen Bay), St. George River (St G), Medomak River (Med), Damariscotta River (Dam), and Kennebec River (Ken) from January 2006 to July 2010. Rivers are listed in order relative to their geographic position from northeast to southwest, with the Penobscot River being the most northeastern river at the top. Water temperature data are from USGS station 01036390 and temperature tags.



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Fig. 3. Transit time, grouped by emigration period, for shortnose sturgeon (tagged with acoustic transmitters) moving between the Penobscot River and Kennebec complex in the Gulf of Maine. Gray triangles are the transit times for tagged sturgeon moving from the Penobscot Estuary to the Kennebec complex, and black triangles are the transit times for tagged sturgeon moving from the Kennebec complex to the Penobscot Estuary. From left to right, transit times are for spring, summer, and fall emigrants.



grants from the Penobscot were detected in the vicinity of Kennebec spawning areas during the spawning window. This includes all three known females from this group that were active for this period. Soon after returning to the Penobscot River, spring emigrants again followed the movement patterns of resident fish. The mean detection period for spring emigrants was 573 days (274–906 days), and the average transit time to the Kennebec complex was 11.4 days (8.0–16.2 days, $n = 5$), with an average return transit time of 14.6 days (6.8–24.1 days, $n = 8$; Fig. 3). No fish were observed making a spring migration in multiple years, and the spring emigration pattern is the only strategy in which fish returned to the Penobscot River during the same year they emigrated. Of the 11 spring emigrants, four were identified as females.

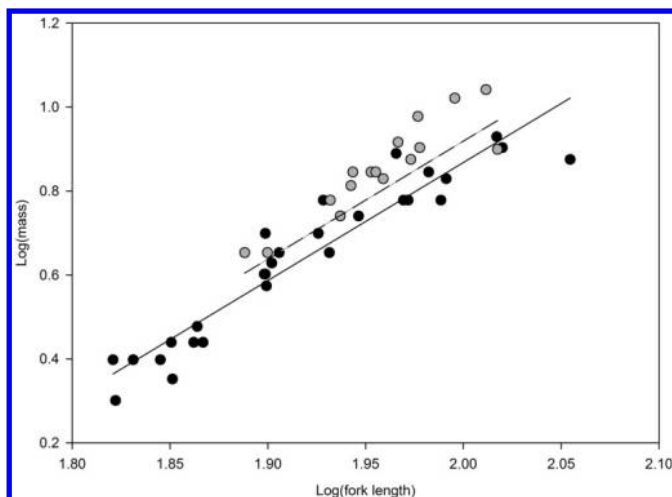
Fall emigrant

Fifteen (of 46, 33%) individuals were classified as “fall emigrants”, which left the system after 9 September, but before fish began to settle in overwintering sites in November. Penobscot River fall emigrants generally followed movement patterns similar to those of resident individuals while in the Penobscot River. However, rather than wintering in the Penobscot River, they utilized wintering areas outside the Penobscot River, presumptively in the Kennebec complex. Receivers were not deployed in the Kennebec complex during winter months, but presence of several fall emigrants was confirmed in wintering areas in the Kennebec River with active tracking through the ice in February 2008. Eighty percent of fall emigrants were documented returning to the Penobscot River, and three fall emigrants were documented utilizing wintering habitats in both the Penobscot and Kennebec rivers in different years (data not shown). The mean detection period for fall emigrants was 569 days (110–749 days), and the average transit time to the Kennebec complex was 12.4 days (5.9–25.6 days, $n = 16$), with an average return time of 14.6 days (6.0–33.8 days, $n = 7$; Fig. 3). Nine of 15 (60%) fall emigrants were previously identified as females with developing eggs.

Summer emigrant

The remaining seven fish (of 46, 15%) were classified as “summer emigrants”. Movements of summer emigrants were less defined than those displaying other movement patterns. Summer emi-

Fig. 4. Regression of $\log(\text{mass})$ (kg) vs. $\log(\text{fork length})$ (cm) for females (gray with dashed regression line) and unknown sex (black with solid regression line) shortnose sturgeon captured in the Penobscot River.



grants were observed leaving the Penobscot River between 1 June and 1 July, after any presumed spawning period and after the water temperature exceeded 16 °C (Fig. 2). Fifty-seven percent of these fish returned to the Penobscot system, and some individuals that emigrated during this period were observed wintering in both the Penobscot and the Kennebec rivers in different years. At least one individual spent a substantial period of time, over 3 continuous months, in coastal river systems between the Penobscot and Kennebec rivers. The mean detection period for summer emigrants was 512 days (14–1090 days), and the average transit time to the Kennebec complex was 36.7 days (8.5–82.9 days, $n = 3$), with an average return transit time of 5.9 days (5.92 days, $n = 1$; Fig. 3). Of the seven summer emigrants, three were identified as females.

Immigration

Of the 33 individual shortnose sturgeon documented emigrating from the Penobscot River, 28 were documented in the Kennebec complex, and 25 were documented returning to the Penobscot River. All of the fish that returned to the Penobscot River emigrated back to the system between 19 April and 7 July, but there was some variation in when various emigration groups returned. In particular, spring emigrants returned to the Penobscot somewhat later in the season (between 25 May and 7 July) than fall (between 19 April and 19 June) or summer emigrants (between 26 April and 8 June). Eighty-one percent of spring emigrants were documented returning to the Penobscot River within 2 months of emigrating (mean residence time in the Kennebec complex, 23.5 days, with a range of 8.1 to 41.5 days); however, one spring emigrant remained outside the Penobscot River Estuary until the year following its initial emigration. Fall emigrants returned to the Penobscot River coincident with increasing water temperatures, opposite of their fall emigration that occurred during declining temperatures.

Movement and fish characteristics

An analysis of covariance (ANCOVA) was performed to compare length-to-mass relationships of fish identified as females with fish of unknown sex. The interaction term, (sex) \times ($\log(\text{fork length})$), was not significant (p value = 0.845) and was dropped from the model. The remaining terms, sex and $\log(\text{fork length})$, were significant ($p < 0.001$). The geometric mean mass of known females and unknown sex were 5.94 kg (SE \pm 1.03 kg) and 4.69 kg (SE \pm 1.02 kg), respectively (Fig. 4).

A logistic regression analysis was performed to determine how the variables of fork length, mass, and sex for individuals affected the odds of emigrating within 1 year of capture. Of these parameters, sex and mass were significant (p value < 0.05). When both parameters were included in a model, however, this model resulted in a higher AIC than the sex only model (AIC = 54.492, AIC = 52.535 respectively), but only sex (known female or not) remained significant as an individual model term (sex: p value = 0.016; mass: p value = 0.834). Sex status alone explained one-third of the variation (Naglekerke's $R^2 = 0.3346$) and predicted that known females were 19.6 times more likely to emigrate from the Penobscot River within the first year after capture than were fish of unknown sex (odds ratio 19.615, 95% CI: 2.3–168.3). The same analysis was performed within the different emigrant patterns, but the results were not significant in any case (p value > 0.050).

Coastal river movements

A total of 13 (28%) active acoustic tagged shortnose sturgeon were documented entering the coastal rivers between the Penobscot and Kennebec rivers (Fig. 2). Six sturgeon were documented in the St. George River, three in the Medomak River, and four in the Damariscotta River in 2008. In 2009, three sturgeon were documented in the St. George River, and two were documented in both the Medomak and Damariscotta rivers. In 2010, four sturgeon were documented in the St. George River, and one was documented in the Damariscotta River. In contrast with the substantial number of Penobscot River emigrants encountered to the west of the Penobscot, only one fish was detected east of the system, an individual recorded in the Narraguagus River in 2010.

Discussion

We documented four migration patterns for shortnose sturgeon captured in the Penobscot River; three of these included coastal migrations. This finding suggests that substantial migratory complexity underlies the demographic and genetic connectivity among sturgeon populations in the putative GoM metapopulation. It is important to note that the fish expressing these migratory patterns are all from the Penobscot River, one river system that may not even afford the full life cycle needs of this species. Evidence to date suggests that these fish likely reproduce in the Kennebec River (Fernandes et al. 2010; Wirgin et al. 2009). Hence, the patterns we describe are for fish that are likely already of migratory origin (Zydlewski et al. 2011). We identified these migration patterns as “resident”, “spring emigrant”, “summer emigrant”, and “fall emigrant” in reference to the Penobscot River where they were captured, with the majority (71%) of fish categorized as one of the three emigrant patterns.

Evidence indicates that emigrant strategies are linked to sexual status, suggesting this is a case of “differential migration” (Dingle and Drake 2007). Subtle variations within seasonal movement patterns further suggest that there is a degree of individual variability or lability associated with each. We did not detect any migratory individuals switching among patterns across years, but the limitations of tag life somewhat restrict this inference. Movements of the residents and the spring and fall emigrants were the most distinctive. The relatively few summer emigrants may represent extreme tail ends of the distributions of the other emigration patterns, specifically the spring or fall patterns. The reimmigration times of these fish are most consistent with a fall migration pattern.

There is strong evidence that the spring emigration events are related to spawning activity in the Kennebec complex. The timing of the spring emigration coincided with the period of time and temperature range when spawning typically occurs in this region, 7 to 18 °C (National Marine Fisheries Service 1998). In addition, most spring emigrants were detected near suspected spawning areas in the Kennebec complex during the spawning period in 2008 through 2010. Although shortnose sturgeon are iteroparous,

those in the north of their range are unlikely to spawn in consecutive years. Spawning periodicity of 2-year intervals for males and 3 to 5 years for females in the Saint John River was reported by Dadswell (1979). If the spring emigration is part of a spawning migration, this spawning periodicity would help to explain why no individuals were documented emigrating during the spring in multiple years. We suggest that the spring movements among rivers in the GoM may be analogous to the “short one-step” migrations described by Kynard (1997), wherein migration is initiated only a few weeks before spawning. The difference between the pattern that Kynard (1997) described and the pattern we document is that the movements described by Kynard occurred within the same river, while the movements we document occurred between coastal river systems that are separated by over 100 km.

Fall emigrants followed an annual migration pattern between the Penobscot and Kennebec systems, with 80% of the individuals repeating this pattern year after year. Like the spring emigrant pattern, these movements may be in part related to spawning in the Kennebec complex. Sixty percent of fall emigrants with active transmitters during 2008 through 2010 were detected near spawning areas in the Kennebec complex during at least one spring, and this includes all eight known females that were active at the time. If these movements are part of a spawning migration, they may be analogous to the “short two-step” migration described by Kynard (1997). Although again initially characterized for in-river movements, the short two-step migration similarly involves a long migration in the fall that brings spawners to a wintering site in close proximity to the spawning habitat they migrate to in the spring.

Though there is evidence that during some years the fall emigrant pattern may be part of an individual's actual spawning migration, shortnose sturgeon generally skip one to several years between spawning events (Dadswell 1979), and it is unlikely that 80% of fall migrants would be in condition to repeatedly spawn on an annual cycle. Studies of Atlantic sturgeon, have shown that some individuals will undergo migrations to reproductive habitats alongside spawners even in years when they do not spawn themselves (Fox et al. 2000; Sulak and Randall 2002). Perhaps some shortnose sturgeon show a tendency toward similar practice migrations. Alternatively, this movement pattern may be part of a highly dispersive strategy that utilizes the summer habitat of the Penobscot River for feeding during the warm months and the overwintering areas of the Kennebec River during the cold months. However, that leaves the question of why these fish do not use the well-populated wintering site in the Penobscot River (Fernandes et al. 2010). One intriguing possibility is that this tendency for some fish to still return to the Kennebec River for overwintering, while others overwinter locally (and some fish do both), reflects a relatively recent origin of the Penobscot wintering aggregation. The Penobscot system suffered more than a century of poor water quality conditions, and dams substantially limited freshwater habitat for juvenile rearing (Opperman et al. 2011). As such, any ancestral Penobscot lineage may have been largely extirpated. Only with improving habitat conditions and a growing Kennebec population may it have been possible for a wintering population to become reestablished in the Penobscot system, and the unknown heritable or social mechanisms that give rise to consistent overwintering habitat use in other river systems may as yet be incomplete for fish using the Penobscot. Of course, high rates of genetic exchange with the Kennebec complex and year-to-year environmental variability may limit the scope for there ever to be a consistent overwintering strategy.

We classified fish whose full record of movements took place entirely within the Penobscot River Estuary as resident because these fish were never documented emigrating from the river. However, longer periods of acoustic monitoring might reveal that these individuals would also ultimately emigrate from the Penobscot River, following one of the three seasonal emigrant patterns. These resident individuals could be between spawning years or

may be an older segment of the population that has abandoned migration, a phenomenon that had been observed in other fish species (e.g., Arctic charr (*Salvelinus alpinus*); Näslund et al. 1993). It is interesting to note that none of the resident individuals were identified as females with developing eggs. Since females have been identified in all other movement categories, this may be evidence of differential spawning migration related to sexual status. Based on this observation, it would appear that females with developing eggs exhibit a greater migratory tendency than the fish of unknown sex (nongravid or male). However, because our methods only allowed us to positively identify females by the presence of maturing eggs, we cannot state conclusively that females in general are more likely to make coastal movements than males.

Variation in habitat and resource availability between rivers may also contribute to the observed movement patterns. Migratory strategies may be influenced by density effects that increase the likelihood that some individuals will seek out additional resources (Secor 1999). It should be noted that dams are currently present in all of the rivers we monitored, restricting access to much of the potential freshwater habitat, and it is interesting to note that the three rivers used for the most time (Penobscot, Kennebec, and St. George rivers) also have the longest unpounded river lengths below the first dam. Minimal use of rivers east of the Penobscot suggests the Kennebec is likely the primary destination for emigrants. To the west of the Kennebec complex, the range of this metapopulation may extend to, or beyond, the Merrimack River in Massachusetts, where four female shortnose sturgeon were documented migrating from the Merrimack to the Kennebec River and back in the spring of 2010 (M. Kieffer, unpublished information, 2011, USGS, Conte Anadromous Fish Research Center, 1 Migratory Way, Turners Fall, MA 01376, USA). Shortnose sturgeon have also been recorded in the Saco River, Maine, a drainage between the Kennebec and Merrimack rivers, where they were encountered by researchers in 2009 and where two individuals implanted with acoustic tags in the Merrimack in 2009 were later detected in 2010 (J. Sulikowski, personal communication, 2011, University of New England, Marine Sciences Center, 11 Hills Beach Road, Biddeford, ME, USA). Movements of females between the Kennebec and Merrimack are of particular interest because spawning has been documented in both systems in recent history (Kieffer and Kynard 1996; M. Kieffer, unpublished data, 2011), indicating that these systems also likely support both migrant and resident components.

Time spent in the coastal rivers between the Penobscot and the Kennebec was typically short (<24 h). The use of small coastal river systems during migration is not currently understood (Zydlowski et al. 2011). Fish may enter these systems as an inadvertent consequence of a near-coast navigational strategy. However, movements appear to occur further up these systems than might be expected based on coastal depth contours alone (Zydlowski et al. 2011). Alternatively, these intermediate rivers may serve as stopover sites, for refuge (e.g., from marine salinities) or foraging, but not the final migratory destination.

We are uncertain whether current coastal movement patterns are a new phenomenon or an ancient part of the life history of shortnose sturgeon at the northern reaches of their range. In all likelihood, both may be true. Such coastal movements have probably always occurred to some degree, but because of advancements in technology they have only come to light recently. Moreover, historic depletion of shortnose sturgeon, and the fact that shortnose sturgeon were rarely distinguished from the extensively migratory Atlantic sturgeon until their listing in the early 1970s, would have reduced the odds of anyone ascribing such movements to shortnose sturgeon. That said, historic disturbance to shortnose sturgeon habitat, including construction of dams, which have restricted access to historical freshwater habitat, may have increased the frequency of migratory life histories because

of the incapacity for some populations to complete all life stages in local rivers. Alternatively, coastal migrations might be a response to increasing regional densities of sturgeon following regional habitat improvements, including removal of dams and reduced pollution. The 1999 removal of Edwards Dam from the Kennebec River restored sturgeon access to spawning areas above the former dam site. This likely aided the growth of the Kennebec sturgeon population potentially to the point where some sturgeon benefit from seeking critical habitat well beyond that system.

Nonetheless, there is anecdotal evidence that some degree of coastal migrations have always occurred in the northern range of shortnose sturgeon, making this seem a less extreme strategy than would arise independently in contemporary time. Anecdotal evidence supporting such migratory strategies is from the 1970s and from another system in the GoM. During his work with shortnose sturgeon in the Saint John River, New Brunswick, Dadswell (1979) noted that 11% (13) of tag returns were from commercial fishermen fishing in the Bay of Fundy and that all of these fish were captured from 1 May to 30 June. Dadswell (1979, p. 2204) suggested that “these recaptures may represent a portion of the SNS population returning to the Saint John River after an overwintering or longer period in the Bay of Fundy.” However, the time period of these captures directly coincides with the time period during which we documented spring emigration and the time period for immigration into the Penobscot River for all of the movement patterns we documented. Therefore, the tag returns from the Bay of Fundy fishermen potentially represent individuals caught in the midst of coastal migrations.

The high degree of coastal mobility and demonstration of specific migratory strategies by shortnose sturgeon in the northern reaches of their range have important implications for the management and conservation of this endangered species. Recognition that GoM shortnose sturgeon rivers are connected in a metapopulation context presents both the opportunity for potential demographic benefits and costs. On the one hand, a metapopulation structure can help to buffer occasional disturbances in component demes by the simple fact that not all demes are likely to face such chance events at the same time (Hanski and Gilpin 1991). On the other hand, if the metapopulation is entirely reliant on a single reproductive source (e.g., Kennebec complex), then threats to reproduction in that source may have wider implications for species status than currently accounted for under the assumption of isolated populations. Recognition of a metapopulation structure for sturgeon in the GoM region also places new requirements on the management and protection of new classes of critical habitat, including coastal corridors and stopover locations. Movements through coastal environments expose sturgeon to a suite of risks that must now be considered with respect to species persistence and recovery. For example, harmful algal blooms recently were ascribed as the cause of a fish kill that claimed more than a dozen shortnose sturgeon at the mouth of Kennebec River in 2009 (Richardson 2009). The migratory tendencies of GoM shortnose sturgeon could either decrease or increase exposure to such localized events. Conversely, protection of these coastal corridors and stopover sites has the potential to facilitate further colonization of regional rivers following suitable habitat restoration. Such colonizations may afford the greatest opportunity for dramatic increases in abundance of this endangered species in the near future.

Much work remains to be done to describe and understand the coastal migrations and migratory patterns of shortnose sturgeon in the northern extent of their range and the implications of complex population structure for species threats and recovery. In the Northeast United States, marking and tagging shortnose sturgeon simultaneously in the Penobscot, Kennebec, Saco, and Merrimack rivers will help to better understand the extent of these

movements and potential population interdependencies. Anecdotal accounts of intersystem movements and recent analyses of genetic population structure (Wirgin et al. 2005, 2009; King et al. 2010) documented elsewhere suggest that coastal migrations may not be restricted to only northern populations. With this in mind, monitoring for coastal movements would be beneficial for this endangered species. Identifying populations with coastal migration strategies will be crucial for managers to determine the potential for regional expansion of populations. Likewise, the identification and characterization of critical coastal habitats for these and other migratory fish are important given the potential role that intersystem movements may play in contributing to overall demographic resilience or risk.

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