Final Report
Period ending: 5/30/2010

Award Details

Award Number: NA07NMF4720053
Recipient Name: Maine Department of Marine Resources
Award Period: 06/01/2007 - 05/30/2010

Program Office: Fisheries Protected Resources Program Office (PRPO)
Program Officer: Lisa Manning ,301 713-1401, lisa.manning@noaa.gov
Project Title: Investigation into the distribution and abundance of shortnose sturgeon in the Penobscot River, Maine
Investigator(s): Kathleen Brosnan, Linda Gosselin, Gail Wippelhauser

Report Type: FR
Progress Reporting Period: 12/01/2009 - 5/30/2010

Final Report: Yes
Report Due Date: 10/27/2010

Investigation into the distribution and abundance of shortnose sturgeon in the Penobscot River, Maine

Gayle B. Zydlewski, Phillip Dionne, and Michael T. Kinnison.

Proposed Scope of Work

The goal of this project was to assess the distribution, abundance and movements of adult and subadult shortnose sturgeon in the Penobscot River in order to inform management needs surrounding the conservation status of this population and delineation of its critical or limiting habitats. Mark-recapture and passive tracking were the primary methods applied.

Funding under this award provided the means to assess the Penobscot River shortnose sturgeon for four consecutive field seasons, 2006 - 2010. Mark-recapture data were used to refine robust design population models to best simulate the population dynamics observed in this river system. The model provides seasonal abundance estimates of shortnose sturgeon in the Penobscot River. Field observations provide important/critical habitats used by individuals.

Technical results are compiled in two manuscripts that will be incorporated in the University of Maine Master's thesis of Phillip Dionne. Drafts of these manuscripts are included as appendices to this report. Once the Master's thesis is defended the thesis will supersede the appended documents and as manuscripts are submitted for peer review those publications will supersede reference to the thesis.

<u>December 1, 2009 – May 31, 2010, progress report:</u>

Data processing:

In 2010, the University of Maine continued to cooperatively manage an acoustic receiver array in the Penobscot River system with NOAA Fisheries and the U.S.G.S. Maine Cooperative Fish & Wildlife Research Unit. The acoustic array of telemetry receivers was retrieved from the Penobscot River and Bay between 4 and 12 December 2009. In December receivers were downloaded and data were compiled for analysis of movement patterns, seasonal distribution, and habitat choices. Netting data from 2009 was compiled and analyses using Pollock's robust design are presented in Appendix 2. Data are still preliminary in nature since they have not been through complete scrutinization of the Master's committee and scientific peer review.

2010 field work preparation:

From December 2009 through May 2010 preparations were made for the 2010 sampling season. Funding for May 2010 field activities were provided with this financial vehicle and continued funding is being provided by a new NOAA-Section 6 grant to the State of Maine Department of Marine Resources. Project field equipment was inventoried, prepared and ordered as needed. This included preparation of over 60 Vemco VR2 and VR2W receivers, 15 transmitters, associated moorings, lines, and surface floats. Nets for summer collection of sturgeon were also prepared during this time.

Field sampling:

Telemetry
Field sampling for 2010 began on 13 March with deployment of the acoustic receiver array in the Penobscot River and Penobscot Bay (Figure 1). From 13 March to 31 May the receiver array was tended on 8 occasions (8 days boat time) for various purposes (data download, receiver maintenance, repair/repositioning after flooding etc.).

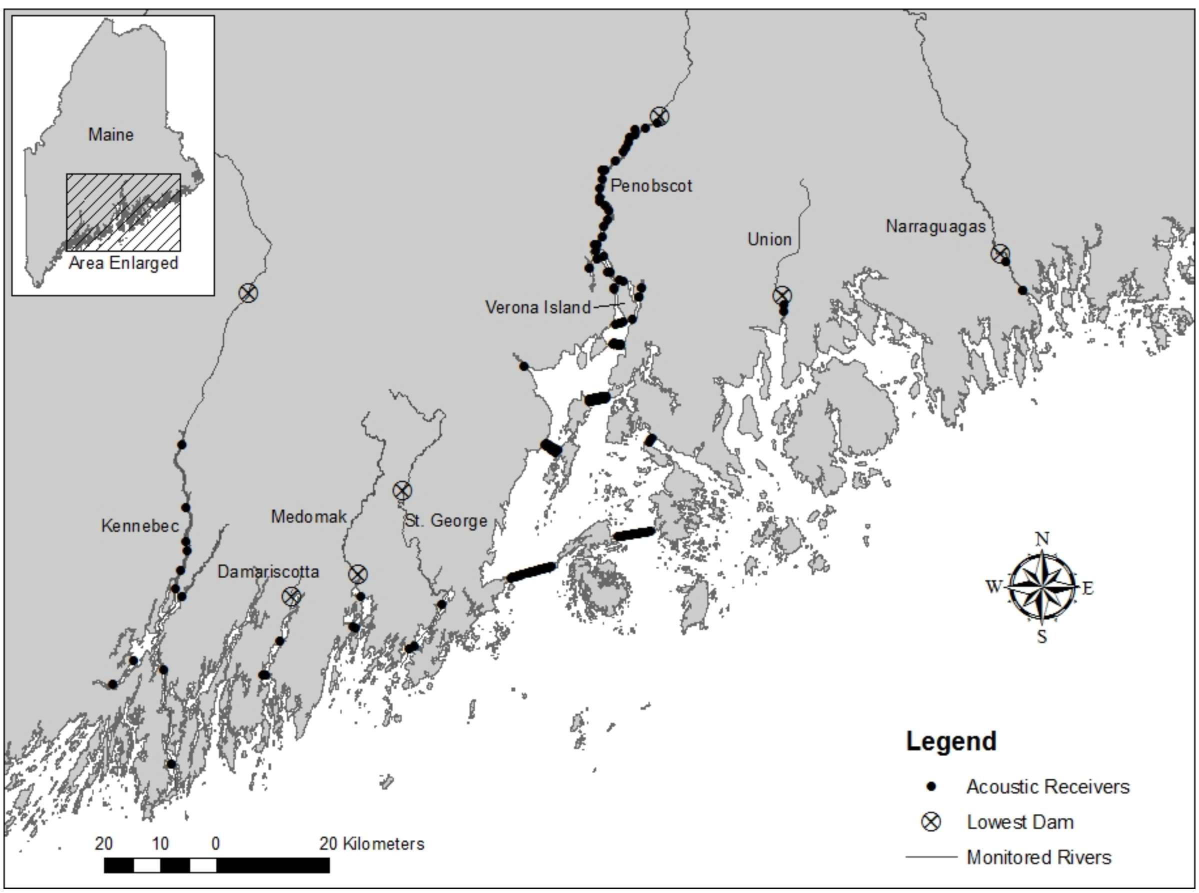

Figure 1: Map of coastal GoM Rivers and acoustic receiver locations. Dark grey lines indicate rivers monitored by acoustic telemetry with the locations of acoustic receivers marked by black circles. The location of the lowest dam on each river is indicated by the circled 'X'.

Based on the documented movements of shortnose sturgeon between the Kennebec and Penobscot Rivers we identified the need to put receivers in coastal rivers between the Kennebec and Penobscot, in an effort to document movements to other adjacent coastal rivers from the Penobscot River. In the middle of May, receivers were deployed in the Damariscotta River, the Medomak River, and the St. George River (2 in each). An additional receiver was deployed in the mouth of the Passagassawakeag River.

Brief Summary of Preliminary Findings:

Findings to date are summarized in the two appendices. Briefly, acoustic telemetry revealed four movement classes for adult shortnose sturgeon tagged in the Penobscot River. Roughly 28% of acoustically tagged fish remained resident in the Penobscot River, albeit seasonally migrating to estuarine and marine habitats in the lower river. None of these fish showed evidence of egg development. Remaining fish showed patterns of emigrating in spring (24%), summer (15%) or fall (33%) and odds of emigration was much greater for females showing early stages of egg maturation (odds ration 19.6). A large proportion (76%) of shortnose sturgeon emigrating from the Penobscot River ultimately returned to that river later in the same year or in the subsequent year. Coastal migration often involved temporary use of smaller coastal rivers between the mouths of the Penobscot and Kennebec Rivers. The amount of time fish spent in these various rivers was positively related to drainage size. A POPAN Jolly- Seber open population model estimated approximately 1654 (95%CI: 1108-2200) adult shortnose sturgeon using the Penobscot River. Robust design analysis with closed periods in the summer and late fall estimated seasonal adult abundance ranging from 636-1285 (weighted mean), with a low estimate of 602 (95% CI: 409.6 – 910.8) and a high of 1306 (95% CI: 795.6 – 2176.4).

Dissemination of findings and outreach:

Publication:

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

Presentations:

Zydlewski, G.B. 2010. Sturgeon of the Penobscot and the Gulf of Maine. Presented to the Veazie Salmon Club on January 28, 2010.

Zydlewski, G.B., M.T. Kinnison, P. Dionne, M. Wegener, J. Zydlewski, G.S. Wippelhauser. 2010. Understanding Habitat Connectivity For Shortnose Sturgeon: From Ocean To Historic Freshwater Habitat In Maine. The 9th International Congress on the Biology of Fishes. Barcelona, Spain, 5-9 Jul.

Dionne,P., G.B. Zydlewski, G. Wippelhauser, J. Zydlewski, M. Kinnison. 2010. Movement Patterns of Shortnose Sturgeon in Coastal Maine Waters. Oral presentation at the Annual meeting of the North American Chapter of the World Sturgeon Conservation Society, Bozeman, MT.

Fernandes, S., G.B. Zydlewski, J. Zydlewski, G.S. Wippelhauser, M.T. Kinnison. 2010. Seasonal Distribution and Movements of Shortnose Sturgeon in the Penobscot River Estuary, Maine. Oral presentation at the Annual meeting of the North American Chapter of the World Sturgeon Conservation Society, Bozeman, MT.

Media Outreach

Spotlight on Sturgeon, on the Penobscot River Restoration Trust website: http://www.penobscotriver.org/content/4067/Spotlight_on_Sturgeon/

Jagels, Richard. 2010. Leaping Living Fossil: The plight of the sturgeon, New England's oldest fish. ***On the Water*** Magazine. January 2010, pages 26-29.

Daigle, Cheryl. 2010. *Penobscot River Restoration Leaps Ahead.* Natural Resources Council of Maine Newsletter article, Summer 2010.

As part of National Marine Fisheries Service's SCUTES (Students Collaborating to Undertake Tracking Efforts for Sturgeon) program, field methods used for collecting sturgeon eggs and larvae were shown and explained to a fourth grade class in March 2010. The class came to the University of Maine to learn about sturgeon field methods: topics included, radio telemetry, surgery, tagging, gill netting, egg collection, DIDSON surveys, and recent findings.

Participation in Penobscot Riverkeepers outreach to Junior High School students. Presentation of sturgeon biology, research, and conservation at the Eddington Salmon Club. May 2010.

Accounting context:

Note that expenses on this project are reported directly from the University of Maine (Office of Research and Sponsored Programs) to the Maine Department of Marine Resources, separately from this progress report.

Non-federal match for this project included boat usage as follows (Total ***during THIS performance period: $19,200):***

- In-kind boat use: **$19,200**
  - Fair market value for rental: $100/h
  - Days used (each day ~12 h): Total = 16 days (> 1 activity on some days)
    - Receiver retrieve (Dec 2009) 3 days
    - Receiver deployment 4 days
    - Receiver tend/download 5 days
    - Tracking 4 days

Match for Section 6	Per Progress Reports						Added to Final Report		
	Year 1		Year 2		Year 3		Amended	Amended	
ITEM	June 2007 - Nov 2007	Dec 2007 - May 2008	June 2008 - Nov 2008	Dec 2008 - May 2009	June 2009 - Nov 2009	**Dec 2009 - May 2010**	**Year 1**	**Year 2**	**Totals**
Non-capital Equipment	$14,500.00	$0.00	$31,290.00	$0.00	$38,410.00				**$84,200.00**
Boat Use	$60,000.00	$0.00	$68,400.00	$19,200.00	$38,400.00	**$19,200.00**			**$205,200.00**
Kinnison Salary					$13,077.00		**$9,400.00**	**$10,088.00**	**$32,565.00**
Indirect Cost Waiver:						**$36,827.00**	**$3,573.00**	**$12,560.00**	**$52,960.00**
									$0.00
	$74,500.00	**$0.00**	**$99,690.00**	**$19,200.00**	**$89,887.00**	**$56,027.00**	**$12,973.00**	**$22,648.00**	**$374,925.00**

Year 1	$87,473.00
Year 2	$141,538.00
Year 3	$145,914.00
Total:	**$374,925.00**

Corrections to previous match reporting:

Technical progress reports for years one and two did not show Dr. Kinnison's matched salary.

$ 9,400 (salary & fringe) in June 2007 – Nov 2007
$10,088 (salary & fringe) in June 2008 – Nov 2008

Indirect cost waiver provided by the University of Maine (not shown in progress reports) was:

$ 3,573 in Year 1
$12,560 in Year 2
$36,827 in Year 3

Appendix 1:

Chapter 1

PARTIAL AND DIFFERENTIAL MIGRATION OF SHORTNOSE STURGEON IN THE GULF OF MAINE

By

Phillip E. Dionne

B.S. Stony Brook University, 2006

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology and Marine Policy)

The Graduate School

The University of Maine

November, 2010

Advisory Committee:

Gayle Zydlewski, Assistant Professor of Marine Science, Advisor

James Wilson, Professor of Marine Policy, Advisor

Michael Kinnison, Associate Professor of Biology & Ecology, Advisor

Teresa Johnson, Assistant Professor of Marine Policy

Joseph Zydlewski, Assistant Professor of Wildlife Ecology

Robert Lilieholm, Associate Professor of Forest Policy

Chapter 1

PARTIAL AND DIFFERENTIAL MIGRATION OF SHORTNOSE STURGEON IN THE GULF OF MAINE

Abstract

Migrations of shortnose sturgeon are generally believed to be restricted to the river and estuary of their natal system. However, in 2007 Fernandes et al. (2010) documented 40% of shortnose sturgeon acoustically tagged in the Penobscot migrating to the Kennebec River, Maine, over 130 km away. Using an extensive array of acoustic receivers in seven coastal rivers draining to the Gulf of Maine, we have documented over 70% of acoustically tagged shortnose sturgeon emigrating from the Penobscot River and utilizing five of the remaining six monitored river systems. By documenting the timing and direction of these migrations we have identified four migration patterns including in-river migrations and three coastal migrations. The variation in migration patterns may be evidence of partial or differential migration strategies within this population. Documentation of high frequencies of coastal migration and specific migratory habitats may have important implications to future management of this endangered species, and we recommend that future research utilize methods that better account for such migrations.

Introduction

Migration is a strategy to cope with the spatial and temporal variation of resource availability and environmental conditions (Gross et al. 1988). Migratory strategies often involve migrations of adults to breeding grounds that provide suitable nursery habitat for offspring, migrations between patches of superior resources, or seasonal migrations between summer and winter habitat. These migrations are undertaken to increase the fitness or chance of survival of either the migrant, or its offspring; however the benefits of migration are not without costs to the individual. Migration can increase the potential that an organism will fall victim to predation (Hvidsten & Møkkelgjerd 1987, Nicholson et al. 1997, Jonsson & Jonsson 1993), and migratory routes may take organisms through environments which increase energetic costs beyond those of locomotion (McKeown 1984). The weight of these costs and benefits may vary for individuals within a population and as a result, migratory strategies may vary within a population due to this heterogeneity.

Where migratory patterns within a population vary by age or sex, it is described as differential migration (Dingle & Drake 2007). The term partial migration is used to describe populations in which some portion of the population does not migrate (Dingle & Drake 2007). Examples of partial and differential migration can be found in birds (Cade & Hoffman 1993, Lundberg 1979), insects (Lawrence 1988), mammals (Stewart 1997, White et al. 2007), and fish (Hutchings & Morris 1985, Nordeng 1983, Secor 1999, Jonsson & Jonsson 1993). In addition to migratory patterns varying by age or sex, partial migration as a strategy may also result from individual plasticity which allows the organism to alter their migration tactic in response to changes in the environment or changes in their resource demands. Partial and differential migration among fishes is not uncommon and has been well documented in some species but is not well understood (Jonsson & Jonsson 1993). Improved methods for monitoring the movements of marine and aquatic species such as acoustic and radio telemetry has enabled us to document such movements in new populations where traditional capture-recapture methods may not detect such movements. One instance where this has occurred is the recent documentation of coastal migrations of the endangered shortnose sturgeon (*Acipenser brevirostrum*) in the Penobscot River, Maine.

The range of the shortnose sturgeon 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 shortnose sturgeon stocks in the early twentieth century. Pollution and the construction of dams which have reduced habitat and blocked passage to spawning grounds have hampered recovery. Now under the Endangered Species Act, shortnose are managed as river specific Distinct Population Segments (DPS), with the largest known populations persisting in the Hudson, St. John, and Delaware Rivers (Kynard 1997). In 2005, 27 years after the last documentation of shortnose sturgeon in the Penobscot River (Squiers 1981), a sturgeon was documented in the Penobscot River, Maine (Holyoke 2005), and in 2006 a capture-recapture and acoustic telemetry study of sturgeon was initiated (Fernandes et al. 2010). Among the shortnose sturgeon captured in 2006 and 2007 were two shortnose sturgeon which had been previously marked in the Kennebec River during the previous decade (Squiers 2003). In addition to these recaptures, ten shortnose sturgeon that had been implanted with acoustic transmitters in the Penobscot River were detected in the Kennebec River (Fernandes et al. 2010), accounting for over 40% of individuals released with transmitters at that time. Though 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, movements between coastal systems over 100 km apart were unexpected because shortnose sturgeon are rarely documented away from the influence of their home river and were accepted as a river-resident species as reflected under their current management (Dadswell et al. 1984, National Marine Fisheries Service 1998). Though life history strategies involving coastal migrations have not been ascribed to shortnose sturgeon in any part of their range, Dadswell et al. (1984) suggested that further studies may reveal extensive marine movements by shortnose sturgeon, and in the past decade exchange between the adjacent Ogeechee and Altamaha Rivers in Georgia have been documented in the southern end of the range (Peterson personal communication).

Since 2006, shortnose sturgeon tagged in the Penobscot River were monitored moving between coastal rivers of the Gulf of Maine by an array of acoustic receivers. In this study we make use of telemetry data to characterize a set of stereotypic migratory patterns for Penobscot River shortnose sturgeon. We also examined the characteristics of size and known sex to determine whether there is a relationship between these characteristics and the migratory patterns we observe. Finally, we also analyzed the role that watershed area may play in influencing the level of use by migratory individuals as a crude measure of potential migratory habitat preference. Documenting and describing the migratory tactics of Penobscot shortnose will help to inform future research of this species and may shine a new light on their population dynamics in this region.

Study Area

The Penobscot River is the largest watershed in the state of Maine, draining an area of roughly 22300 km^2 into the Gulf of Maine (GoM). The first impoundment of the river is the Veazie Dam. Constructed in 1910, the Veazie Dam is located near the head of tide and is the upriver extent of sturgeon movement in the river. The watershed was used extensively by the lumber industry for mill operations and the transportation of lumber. These activities impacted the substrate composition, hydrology, and water quality of the river (Heafner 1967). Water quality standards have improved since the 1960's but much of the woody debris and structures associated with the lumber industry remain.

Methods

Field Methods

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

Once captured, shortnose sturgeon where placed into a floating net pen (1.22 x 1.22 x 0.61 meters) prior to processing. Measurements taken were fork length (cm), total length (cm), mass (g), interorbital width (mm), and inner and outer mouth widths (mm). Photos were taken of the head and body. A small clip of dorsal fin tissue was collected for population genetics analysis. 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. When possible, to assess sex and maturity an endoscopic examination was performed following the methods of Kynard and Kieffer (2002). This method allowed identification of females with developing eggs only. When eggs were not observed, the individual was characterized as "unknown" gender. In some cases, the presence or absence 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°C and 25°C, and dissolved oxygen was 5ppm or greater. Surgery was not performed on sturgeon that were considered to be in pre-spawning condition during the spring. Surgeries were performed in a 75 to 113 L holding tank filled with river water, with about a 50 mg/L buffered solution of MS-222 (tricaine methane sulfonate) and equipped with an aerator. Each sturgeon was placed in the tank with its head and gills submerged and its body supported by a cloth sling in such a way that the ventral surface was exposed. The head and any exposed flesh beyond the area of implantation were draped with wet towels to avoid drying and sun exposure. Once the fish was still and minimally responsive to touch, a number 10 surgical blade was used to make a 3-4 cm incision to one side of the medial vental line. The transmitter was inserted through the incision and pushed anteriorly. The incision was closed with two sets of sutures. The first set of sutures was absorbable braided Vicryl® passed through the peritoneum and the outer dermal layer, and the second set were made of a non-absorbable braided silk only passed through the dermal layer. After surgery, the fish were returned to the floating net pen for at least 15 minutes and allowed to recover prior to release at the location of capture.

Sixty-eight shortnose sturgeon were implanted with coded acoustic transmitters in 2006 (21), 2007 (19), 2008 (17), and 2009 (11). Coded transmitters were Vemco V9P-2L, V13TP-1L, or V13TP-1H acoustic transmitter. The V9P-2L acoustic transmitters measured 9mm by 47mm and weigh 6.4g in air. The V13TP-1H and V13TP-1L acoustic transmitters measured 13mm by 45mm and weigh 12g in air. All coded acoustic transmitters had a minimum battery life of 250 days, operated at 69 kHz, and provided a means to identify individual sturgeon by the identification code transmitted. In addition to coded acoustic transmitters, most shortnose sturgeon (n = 61) were also implanted with either a continuous Vemco V16-1H acoustic transmitter (n = 46), or a Lotek MCFT-7A radio transmitter (n = 15). Both of these transmitters were used to enable active tracking with portable receiver equipment. The V16-1H continuous acoustic transmitters measured 16mm by 54mm, weigh 20g in air, and operated on a frequency between 51 kHz and 81 kHz. The MCFT-7A radio transmitters were prepared for internal implantation, following protocols for handling shortnose sturgeon, Moser et al. 2000. Preparation involved coiling the antenna in a helical fashion and coating the entire transmitter and antenna in a biologically inert flexible elastomer (M. Kieffer, unpublished). Once prepared, the radio transmitters measured about 17mm at the widest diameter by approximately 155mm long, including the flexible antenna, and weighed about 40g in air.

The Penobscot River/Bay acoustic receiver array (transmitter detection system) deployed for this study consisted of Vemco VR2 and VR2W units (Figure 1). 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 (river km 47 to 0) and Bay (river km 0 to 49) array was essentially unchanged from 2006 through 2010, with the exception of lost receivers and station enhancement with additional receivers. Between 82 and 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 km south of Verona Island, towards the GoM. Receivers were typically in place from April through October. The array in the Penobscot system (the Penobscot River Estuary and Bay) was cooperatively managed by the University of Maine, NOAA Fisheries, and the USGS Fish & Wildlife Cooperative Research Unit.

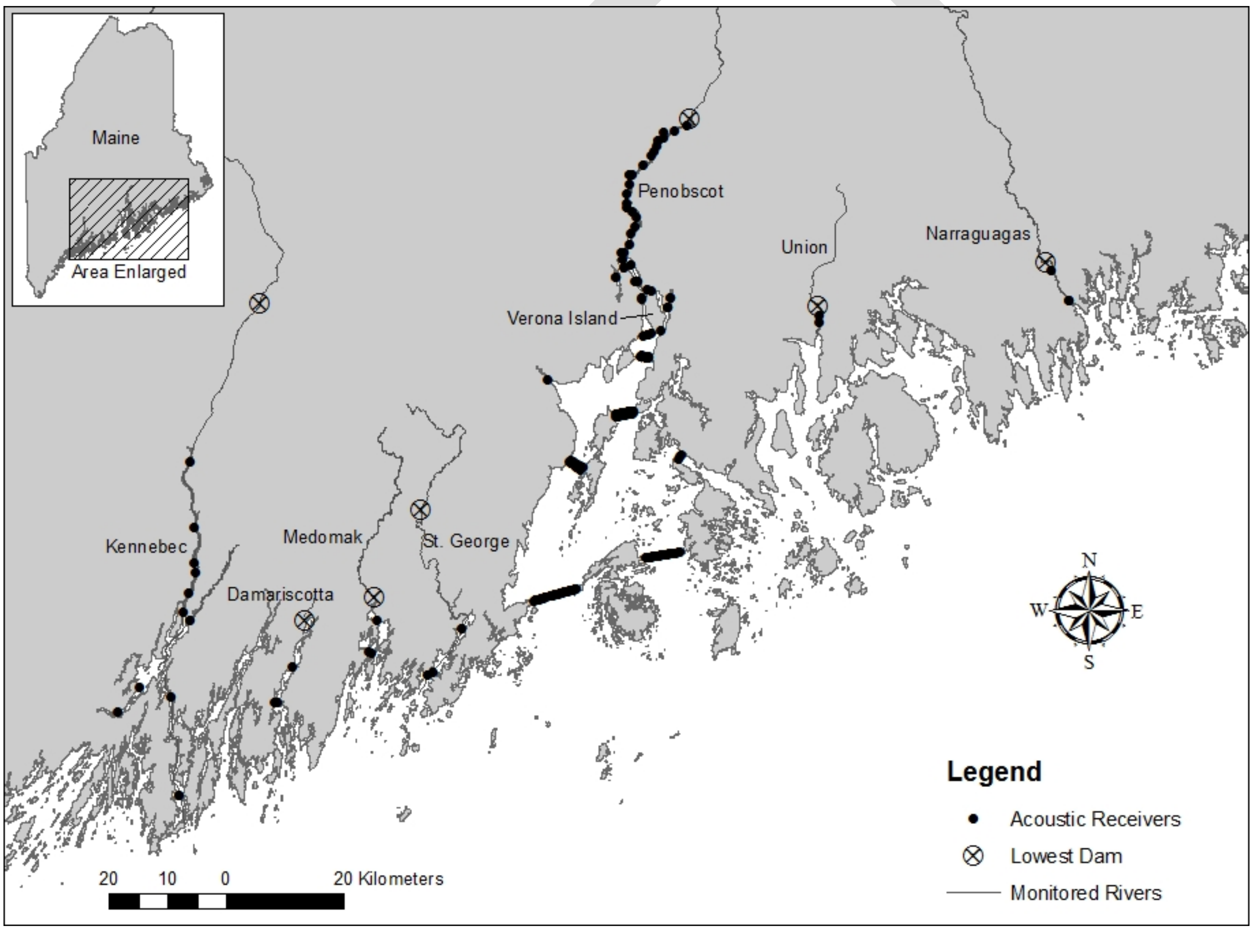

Figure 1: Map of coastal GoM Rivers and acoustic receiver locations. Dark grey lines indicate rivers monitored by acoustic telemetry with the locations of acoustic receivers marked by black circles. The location of the lowest dam on each river is indicated by the circled 'X'.

Since 2007 the Maine Department of Marine Resources has maintained a similar acoustic array in the Kennebec/ Androscoggin system, and since 2008 the University of Maine and NOAA Fisheries maintained from one to three receivers in coastal Maine rivers between the Penobscot and Kennebec Rivers: the Damariscotta, Medomak, and St. George rivers, as well as in the Union, and Narraguagus rivers to the east of the Penobscot (Figure 1). One to three receivers were also deployed in the Penobscot River during the winters of 2007, 2008, and 2009, near Rkm 36 (Table 1).

	2006		2007		2008		2009		2010
	Receivers Present		Receivers Present		Receivers Present		Receivers Present		Receivers Present
	Start	End	Start	End	Start	End	Start	End	Start
Penobscot Estuary	May-16	Dec-09	Apr-11	Nov-30	Apr-03	Nov-26	Apr-08	Dec-11	Mar-13
Penobscot Bay	Apr-12	Nov-16	Apr-20	Nov-09	May-01	Nov-10	Apr-08	Nov-09	Apr-21
Kennebec River	-	-	May-30	Nov-30	Apr-10	Nov-13	Apr-16	Dec-02	Mar-10
Narraguagus River	-	-	-	-	Apr-26	Dec-03	Apr-30	Nov-03	May-14
Union River	-	-	-	-	Apr-28	Dec-03	Apr-30	Nov-03	May-14
St. George River	-	-	-	-	May-09	Nov-24	May-18	Dec-12	Mar-17
Medomak River	-	-	-	-	May-09	Nov-24	May-18	Dec-12	Mar-17
Damariscotta River	-	-	-	-	May-13	Dec-01	May-13	Dec-04	Mar-24

Table 1: Monitoring Periods. Annual periods when acoustic receivers were present in each of the monitored coastal rivers.

Analysis

Acoustic Data Processing. To characterize migration patterns of shortnose sturgeon, the spatial and temporal extent of movements were documented using coded acoustic transmitter detections from stationary acoustic receivers. All acoustic data recorded were from transmitters implanted in shortnose sturgeon captured and released in the Penobscot River. No other research projects were actively tagging shortnose sturgeon in this region, and we did not detect acoustically tagged shortnose sturgeon released by other researchers.

To characterize migratory patterns we defined emigration and immigration as specific events. Emigrations are movements that take an individual outside of the Penobscot River Estuary. Immigrations are those movements of an individual into the Penobscot River Estuary. Since all individuals were initially implanted with acoustic transmitters while in the Penobscot River Estuary, all immigrations were preceded by emigrations. The date of emigration was the last date an individual was detected upriver of Rkm 5, prior to leaving the Penobscot River Estuary (where leaving is defined as being detected outside of the Penobscot system or going unaccounted for a minimum of 14 days after a downriver movement to below river kilometer 5). All individuals last detected below Rkm 5 were considered potential emigrants. Individuals that moved below Rkm 5, but remained in Penobscot Bay prior to returning back up river were not considered emigrants. Immigration date was defined as the date of the first detection of an individual upstream of Rkm 5 after emigrating.

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 of a single detection greater than 20 Rkm from the previous legitimate detection event, were considered a false detection and filtered out of the dataset. Transmitters that were not detected on at least three occasions within 10km and over 24hrs were also filtered out of the dataset. For the purpose of this study, unless detected emigrating from the Penobscot River Estuary, coded acoustic transmitters that were not actively moving in the system for a minimum of seven months were disregarded, to avoid including records from shed transmitters or expired fish. This time period was chosen because it was near the minimum expected battery life for the coded acoustic transmitters used, and any period of seven months would overlap with at least one of the time periods that we observed emigration to occur. Coded acoustic transmitters were considered inactive if their movement ceased for a period of greater than eight weeks between the months of March and November and did not resume movement. In this region, shortnose sturgeon gather in wintering areas from November through March, during which time their movements are minimal. Seasonal and yearly movement data only include coded acoustic transmitters that were active during the time from March through November.

<u>Analysis of Movement Patterns.</u> Movement patterns were initially divided into two major groups of either 'resident' or 'migrant' individuals, and three migrant sub-groups. Individuals were categorized under these movement patterns based on the entire detection period of each fish. Residents are defined as individuals that were never observed leaving the Penobscot River during the course of the study (2006 – 2010). Migrants are individuals documented leaving the Penobscot River. Migrant sub-groups are defined by the time which they left the Penobscot River: 'Spring' emigrants were classified as those individuals emigrating from March through May; 'summer' emigrants as those emigrating from June through August; and 'fall' emigrants as those emigrating between September through November. These periods were based on observed individual movement patterns (Figures 2-4).

<u>Temperature Data</u>. Water temperature data for the Penobscot River, after Augusts 16, 2007 are based on mean water temperature values collected from USGS gauging station 01036390 on the Penobscot River, in Eddington, Maine. Prior to USGS water data being available, water temperature data for the Penobscot River is based on values collected from acoustic transmitters that were equipped with temperature sensors and present in the upper estuary at the time.

<u>Movements and Fish Characteristics.</u> The length weight relationship of females and those of unknown sex were compared using ANCOVA (ANCOVA; general linear model (GLM), *Log (Weight) = Constant + sex+ Log (Fork Length) + (sex) X (Log (Fork Length))*. Where sex is the sexual status of an individual inferred from endoscopic examination (maturing female versus all other individuals. To predict the probability of emigration based on fish characteristics, i.e. FL, weight, and known sex, logistic regression was used. Fish that emigrated from the Penobscot River within one year of their capture, and those that remained in the river for at least one year after capture were used in this analysis. The best models were selected based on AIC values, models with lower AIC's were expected to be more parsimonious. The percent of variation explained by these variables was assessed by Naglekerke's R-square.

Fish Movement Patterns and Watershed Characteristics. From 2008 – 2010 the percent time shortnose sturgeon acoustically tagged in the Penobscot River spent in coastal river systems (including the Penobscot River) was calculated for each fish that moved among rivers while the coastal receivers were operating. Monitoring times included: May 13 through November 24 in 2008, May 18 through December 12 in 2009, and March 26 through July 1 in 2010.The time period between leaving a river and being detected in a different river was recorded and the total time outside of river systems (i.e. in the coastal environment) was reported as the percent of time 'at large'. Percent times spent in each river system were compared with the area of each watershed, and the distance to the first dam. A linear regression was applied to determine if there was a relationship between watershed size and percent time the river was used by Penobscot-migrant sturgeon, or distance to the first dam and percent time. Watershed areas were calculated from watershed shape files available at MEgis.maine.gov using ArcGIS. Distance to the first dam was calculated as a path from the first point where the total width of the river was 3 km or less to the dam using ArcGIS software. The distance from the Penobscot River to each coastal river was estimated by drawing the shortest path between the mouth of the Penobscot River and each coastal river mouth, using ArcGIS software (Table 2).

River Name	Watershed Area (km^2)	Minimum Distance to Mouth of Penobscot (km)
Narraguagus River	630	130
Union River	1345	85
Penobscot River	22300	0
St. George River	718	88
Medomak River	271	100
Damariscotta River	277	116
Kennebec River	15203	132

Table 2: Watershed area and distance to Penobscot River. The approximate watershed area of each river monitored, and the approximate shortest distance from the mouth of each river to the mouth of the Penobscot River at the southern end of Verona Island.

Results

From 2006 – 2009, 454 individual adult (total length > 45cm) shortnose sturgeon were captured and marked in the Penobscot River. Of these, 68 were implanted with acoustic transmitters: 22 in 2006, 19 in 2007, 17 in 2008, and 11 in 2009. The first acoustic tag was deployed on June 14, 2006, and movement data collected until July 1, 2010 are included in these analyses. Twenty two of the 68 acoustically tagged fish were removed from our analysis because they were no longer mobile (detected moving within the arrays, or documented leaving the Penobscot River) for a minimum of seven months at some point in the study window. With the exception of two cases, we were unable to confirm the reason that a transmitter became immobile. In one case we observed a grey seal (*Halichoerus grypus*) eating an acoustically tagged individual (Fernandes 2008), and in a second case we recaptured an individual which had rejected its tag. Scenarios other than predation and tag rejection which may lead to immobile transmitters include post-tagging or natural mortality, or tag malfunction. The mean detection period of acoustic tags, i.e. the period between the first and last detection of the tag, was 546 ± 35 days (mean ± SE). The mean weight and fork length of acoustically tagged individuals were 5.6 ± 0.3 kg and 85.9 ± 1.7 cm. Of the 46 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). Of the 46 active acoustically tagged individuals, 13 undertook annual migrations that never extended beyond the Penobscot River/Estuary/Bay and were classified as Penobscot River 'resident'. Resident fish followed an in-river migration 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 (Fernandes et al. 2010). The mean detection period for resident fish was 516 days (SE± 60 days). We were unable to determine the sex of any resident individuals, i.e. all fish in this group were categorized as 'unknown sex'.

Spring emigrant. Eleven acoustically tagged individuals were classified as 'spring emigrant'. Spring emigrants followed an in-river movement pattern similar to resident fish. However, each individual was documented making a single migration 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 April 12 to May 11 before water temperatures reach 16ºc (Figure 2). All spring emigrants documented returning to the Penobscot River (81%) immigrated back from May 25 to July 7, generally within two months of emigrating, however one spring emigrant was observed to remain outside the Penobscot River Estuary until the year following its initial emigration (not shown in figure). Soon after returning to the Penobscot River, spring emigrants continue to follow the movement patterns of resident fish. The mean detection period for spring emigrants was 573 ± 69 days. No fish were observed making a spring migration in multiple years. Of the eleven spring emigrants, four were identified as females.

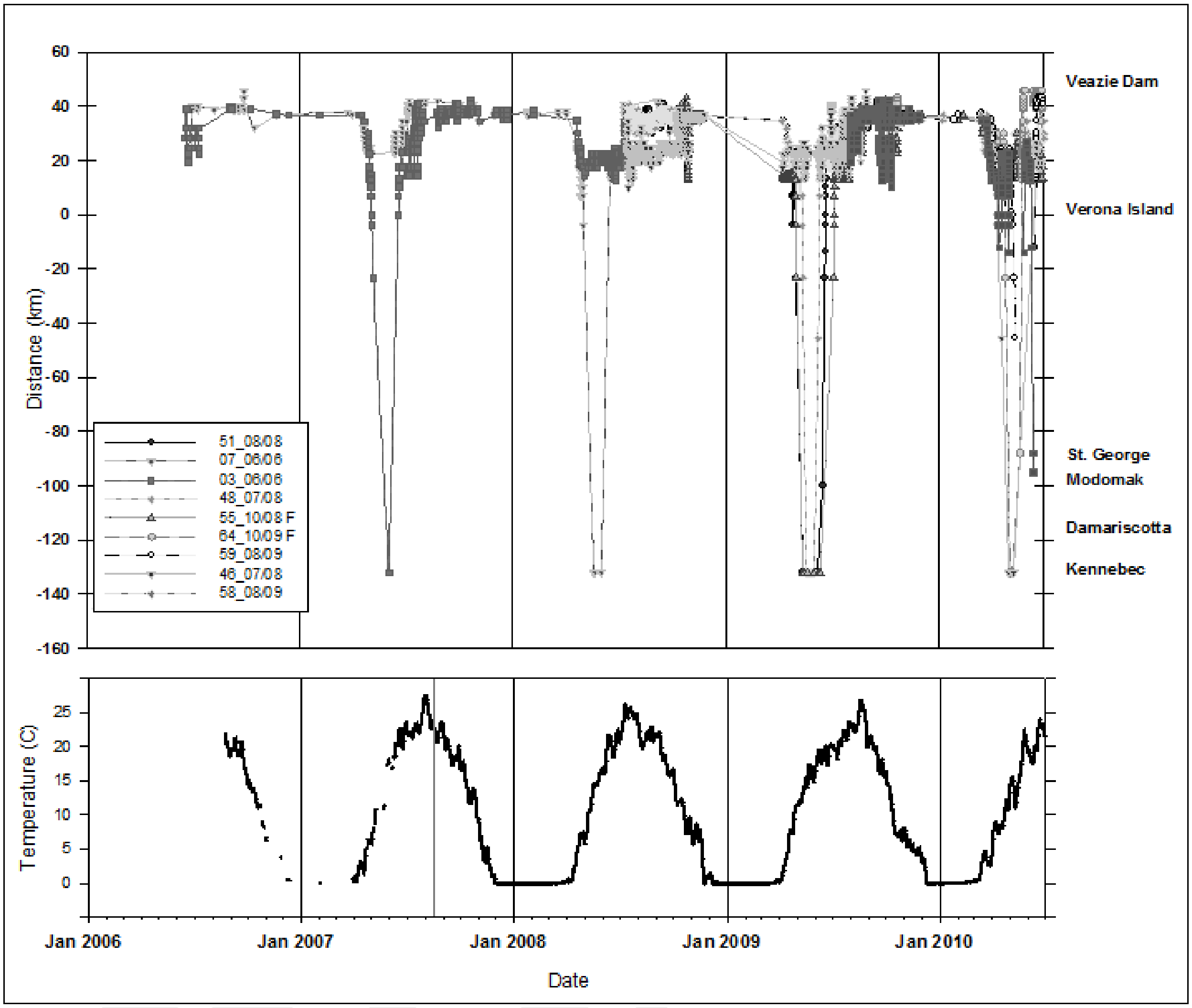

Figure 2: Spring emigrant movements and mean daily temperature. The upper panel represents the documented movements of spring emigrants. Individuals were labeled as: *ID#_month captured/ year captured.* The letter 'F' after the label indicates that the individual was identified as a female. Distances greater than '0' are detection events in the Penobscot River Estuary. Distances between '0' and '-50' are detection events in Penobscot Bay. The distances '-88', '-100', '-116', and '-132' are detection events in the St. George, Medomak, Damariscotta, and Kennebec Rivers respectively (the single detection event in the Narraguagus is not included). The lower panel represents the mean daily temperature in the upper Penobscot Estuary. Temperatures on days prior to August 16, 2007 (the thin gray line) were reported by acoustic tags equipped with temperature sensors. Temperatures on days after August 16, 2007 were recorded by USGS gauging station 01036390 on the Penobscot River, in Eddington, Maine.

Fall emigrant. Fifteen individuals were classified as 'fall emigrant'. Penobscot River fall emigrants generally followed movement patterns similar to those of resident individuals while in the river. However, rather than wintering in the Penobscot River, they utilized the wintering areas in the

Kennebec River. In general, fall emigrants utilized the Penobscot River from mid-spring, immigrating into the Penobscot between April 19 and June 19 as water temperatures increased, before emigrating again between September 9 and November 4 as water temperatures decreased (Figure 3). Eighty percent of fall emigrants were documented returning to the Penobscot River, and three fall emigrants were documented utilizing winter habitat in both the Penobscot and Kennebec River in different years (not shown in figure). The mean detection period for fall emigrants was 569 days (SE± 56 days). Nine of fifteen fall emigrants were identified as female.

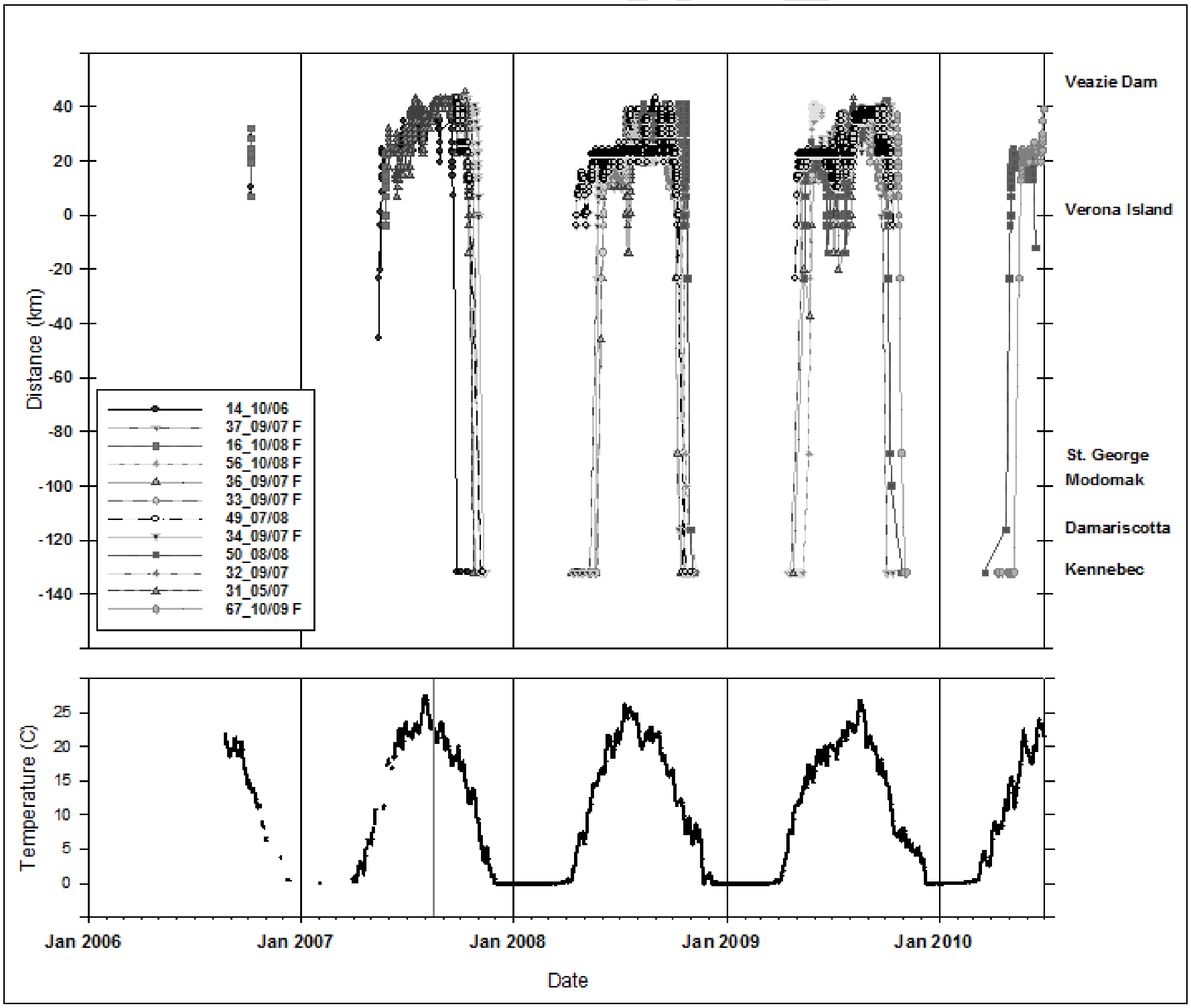

Figure 3: Fall emigrant movements and mean daily temperature. The upper panel represents the documented movements of fall emigrants. Individuals were labeled as: *ID#_month captured/ year captured*. The letter 'F' after the label indicates that the individual was identified as a female. Distances

greater than ‘0’ are detection events in the Penobscot River Estuary. Distances between ‘0’ and ‘-50’ are detection events in Penobscot Bay. The distances ‘-88’, ‘-100’, ‘-116’, and ‘-132’ are detection events in the St. George, Medomak, Damariscotta, and Kennebec Rivers respectively. The lower panel represents the mean daily temperature in the upper Penobscot Estuary. Temperatures on days prior to August 16, 2007 (the thin gray line) were reported by acoustic tags equipped with temperature sensors. Temperatures on days after August 16, 2007 were recorded by USGS gauging station 01036390 on the Penobscot River, in Eddington, Maine.

Summer emigrant. The remaining seven fish were ‘summer emigrants’. The movements of summer emigrants were less well defined than those of the other movement patterns. Summer emigrants were observed leaving the Penobscot River between June 1 and July 1 while the water temperature was increasing and after it has exceeded 16°C during (Figure 4). Individuals that emigrated during this period were observed over wintering in both the Penobscot and the Kennebec Rivers. Those individuals that have been documented returning to the Penobscot River (57%) were observed doing so between April 26 and June 8. At least one individual spent a substantial period of time, over three months, in coastal river systems between the Penobscot and Kennebec Rivers. The mean detection period for summer emigrants was 512 days (SE± 140 days). Of the seven summer emigrants, three were identified as female.

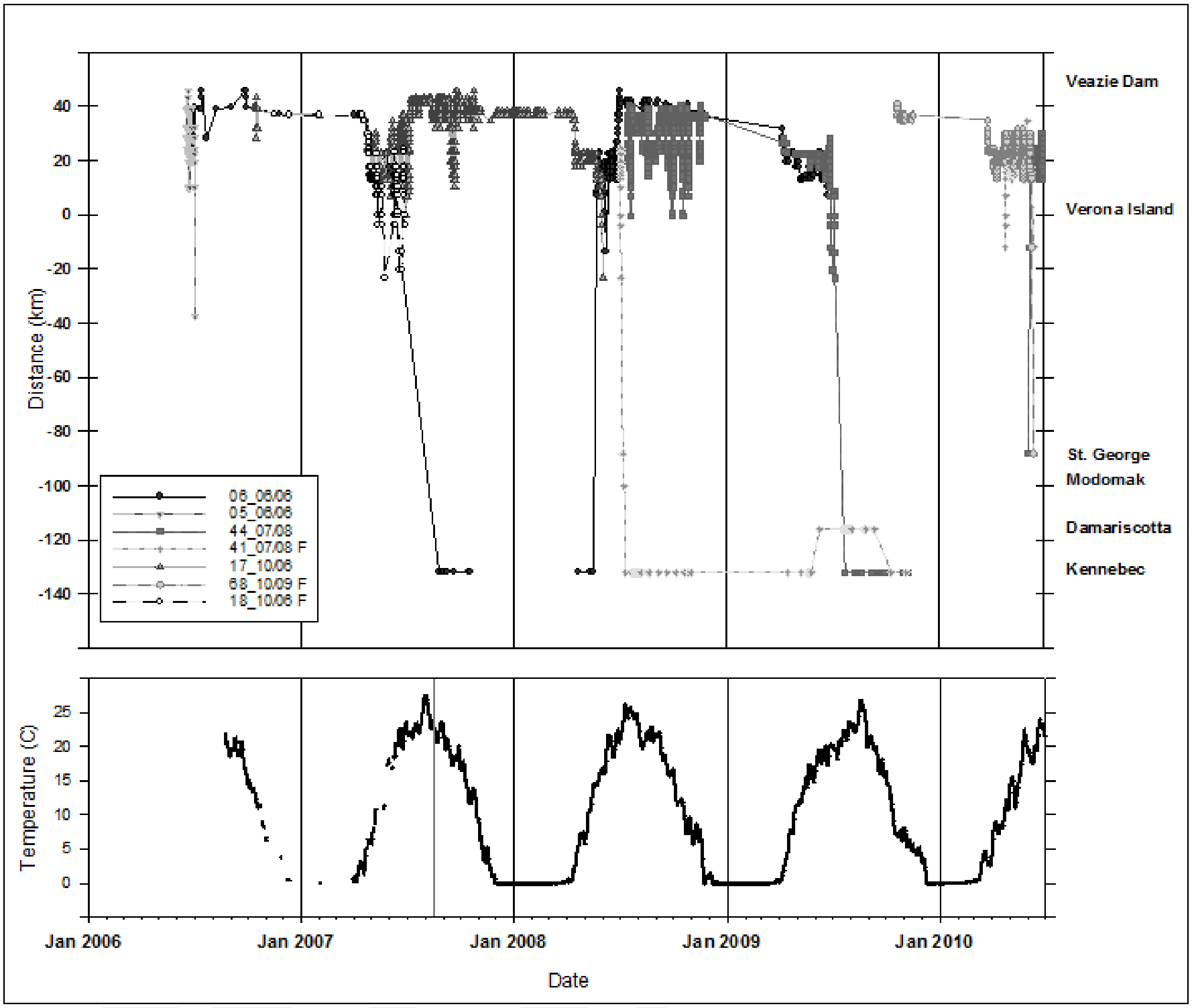

Figure 4: Summer emigrant movements and mean daily temperature. The upper panel represents the documented movements of summer emigrants. Individuals were labeled as: *ID#_month captured/ year captured.* The letter 'F' after the label indicates that the individual was identified as a female. Distances greater than '0' are detection events in the Penobscot River Estuary. Distances between '0' and '-50' are detection events in Penobscot Bay. The distances '-88', '-100', '-116', and '-132' are detection events in the St. George, Medomak, Damariscotta, and Kennebec Rivers respectively. The lower panel represents the mean daily temperature in the upper Penobscot Estuary. Temperatures on days prior to August 16, 2007 (the thin gray line) were reported by acoustic tags equipped with temperature sensors. Temperatures on days after August 16, 2007 were recorded by USGS gauging station 01036390 on the Penobscot River, in Eddington, Maine.

<u>Immigration.</u> Of the thirty three shortnose sturgeon documented emigrating from the Penobscot River, twenty eight were documented in the Kennebec River, and twenty five were documented returning to the Penobscot River. All of the fish that returned to the Penobscot River immigrated between April 19 and July7.

<u>Movement and Fish Characteristics.</u> Partial and differential migratory strategies have been linked to sex and condition. An analysis of co-variance (ANCOVA) was performed to compare length to weight relationships of fish identified as females with fish of unknown sex. The interaction term, *(Sex) X (Log (Fork Length))*, was not significant (P = 0.845), and was dropped from the model. The remaining terms, *Sex*, and *Log (Fork Length)*, were significant with p-values less than 0.001. The geometric mean weight of known females, and unknown sex were 5.94kg (SE± 1.03 kg), and 4.69kg (SE± 1.02 kg) (Figure 6).

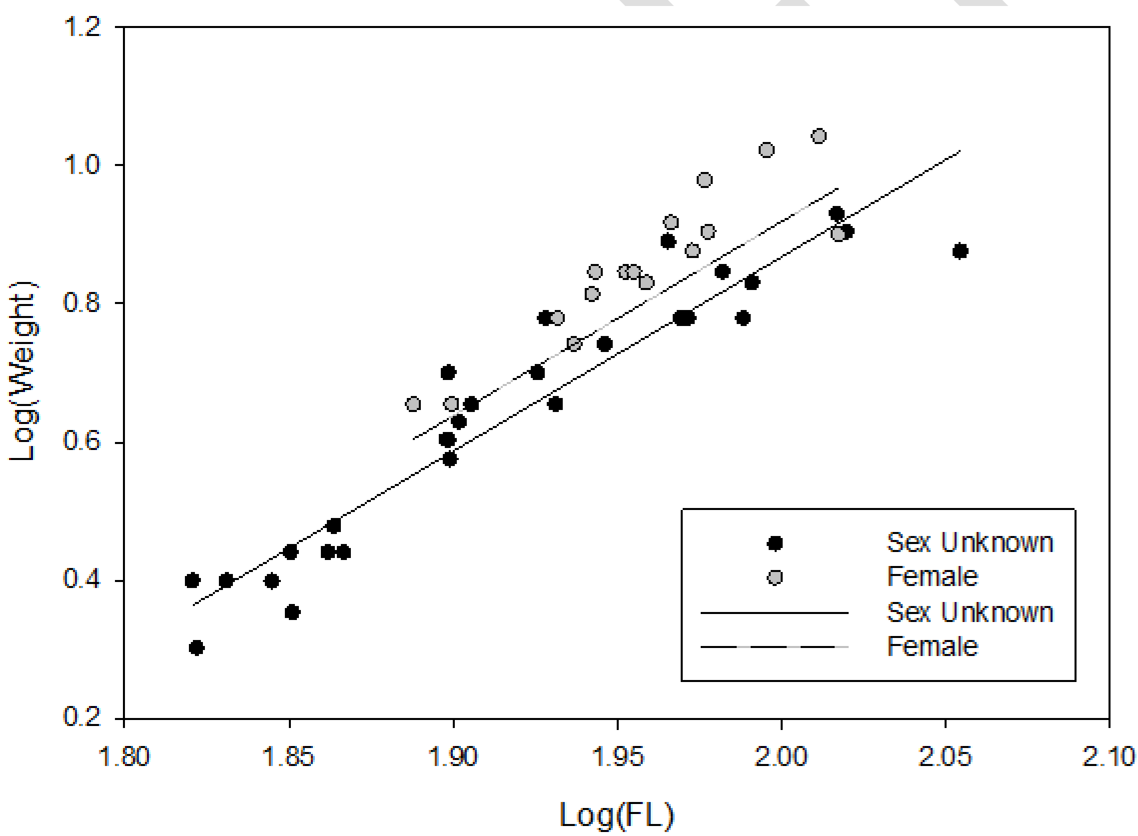

Figure 6: Regression of Log (Weight) vs. Log (Fork Length) for females and unknown sex. Plot of the log (weight) vs. log (fork length) for known females in grey with dashed regression line. Plot of the log (weight) vs. log (fork length) for unknown sex in black with solid regression line.

A logistic regression analysis was performed to determine how the variables of fork length, weight, and sex for individuals affect the odds of emigrating within one year of capture. Of these parameters, sex and weight were significant ($P < 0.05$). 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), and only sex (known female or not) remained significant when in the model with both terms ($P = 0.016$). Sex status alone explained one third of the variation (Naglekerke's R-square = 0.3346), and predicts that known females are 19.6 times more likely to emigrate from the Penobscot River within the first year after capture than are fish of unknown sex (Odds Ratio 19.615, 95% CI: 2.286731 - 168.259079). The same analysis was performed to compare within different emigrant patterns, but the results were not significant ($P > .050$).

<u>**Movement Patterns and Watershed Characteristics.**</u> Differences between rivers are likely to influence if and how each river is utilized by shortnose sturgeon during coastal migrations. From 2008 through the spring of 2010, 28% (13) of active acoustically tagged shortnose sturgeon were documented in the coastal rivers between the Penobscot and Kennebec Rivers. Seven fish in 2008, six in 2009, and five in 2010 were documented in the coastal rivers between the Penobscot and Kennebec Rivers (Table 3). In 2008, 2009, and 2010 acoustic receivers were also present in rivers to the east of the Penobscot River, the Narraguagus and Union Rivers. Only one individual was detected in the Narraguagus River, to the east of the Penobscot. For the five remaining rivers, the Penobscot, Kennebec, St. George, Medomak, and Damariscotta, as watershed size increased the percent of time spent in that watershed increased ($R^2 = 0.796$, $p < 0.001$) (Figure 7).

River Name	2008			2009			2010		
	Number of Fish Detected	Mean Observed Residence (hr:min)	Max Observed Residence (hr:min)	Number of Fish Detected	Mean Observed Residence (hr:min)	Max Observed Residence (hr:min)	Number of Fish Detected	Mean Observed Residence (hr:min)	Max Observed Residence (hr:min)
Narraguagus River	0	0:00	0:00	0	0:00	0:00	1	1:42	1:42
Union River	0	0:00	0:00	0	0:00	0:00	0	0:00	0:00
St. George River	6	19:18	25:16	3	5:18	9:20	4	11:09	6:55
Medomak River	3	2:56	7:42	2	2:02	3:48	0	0:00	0:00
Damariscotta River	4	13:14	18:58	2	16:39	3:15	1	9:10	9:10

Table 3: Number of shortnose sturgeon documented in coastal rivers. Coastal rivers other than the Penobscot and Kennebec Rivers are listed from east to west, and the number of fish detected and the mean and maximum documented residence time are listed by year.

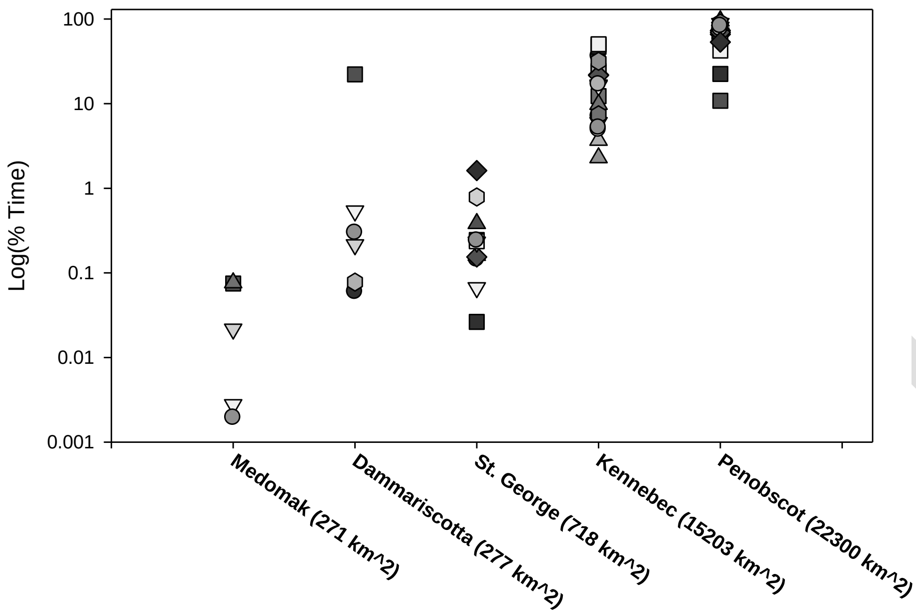

Figure 7: Watershed vs. Log (% time in river). The Log (% time in river) plotted for each river in order of watershed area to illustrate the trend of increasing use with watershed area.

Discussion

We documented four migration patterns for shortnose sturgeon captured in the Penobscot River; three of these include coastal migrations. Though shortnose sturgeon have been documented in marine habitats, they are rarely documented beyond the influence of their natal rivers, so the extent of coastal migrations we documented were somewhat unexpected. We identified these migration strategies as 'resident', 'spring emigrant', 'summer emigrant', and 'fall emigrant' strategies, with the majority (71%) of fish categorized as one of the three emigrant strategies. The presence of both resident and coastal migratory strategies in this population is evidence of partial migration, and there is also evidence of differential migration linked to sexual status. Subtle variations within seasonal movement patterns suggests that there is also a degree of lability associated with potential genetic variation or plasticity. Movements of the resident strategy and the spring and fall emigrants are the most distinctive, while the movement patterns of the summer emigrants are less uniform and represented by the smallest number of fish making it difficult to characterize this movement pattern as distinctly. These fewer summer emigrants may represent an intermediate or imperfect timing pattern that is less optimal than the more frequent spring and summer patterns.

We classified fish whose full record of migrations 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 will also emigrate from the Penobscot River, following one of the three seasonal emigration patterns. If this were the case these individuals would most likely follow the movement patterns classified as spring or summer emigrant, as we documented fall emigrants migrating in consecutive years regardless of their sex. Alternatively, these individuals may be an older segment of the population which has abandoned migration; a phenomenon that has been observed in other fish species (Näslund 1993). It is interesting to note that none of the resident individuals were identified as females. Since females have been identified in all other movement categories, this may be evidence of differential migration related to sex. However, since our methods only allow us to positively identify females by the presence of maturing eggs we cannot state this conclusively. There is the potential that although all shortnose sturgeon captured during this study were of adult size, these resident individuals may have never attained some necessary physiological threshold for migration and reproduction during the period which they were monitored. If emigration is largely driven by the drive to spawn in a river outside of the Penobscot, then the absence of maturing females could suggest that the resident fish lacked the physiological status required for maturation and migration.

There is strong evidence that the spring emigration event that occurs as part of the spring emigrant pattern is related to spawning activity in the Kennebec River. The timing of the spring emigration coincides with the period of time and temperature range when spawning typically occurs in this region, 7ºC to 18ºC (National Marine Fisheries Service 1998). Also, from 2008 through 2010, when receivers were present in the Kennebec River during the spring, 78% of the spring emigrants were detected near suspected spawning areas during the spawning period. This includes all three known females from this group that were active for this time (Wippelhauser, personal communication). Though iteroparous, shortnose sturgeon 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 St. John River was estimated 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. Such a spawning migration would be similar to the "short 1-step" migration as described by Kynard (1997) in which the migration is initiated only a few weeks before spawning. The difference between the pattern that Kynard (1997) has described, and those that we documented is that the movements described by Kynard occur within the same river, while the movements we documented occur between coastal river systems that are separated by over 100 km.

Fall emigrants follow an annual migration pattern between the Penobscot and Kennebec Rivers with 80% of the individuals documented utilizing both rivers each year. Like the spring emigrant strategy, these movements may be related to spawning in the Kennebec River. Sixty percent of fall emigrants with active transmitters during 2008 through 2010 were detected near spawning areas in the Kennebec River during at least one spring, this includes all eight known females that were active at the time. If these movements are part of a spawning migration, they would be similar to the "short 2-step" migration described by Kynard (1997) in which a long migration in the fall brings spawners nearer to the spawning area where they winter before a short migration to the spawning area in the spring. Once again, the primary difference between the pattern described by Kynard (1997) and the pattern we documented is that the long fall migration we've documented occurs between coastal river systems rather than within them. Though there is evidence that during some years the fall emigrant pattern may be part of an individual's spawning migration, since both known females and fish of unknown sex were documented following these movement patterns in consecutive years, it is unlikely that all individuals emigrating in the fall are in condition to spawn in the spring due to the long spawning periodicity of this species. Alternatively, this movement pattern may be part of a broader pattern that utilizes the summer habitat of the Penobscot River for feeding during the warm months, and the over-wintering areas of the Kennebec River during the cold months. However, that leaves the question as to why these particular fish do not make use of the well populated wintering site that already exists in the Penobscot (Fernandes et al. 2010).

In many species of fish, females are documented to have a greater migratory tendency than males (Campbell 1977, Jonsson & Jonsson 1993). It is believed that this may be related to females maturing at a later age and larger size than males, and so they are driven to seek superior resources to support this additional growth (Jonsson 1989). It is also possible that since size is so closely linked to fitness in females, i.e. larger females produce more eggs, that the potential benefits of migration are greater for females than males (Jonsson & Jonsson 1993, Lobon-Cervia et al. 1997). Over the course of this study, we documented all females with active transmitters emigrating from the Penobscot River, while 13 fish of unknown sex never left the river. Based on this observation it would appear that females in this population do exhibit a greater migratory tendency than the fish of unknown sex. However, our methods only allow us to identify females if developing eggs are present and we are unable to identify males. Therefore the increased probability of movement we documented for known females may also be related to maturation state. It is possible that many males that are approaching spawning condition may have similar migration probability to females approaching spawning condition.

Variation in habitat and resource availability between rivers may contribute to the migratory strategies we documented. Migratory strategies may also be influenced by density effects which could increase the likelihood that some individuals will seek out additional resources. Watershed area was used a simple index of the potential resource availability for each river. A linear regression of the percent of time spent in coastal rivers versus watershed shed area showed that larger watersheds were used for a greater percent of time during monitoring periods with the exception of the two acoustically monitored rivers to the east of the Penobscot where only one shortnose sturgeon was documented. It should be noted that as with many of the rivers in this region, dams are currently present in all of the rivers we monitored, restricting access to much of the potential freshwater habitat (Figure 1). Insufficient data was available to accurately measure freshwater reaches below dams in each river, however it is interesting to note that the three rivers used for the most time (Penobscot, Kennebec, and St. George Rivers), also have the longest un-impounded river lengths below the first dam.

Minimal use of rivers east of Penobscot suggests the Kennebec may be the primary destination for emigrants. To the west of the Kennebec River, the range of this population potentially extends to or beyond the Merrimack River in Massachusetts where a shortnose sturgeon originally marked in the Kennebec was recovered in 2009(Kieffer, personal communication). Shortnose sturgeon were also documented between the Merrimack and Kennebec Rivers in the Saco River, Maine where they were encountered by researchers in 2009, and where an individual acoustically tagged in the Merrimack in 2009 was later detected in 2010 (Sulikowski, personal communication).

The time spent in the coastal rivers between the Penobscot and the Kennebec is typically short (< 24hrs). Utilization of these intermediate systems appears to be part of migrations between the Penobscot and the Kennebec Rivers where the intermediate rivers serve as stop-over sites, but usually not the final destination. The utilization of small coastal river systems during migration is not currently understood. Shortnose sturgeon may venture into these coastal rivers in search of resources, or as part of their navigational or osmotic strategy to move back and forth between distant river systems. Remaining near the coast may also reduce exposure to marine predators.

It is unclear whether coastal migrations are a new phenomenon, or regular part of the life-history of shortnose at the northern reaches of their range. These migrations may have always occurred, but either because of low numbers, advancements in technology, or increased study interest; they have only come to light recently. If these migrations strategies are new, they could reflect a response to environmental disturbances such as dams, which restrict access to historical fresh water habitat and force sturgeon to seek resources elsewhere. Alternatively, efforts to restore river systems by reducing pollution and removing dams (e.g. 1999 removal of Edwards Dam), might be aiding growth of the Kennebec population, and these migrations might be in response to increasing local densities of fish in the Kennebec Rivers. However, it seems likely that some degree of coastal migrations occurred in the northern range of the shortnose sturgeon for decades if not longer, else such an extreme strategy would be unlikely to even arise in contemporary time. During his work in the St. 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 May 1 to June 30. Dadswell (1979) 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 migratory strategies we documented. Therefore, these tag returns from the Bay of Fundy potentially represent individuals caught in the midst of coastal migrations similar to those we documented to the west in the Penobscot River.

The high degree of coastal mobility by shortnose sturgeon in the northern reaches of their range has significant implications for the management and restoration of this endangered species. The identification of coastal corridors and stop-over locations would represent a substantial expansion of the perceived critical habitat of this species. Locally, knowledge of these movements is critical to any appreciation of the potential population dynamics of GoM shortnose, and the potential consequences of what might have previously been seen as local challenges to recovery. Movements through coastal environments expose sturgeon to a whole new suite of risks that must now be considered with respect to species persistence and recovery. For example, harmful algal blooms were recently ascribed as the cause of a fish kill that claimed a dozen shortnose sturgeon at the mouth of Kennebec River in 2009 (John Richardson, 2009). The migratory tendencies of GoM shortnose could either decrease or increase the risk of the species to such chance events. Beyond the additional risks to the individuals to consider, it is also important to consider the potential impact the coastal movements have on the ability to colonize and re-colonize regional rivers, and the important role that smaller river systems may play in facilitating these metapopulation dynamics.

Much work is still to be done to describe and understand the coastal migrations of shortnose sturgeon in the northern extent of their range and elsewhere. In the North East United States, marking and acoustically 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. Movements documented elsewhere, between the Ogeechee and Altamaha Rivers in Georgia, suggest that coastal migrations are not restricted to only northern populations, even if they turn out to serve a particularly critical role in population resilience or risk in the North East. With this in mind, monitoring for coastal movements should become a part of research for this species in all rivers. Identifying populations with coastal movement strategies will be crucial for managers to determine the potential for regional expansion of populations. Likewise, the identification and characterization of critical coastal habitats should be a priority for these fish given the potential role that intersystem movements may play in contributing to overall demographic resilience.

REFERENCES

Cade, B. S., and Hoffman, R. W. 1993. Differential migration of blue grouse in Colorado. The Auk 110: 70-77.

Campbell, J. S. 1977. Spawning characteristic of brown trout and sea trout *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland. Journal of Fish Biology 11: 217-229.

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., Taubert, B. D., Squiers, T. S., Marchette, D., and Buckley, J. 1984. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818. Washington D.C., National Oceanic and Atmospheric Administration.

Dingle, H., and Drake, V. A. 2007. What is Migration? BioScience 57: 113-121.

Fernandes, S. J. 2008. Population demography, distribution, and movement patterns of Atlantic and shortnose sturgeons in the Penobscot River estuary, Maine. M.Sc. thesis, Department of Ecology and Environmental Sciences, The University of Maine, Orono, ME.

Fernandes, S. J., Zydlewski, G. B., Zydlewski, J. D., Wippelhauser, G., Kinnison, M. T. 2010. Seasonal Distribution and Movements of Shortnose and Atlantic Sturgeon in the Penobscot River Estuary, Maine. Transactions of the American Fisheries Society 139: 1436-1439.

Gross, M. R., Coleman, R. M., and McDowall, R. M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239: 1291-1293.

Haefner, P. A. 1967. Hydrography of the Penobscot River (Maine) esturary. Journal of the Fisheries Research Board of Canada 24: 1553-1571.

Holyoke, J. Brewer angler hooks five-foot sturgeon during lunch break. Bangor Daily News. July 9, 2005.

Hutchings, J. A., and Morris, D. W. 1985. The influence of phylogeny, size and behavior on patterns of covariation in salmonid life histories. OIKOS 45: 118-124.

Hvidsten, N. A., and Møkkelgjerd, P. I. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. Journal of Fish Biology 30: 273-280.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (Salmo trutta). Freshwater Biology 21: 71-86.

Jonsson, B., and Jonsson N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

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 Kieffer, M. 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.

Lawrence, W. S. 1988. Movement ecology of the red milkweed beetle in relation to population size and structure. Journal of Animal Ecology 57: 21-35.

Lobon-Cervia, J., Utrilla, C. G., Rincón, P. A., and Amezcua, F. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. Freshwater Biology 38: 277-288.

Lundberg, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. Oecologia 41: 273-281.

McKoewn, B. A. 1984. Fish Migration. Pages 87-106 Chapter 4: Bioenergertics. London. Croom Helm.

Näslund, I., Milbrink, G., Eriksson, L. O., and Holmgren, S. 1993. Importance of habitat productivity differences, competition and predation for the migratory behavior of Arctic charr. OIKOS 66: 538-546.

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

Nicholson, M. C., Bowyer, R. T., and Kie, J. G. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78: 483-504.

Nordeng, H. 1983. Solution to the "char problem" based on arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 1372-1387.

Richardson, J. 2009. July red tide was deadliest of deadly trend. Portland Press Herald, November 14, 2009.

Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fisheries Research 43: 13-34.

Squiers, T. S., Smith, M., and Flagg, L. 1981. Distribution and abundance of shortnose and Atlantic sturgeon in the Kennebec River estuary. Research Reference Document: 81/11 Maine Department of Marine Resources.

Squiers, T. S. 2003. Completion Report: Kennebec River shortnose sturgeon population study 1998-2001. Maine Department of Marine Resources.

Stewart, B. S. 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. Journal of Mammalogy 78: 1101-1116.

White, P. J., Davis, T. L., Barnowe-Meyer, K. K., Crabtree, R. L., and Garrott, R. A. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation 135: 502-510.

Appendix 2:

Chapter 2

SEASONAL ABUNDANCE OF SHORTNOSE STURGEON IN THE PENOBSCOT RIVER, MAINE

By

Phillip E. Dionne

B.S. Stony Brook University, 2006

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology and Marine Policy)

The Graduate School

The University of Maine

November, 2010

Advisory Committee:

Gayle Zydlewski, Assistant Professor of Marine Science, Advisor

James Wilson, Professor of Marine Policy, Advisor

Michael Kinnison, Associate Professor of Biology & Ecology, Advisor

Teresa Johnson, Assistant Professor of Marine Policy

Joseph Zydlewski, Assistant Professor of Wildlife Ecology

Robert Lilieholm, Associate Professor of Forest Policy

Chapter 2

SEASONAL ABUNDANCE OF SHORTNOSE STURGEON IN THE PENOBSCOT RIVER, MAINE

Abstract

Shortnose sturgeon (*Acipenser brevirostrum*) once inhabited many of the large rivers of the east coast of the United States. Due to population declines from exploitation, habitat loss and degradation, the shortnose sturgeon has been listed as endangered under the Endangered Species Act of 1973. In 2006, shortnose sturgeon were captured in the Penobscot River, Maine for the first time since the 1970s. Initial abundance estimates of this population were based on closed population models, however acoustic telemetry indicated that a high proportion of acoustically tagged individuals emigrated out of the river in 2007. Based on these observations, 2008 acoustic telemetry has been applied to identify periods of migration. In addition, mark-recapture sampling was redesigned to apply a robust design population model. The model provides a seasonal assessment of abundance. The design includes two annual primary periods, therefore estimating abundance during those periods (here, summer and fall) between periods of migration. We also used acoustic telemetry to quantify the proportion of shortnose sturgeon that migrated seasonally. Observed migration using telemetry was incorporated in the robust design population model. Seasonal estimates of abundance from the top model (selected based on Akaike's information criterion) ranged from 602 to 1306, and fluctuated by season (lower in the fall, higher in the summer). Despite the low encounter rates often associated with endangered species, combining capture, mark-recapture methods with acoustic telemetry data allowed us to provide more biologically realistic estimates of shortnose sturgeon abundance in this river.

Introduction

Estimating the population abundance of endangered species is critical to their restoration and conservation. These species are often cryptic in nature and low population numbers make encountering them even more challenging. This is especially true for aquatic and marine species that are not easily observed in their environment. Capture methods are often used to estimate the abundance of such species, but these methods could be potentially harmful to the organism and so researchers must balance the risks of handling the animal with the need for accurate information. In addition to capture, mark-recapture methods, researchers can gain greater insight into the population dynamics of a species through the use of acoustic, radio, or satellite telemetry (Pine et al. 2003, Powell et al. 2000). Though these methods may pose a greater risk to the individual, the information gained from each individual can provide a better understanding about the population in a shorter period than the use of capture, mark-recapture methods alone. Combining telemetry methods with capture methods can help researchers identify characteristics of populations that may otherwise be missed using capture, mark- recapture methods alone.

Models used to estimate abundance using capture, mark-recapture techniques generally belong to one of two categories: closed and open population models. Closed capture models assume that a population is closed to additions and subtractions, such as death and birth, or emigration and immigration, during the time when the population is being sampled. This assumption may be violated by long term studies (Pine et al. 2003). Open population models do not make these assumptions about additions and subtractions to the population. However, they do make the assumption that any subtractions from the population are permanent. Both model types assume that all animals are equally likely to be caught in each sample (Cooch and White 2010).

Closed capture models are commonly used to estimate the abundance of shortnose sturgeon (*Acipenser brevirostrum*) (Dadswell et al. 1984), one of the first species to be listed under the

Endangered Species Act (ESA) of 1973. This long lived species is slow to mature, rarely seen, and believed to spend most of its life on the bottom of rivers and estuaries of their natal ecosystems. As such shortnose sturgeon in the Penobscot River, Maine, are managed as one of 19 river-specific, distinct population segments under the ESA. Based on capture, mark – recapture data collected in 2006 and 2007, Fernandes (2008) estimated a population of 1531 (95%CI: 885-5681) shortnose sturgeon in the Penobscot River using a Schnabel's closed capture estimate. However, using acoustic telemetry, Fernandes et al. (2010) also documented that 42% (N= 28) of the acoustically tagged shortnose sturgeon emigrated from the Penobscot River in 2007. These and further telemetry work in the Penobscot (Appendix 1) suggest that closed capture population estimates are not appropriate for estimating the abundance of shortnose sturgeon in the Penobscot River.

Ongoing acoustic monitoring of acoustically tagged shortnose sturgeon though the summer of 2010 documented 71% (33 of 46) of individuals emigrating out of the Penobscot River (Appendix 1). Of these emigrants, 84% (28 of 33) were documented in other coastal river systems, and 75% were documented returning to the Penobscot River the following spring. Temporary emigration is a common strategy among shortnose sturgeon captured in the Penobscot River (Appdendix 1). However, temporary emigration violates the permanent emigration assumption of open population models. A third (mixed) population model, the robust design, combines aspects of open and closed models in such a way that temporary emigration can be accommodated (estimated or set) along with abundance (Kendall et al. 1997).

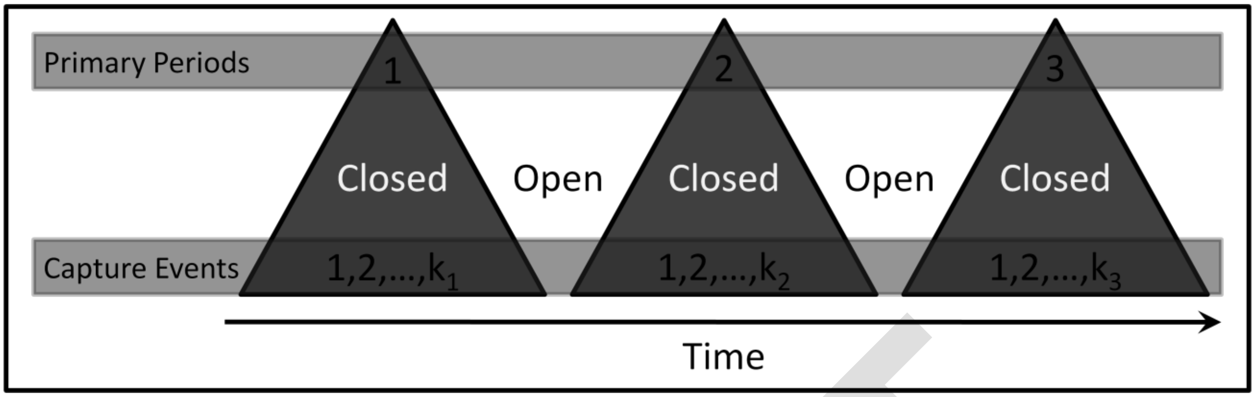

Figure 1: Robust design. This figure depicts the hierarchical design of the robust design model in with multiple capture events within each primary period. The figure also illustrates that the population is closed during primary periods and open between primary periods (Adapted from Cooch & White 2010, and Pollock 1982).

The robust design model relies on a hierarchical sample design in which multiple capture events occur during each primary period, when the population is assumed to be closed. Primary periods are separated by times when the population can be open (Figure 1). Acoustic telemetry analysis by Fernandes et al. (2010) identified two periods when shortnose sturgeon were documented leaving the Penobscot River, and one period when they were documented reentering the river, these periods are times when the population was considered open. Periods of emigration occurred in the spring and fall from mid-April to early July, and from mid-September to early November. Sturgeon were only documented returning (immigrating) in the spring from mid-May to late June. These telemetry data indicate that the population is closed from early July to mid-September (summer).

In the summer shortnose sturgeon are located between Rkm 24.5 and 42.2 in July and between Rkms 32 and 45 in August (Fernandes et al. 2010). This is preceded by a downriver movement in the early spring to the reach of the river between Rkm 10 and 24.5. In the fall, September and October, Fernandes et al. (2010) noted increased movement among fish remaining in the system with an increased distribution and a small downriver shift in location. This increased movement coincides with the fall period of emigration when some individuals leave the river entirely. Fish that remain in the river concentrate at a single wintering location near Rkm 36.5 by mid-October, where they remain until the following spring.

Zehfuss et al. (1999) emphasized the utility of telemetry in testing the assumption of population closure during sampling periods. With the goal of estimating seasonal abundance (summer and fall) while accounting for temporary emigration of shortnose sturgeon in the Penobscot River, capture, mark-recapture sampling periods were selected to coincide with the closed periods identified by Fernandes et al. (2010). Acoustic telemetry data was used to further refine these sampling periods and provided rates of temporary emigration and immigration. A robust design model that allowed estimation of temporary migration was used to estimate seasonal abundance. Five candidate models were considered under the Huggins robust design model and compared using Akaike's information criterion (AIC) to select the model that best described the data. In addition to the Huggins robust design model, a POPAN Jolly-Seber open population model was used to estimate the total number of shortnose sturgeon using the Penobscot River over all seasons. Application of this model was in violation of the assumptions of instantaneous sampling (especially in the summer season) and permanent emigration.

Methods

Capture, mark-recapture. Shortnose sturgeon were captured in the Penobscot River estuary, 47 river km (Rkm) downstream of the Veazie dam (Figure 2). River km 0 is defined as the southern end of Verona Island. Adult shortnose sturgeon were captured using multifilament gillnets with 16.2 cm or 30.5 cm stretch mesh. Nets were 2.44 m tall and 45 m or 90 m long. Nets were fished on the river bottom between Rkm 7 and 46 for 0.2 to 23.8 hours from May through November in 2006 and 2007 while Fernandes (2008) searched for areas used by shortnose sturgeon. From 2008 – 2010, once areas used by sturgeon were defined, nets were fished between Rkm 20 and 42 for 0.2 to 3.7 hours from May through October.

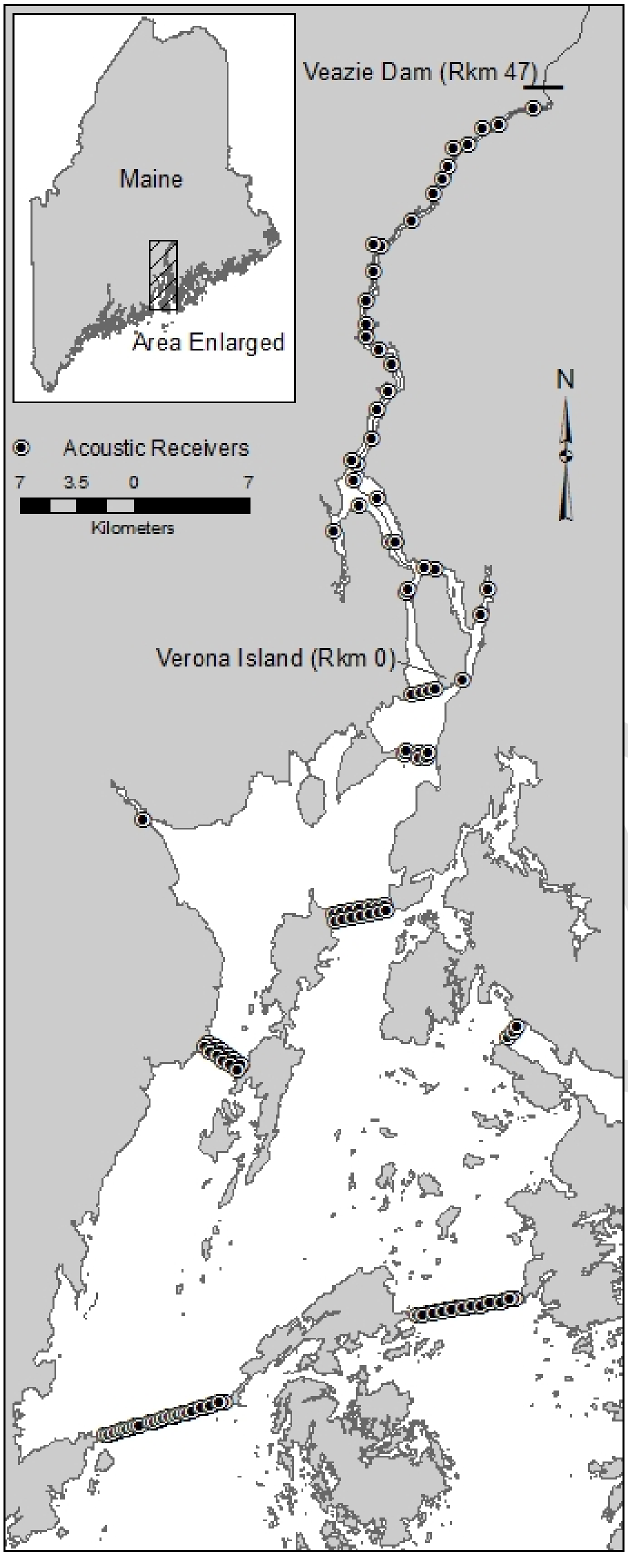

Figure 2: Map of Penobscot River, Maine and acoustic receiver locations. The locations of acoustic receivers are marked by dark circles.

All shortnose sturgeon were marked upon capture. 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, 11.5 mm long PIT tag was implanted intramuscularly just anterior and distal to the dorsal fin. An external Carlin dangler tag with an individual identification number was attached to every fish just below and forward of the dorsal fin on the side opposite of the PIT tag, or through the base of the dorsal fin. However, on two occasions encounter rates and time restriction forced us to skip the procedure on some fish. A total of 77 shortnose sturgeon were released without Carlin dangler tags. Once captured, measurements of fork length (cm), total length (cm), mass (g), interorbital width (mm), and inner and outer mouth widths (mm) were taken. Photos were taken of the head and body, and a small clip of dorsal fin tissue was collected for population genetics analysis.

<u>Telemetry: estimating migration.</u> Vemco acoustic transmitters were surgically implanted into the body cavity of a subset of shortnose sturgeon. A total of 79 shortnose sturgeon were implanted with transmitters from 2006 through the summer of 2010 (2006: 21, 2007: 19, 2008: 17, 2009: 11, and summer 2010: 11). The battery life of acoustic transmitters varied by model with expected battery lives ranging from 250 days to 5 years. The acoustic transmitters were programmed to emit a unique identification coded at 69 kHz over a random time period ranging from 40 to 120 seconds. The unique code provided a means to identify individual sturgeon when detected.

The Penobscot acoustic receiver array deployed for this study consisted of Vemco VR2 and VR2W units. 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 (river km 47 to 0) and Bay (river km 0 to -49) was essentially unchanged from 2006 through 2010, with the exception of lost receivers and station enhancement with additional receivers. Between 82 and 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 km downriver of Verona Island, towards the Gulf of Maine (GoM) (Figure 2). Receivers were typically deployed from April through November of each year. The array in the Penobscot River Estuary and Bay has been cooperatively managed by the University of Maine, NOAA Fisheries, and the USGS Fish & Wildlife Cooperative Research Unit. Since 2007 receiver arrays have also been deployed in up to six additional coastal rivers in the region.

Analysis

Model Choice. Two model types were selected to estimates abundance of shortnose sturgeon in the Penobscot River. The robust design model was selected because it provided a method to estimate temporary migration and seasonal abundance. A POPAN Jolly-Seber open population model was selected to provide an estimate of the number of shortnose sturgeon in the Penobscot River across seasons.

The robust design model is based on a two-tier hierarchal sample design in which there are multiple capture events within each primary period (Pollock 1982). This allows capture probability (p), recapture probability (c), and abundance (*N-hat*) to be estimated within primary periods using closed capture estimates while apparent survival (ϕ) and temporary migration (γ'' = probability of emigrating, $1-\gamma'$ = probability of returning) can be estimated for the periods between the primary sessions. Five model variations were considered under the Huggins robust design model using the program MARK. A Markovian movement model in which temporary migration was estimated with time dependence ($\phi(.)\ \gamma''(t)\ \gamma'(t)\ p(t)=c(t)$); a random movement model in which temporary migration was estimated randomly ($\phi(.)\ \gamma''(t) = \gamma'(t)\ p(t)=c(t)$); an even flow movement model in which temporary emigration estimation was balanced by the rate of immigration ($\phi(.)\ \gamma''(t) = 1-\gamma'(t)\ p(t)=ci(t)$); a 'reduced Markovian' movement model in which temporary migration was seasonally dependant ($\phi(.),\ \gamma''_{1,3,5}(.)\ \gamma''_{2,4}(.)\ \gamma'_{1,3}(.)\ \gamma'_{2,4}(.)\ p(t)=c(t)$); and an 'observed movement' model in which the parameters of temporary emigration were fixed to reflect the temporary migration documented by acoustic telemetry during the periods between primary sessions ($\phi(.)$ γ''(observed) γ'(observed) $p(t)=c(t)$). All models assumed that survival did not vary between periods, and that probability of capture and recapture are equal during each capture event. AICc was used to compare models and to determine the model that best fit the data. The weighted mean of seasonal abundance estimates of all models under Huggins robust design was calculated using the AICc weight of each model.

Secondary sample events were combined within primary sampling sessions and were used in an open population POPAN Jolly-Seber model with constant survival and time variable capture probability ($\phi(.)$, $p(t)$). The program RELEASE, was used to perform a goodness-of-fit test as a general assessment of the fit of the data to the POPAN Jolly-Seber model (Cooch & White 2010). Since the robust design model does not have a standard goodness-of-fit test, the results of this test were also used as a general assessment of the fit of the data to the robust design model as in Dinsmore et al. (2003).

Open and closed periods. To identify open migratory periods of shortnose sturgeon, timing and direction of migrations were assessed using coded acoustic transmitter detections recorded on stationary receivers. All acoustic data analyzed were from transmitters implanted in shortnose sturgeon captured and released in the Penobscot River.

To identify migratory periods we have defined emigration and immigration as specific dates for each individual as described by Dionne (Appendix 1). For the purpose of this study, unless detected emigrating from the Penobscot River, coded acoustic transmitters that did not remain active (detected moving within the arrays) for a minimum of seven months were disregarded to avoid including records from shed transmitters, expired fish, and recently deployed transmitters. This period was chosen because it is near the minimum expected battery life for the coded acoustic transmitters used, and any period of seven months would overlap with at least one of the time periods that we have observed emigration to occur. Inactive transmitters were identified by the same means described by Dionne (Appendix 1). Estimates of emigration and immigration based on acoustic telemetry only include coded acoustic transmitters that were active during both time periods.

Capture, mark-recapture closed/primary periods. From 2008 through the summer of 2010, we aimed to perform capture-recapture sampling only during periods when the Penobscot River was closed to migration in summer and fall. This was done in order to estimate the abundance of shortnose sturgeon in the river during these periods, and estimate the probability of temporary migration between these periods. Closed capture periods in the summer were defined as beginning the day after the last documented spring/early-summer emigration/immigration date as defined by Dionne (Appendix 1) and ending the day before the first fall emigration date.

Closed capture periods were separated by a minimum of 25 days (open periods), during which time migration events occurred. Sturgeon captures that occurred outside the bounds of the closed periods were not used in the analyses To approximate a closed capture period in the fall we focused sampling during a narrow time periods (≤10 days) in mid to late October. At this time water temperatures approached the 7°C threshold and shortnose sturgeon were most likely to be concentrated in or near the wintering area. Sampling was conducted in this manner due to ESA permit restrictions: netting was not permitted when water temperatures were below 7°C. This prohibited sampling during the winter when the population was closed to migration.

Captures from 2006 and early 2007 were not included in analyses due to differences in effort and sampling design. However, captures from the summer and fall of 2007 were included as a single primary sampling session. This was done to enable estimates of immigration after the second period since the robust design model can only estimate immigration after the second period because is the model assumes that there are no marked fish at large until the second period.

The sample areas have been defined as the area between 3 Rkm upriver of the most upriver netting site, and 3 Rkm downstream of the most downstream netting site for each primary period. Sturgeon that were detected within this range between the first and last samples of the primary period were considered available for capture– (Table 1). Geographic dissimilarity between areas of the summer and fall sample periods was the result of efforts to sample the shifting distribution of sturgeon during the closed summer season, and allowed us to adjust to seasonal variations in location while trying to sample as much of the population present in the river at that time.

Observed migration rates were quantified by classifying each active acoustic tag as either available or unavailable in the sample area for each primary period. A transition from available to unavailable or vice versa across two primary sample periods was recorded as an emigration or immigration respectively. We calculated emigration rate between primary periods as the percentage of active acoustic tags that were available at period *i*, and remained active but were unavailable at period *i*+1. Acoustic tags that were known to be active outside of the Penobscot River (unavailable) were used in the same manner to calculate the immigration probability. Although the fall sampling periods occurred before the system became truly closed for the winter, all acoustically tagged sturgeon that were observed emigrating from the Penobscot River in the fall, were already beyond the sample area and unavailable by the first sample event of the period in both fall 2008 and fall 2009. Additionally, no acoustically tagged shortnose sturgeon that were unavailable during the fall sample periods were ever documented entering the sampling area during the fall primary period.

<u>Results</u>

The numbers of shortnose sturgeon encountered during each primary period ranged from 38 to 130 (Table 1). The first primary sampling period (Period 1) began on July 7, 2007, ended on November 2, 2007 and consisted of eleven encounter events (11 days of sampling). The encounter history for this period was adjusted because the final six encounter events occurred during a period of emigration. Kendall (1999) showed that estimates of *p* will remain unbiased even in the case of emigration within a primary period "*if the entire population is present at the first session within a period but begins to leave before the last session, if detection histories are pooled for all sessions that follow the first exit from the study area*" (Cooch & White 2010). The final six encounter events of Period 1 were pooled into a single event leaving a total of six sample events for the period, five during the closed summer period and one representing the fall open period. Data from this period were sparse, and abundance estimates failed to converge and are therefore not reported for Period 1. This period was included in the model to enable estimates of both γ parameters to be used for the time between periods 2 and 3. The remaining five primary periods are represented by their complete encounter history for the robust design model (Table 1).

Period	Season	# Captured	# Recaptured	Capture Events	Dates	River Reach (Rkm)
1	Summer/Fall '07	38	2	11	06/30-11/02	19-44
2	Summer '08	79	6	17	07/04-09/17	20-40
3	Fall '08	100	15	5	10/10-10/17	32-40
4	Summer '09	130	31	15	07/08-09/24	19-40
5	Fall '09	90	27	3	10/16-10/21	33-40
6	Summer '10	76	17	10	06/18-09/13	19-40

Table 1: Capture, mark-recapture results. Table of the season, dates, number of capture events, number of shortnose sturgeon captured and recaptured, and the reach of the Penobscot River sampled during each primary period.

Closed summer periods were approximated using acoustic telemetry data. The closed period in 2008 (Period 2) began on July 4, ended on September 17, and consisted of seventeen capture events between these dates. The closed summer period in 2009 (Period 4) began on July 8, ended on September 24, and consisted of fifteen capture events between these dates. The closed summer period in 2010 (Period 6) began on June 18, ended on September 13, and consisted of ten capture events between these dates.

Fall sample periods occurred prior to the population being closed in the winter. To minimize the effect of migration during these samples, they were restricted to short time periods (≤ 10 days).

The fall sample period in 2008 (Period 3) began on October 10, 2008, ended on October 17, 2008, and consisted of five capture events. The fall sample period in 2009 (Period 5) began on October 16, 2009, ended on October 21, 2009, and consisted of three capture events. The total number of encounter events in the encounter history for the robust design model was fifty six.

Encounter events were pooled within each period to provide encounter histories for the POPAN Jolly-Seber model and goodness-of-fit tests. The cumulative results of tests performed in the program RELEASE indicated that there was a good fit of the data to the models ($\chi^2 = 5.23$, degrees of freedom = 10, P = 0.88).

From 2006 through 2010, 641 adult (fork length ≥ 45 cm) shortnose sturgeon were captured in the Penobscot River including the 515 captures that occurred during the six sample periods included in this study from 2007 to 2010. Of these 515 captures, 97 were recaptures. Tag retention, assessed based on 116 recaptures of double tagged shortnose sturgeon from the period 2006 to 2009, indicated that tag retention was good. PIT tag retention among these fish was 97.4%, and Carlin dangler tag retention was 91.4%. The movements of acoustically tagged shortnose sturgeon indicated that summer and late fall were time periods for sampling when the population was closed or nearly closed to migration. Acoustically tagged sturgeon that remained active for consecutive primary periods were used to calculate the proportion of individuals that left (emigrated) or returned (immigrated) to the Penobscot River between primary periods. These proportions were used as the parameter estimates γ'' and γ' in the observed movement model (ϕ(.) γ''(observed) γ'(observed) *p*(t)=*c*(t)). The proportion of acoustically tagged shortnose sturgeon observed migrating between periods ranged from 0.154 to 0.40 for γ'' (emigration), and 0 to 0.833 for 1- γ' (immigration) (Table 2). The greatest proportions of emigrants were observed in the times going from summer to fall, and returning immigrants were only observed in the time from fall to summer. Note that there was no estimate of γ' for Period 1-2 because it is assumed that there are no marked individuals outside of the sample area prior to this time interval.

	Period 1-2	Period 2-3	Period 3-4	Period 4-5	Period 5-6
γ''(observed)	4/15 (.267)	7/22 (.318)	2/13 (.154)	6/15 (.40)	2/12 (.167)
$1-\gamma'$(observed)	-	1/1 (0.0)	5/6 (.833)	2/2 (0.0)	3/5 (.60)

Table 2: Observed migration. Table of the proportion of acoustically tagged shortnose sturgeon that emigrated (γ''), or returned (1-γ') between each primary period.

Based on AICc, the model that best explained the data was the 'observed movement' model in which the γ parameters of temporary migration were set equal to the proportions of acoustically tagged individuals documented emigrating/ immigration between periods (Table 3). The next most likely model and the only one competing with the top model (ΔAICc < 2), was the 'reduced Markovian' movement model (ΔAICc = 1.88) that grouped γ parameters of temporary migration based on season, which reflects the pattern of movement documented using acoustic telemetry. Estimates of the γ parameters in this model did not converge with the exception of the estimate of emigration between summer and fall periods which was estimated at 0.313 (SE ± 0.111). The next most likely model was the even flow model (ΔAICc = 4.11), and the remaining models were not supported by the model selection criterion (ΔAICc > 10) (Table 3).

	Model	AICc	ΔAICc	AICc Weight	*K*
Observed	$\phi(.)\ \gamma''(\text{observed})\ \gamma'(\text{observed})\ p\,(t) = c\,(t)$	2351.07	0.00	0.66	57
Reduced Markovian	$\phi(.)\ \gamma''_{1,3,5}(.)\ \gamma''_{2,4}(.)\ \gamma'_{1,3}(.)\ \gamma'_{2,4}\,(.)\ p\,(t) = c\,(t)$	2352.95	1.88	0.26	61
Even Flow	$\phi(.)\ \gamma''(t) = 1-\gamma'(t)\ p\,(t) = c\,(t)$	2355.18	4.11	0.08	62
Markovian	$\phi(.)\ \gamma''(t)\ \gamma'(t)\ p\,(t) = c\,(t)$	2366.07	15.00	0.00	66
Random	$\phi(.)\ \gamma''(t) = \gamma'(t)\ p\,(t) = c\,(t)$	2371.20	20.13	0.00	66
Global	$\phi(t)\ \gamma''(t)\ \gamma'(t)\ p\,(t)\ c\,(t)$	2489.42	138.35	0.00	117
(.)	$\phi(.)\ \gamma''(.) = \gamma'(.)\ p\,(.) = c\,(.)$	2862.10	511.03	0.00	3

Table 3: Model ranks. Each of the robust design models are listed in order of the AICc. ΔAICc indicates the model's difference in AICc compared to the top model. AICc Weight is a measure of relative model strength. *K* indicates the number of parameters estimated.

The weighted mean of seasonal abundance estimates of all models under Huggins robust design for periods 2 through 6 are summer '08: 851, fall '08: 649, summer '09: 893, fall '09 636, and summer 2010: 1285 (Table 4). The total abundance estimate of shortnose sturgeon in the Penobscot River across all six periods using the POPAN Jolly-Seber open population estimate was 1654 (95% CI: 1108 – 2200). The apparent survival estimate across periods from this model was estimated at 0.969 (SE± 0.0199).

Period	Observed Movement		Reduced Markovian		Weighted Mean
	N-hat	95% CI	N-hat	95% CI	N-hat
2	812	396.16 - 1768.92	926	448.59 - 2017.02	851
3	641	399.41 - 1074.32	679	408.21 - 1183.49	649
4	902	631.45 - 1315.63	883	611.51 - 1304.97	893
5	602	409.59 - 910.77	666	404.31 - 1144.08	636
6	1306	795.56 - 2176.39	1196	690.89 - 2116.24	1285

Table 4: Robust design results. Seasonal abundance estimates (N-hat) for periods 2 through 6 for the top two models, the 'observed movement' model and the 'reduced Markovian' movement model as well as the weighted mean of all of the models. Periods 2, 4, and 6 were summer and 4 and 5 were fall.

<u>Discussion</u>

The robust design models that best described the data were the 'observed movement' and the 'reduced Markovian' movement models. The seasonal abundance estimates fluctuated with higher abundance estimated for the summer periods than the fall periods (636 -1285 weighted mean). The POPAN Jolly-Seber model estimated that the abundance of the population utilizing the Penobscot River across all periods was 1654 (95% CI: 1108 – 2200).

Fluctuations in seasonal abundance coincided with observed patterns of migration. The pattern of fall abundance estimate below the previous summer's abundance estimate was observed not only in the 'observed movements' model, but also in both of the other top candidate models and a similar pattern was seen in the remaining two models. However, abundance during period 5 was estimated to be higher than period 4 in both the random and Markovian movement models. Estimates of migration from acoustic telemetry supported the finding of Fernandes et al. (2010) that emigration occurs during the spring/ early summer and fall, and that immigration only occurs during the spring (Appendix 1). However, the movements of individuals emigrating in the spring had little influence on estimates of migration between primary periods because these individuals typically left the Penobscot River after the fall sample period and returned before the following summer sample period. Due to the timing of the primary sample periods, migration estimates primarily reflected the movements of fish that emigrated during the fall. Fall emigrants represent about one third of the acoustically tagged shortnose sturgeon that we monitored, and it appears that unlike fish that emigrate during other seasons, fish that emigrate during the fall do so annually with annual spring immigration. This annual pattern could result in the seasonal fluctuations in estimated abundance in the model.

While the seasonal fluctuation of abundance coincides with the patterns of migration we documented using acoustic telemetry, a t-test performed to compare abundance estimates between summer and fall periods indicated that there is not a significant difference between seasons ($p > 0.05$). Fluctuations in abundance could also be the result of heterogeneity of capture probabilities between seasons due to seasonal variation in density or effort. Under-estimation of capture probability can result in over-estimation of abundance (Cooch & White 2010), and capture probabilities during summer periods were lower than fall periods. Seasonal variation in sampling area and duration were a potential source of bias in encounter probabilities.

The simplest way to reduce problems associated with heterogeneous capture probability is to increase the capture probability by capturing more fish in each season (Cooch & White 2010). Efforts were made to maximize capture probabilities during each primary period, however permitting restrictions allowed for only 200 shortnose sturgeon to be handled annually from 2008 through 2010, and 100 annually in 2006 and 2007. Sampling efforts were restricted to times when capture probabilities were highest to avoid violating the permit. Low capture probabilities also contributed to data sparseness which may be the reason that some parameter estimates of the robust design models failed to converge. Data sparseness is a problem in complicated models that have a large number of parameters such as the robust design model (Pine et al. 2003; Cooch and White 2010). Under these conditions, use of telemetry data enabled us to identify times when the population was open to migration and estimate the proportion of migrants between periods. It is unlikely that this would have been feasible with the data we gathered using capture, mark-recapture methods alone within this time period.

One of the limitations of the robust design model is that it relies on individuals captured and marked in a single study area to estimates immigration. This means that for an individual to be documented as an immigrant, it must first be marked, and then emigrate before immigrating. If permitted to sample simultaneously in the Penobscot River and Kennebec River (the primary destination for emigrants), future research efforts could combining a multi-state model to estimate with a Jolly-Seber model similar to the approach used by Caroffino et al. (2009). This would provide a better opportunity to estimate the rate of exchange between both rivers and lend further insight into the population dynamics and abundance of the sturgeon in this region. Alternatively, under the current sampling restrictions, a sample design which included only one primary period per year in order to increase the capture probability during that period could provide better confidence in abundance estimates for that period. The fall period, would likely be the best choice for such an approach because capture probabilities are higher, and the individuals that remain in the river are more concentrated during this time as they congregate in the wintering area. However, this estimate would likely under estimate the number of individuals using the system during a given year due to fall emigration. In addition to capture, mark-recapture, and acoustic telemetry methods, other technologies such as acoustic imaging may provide a non-invasive means to estimate abundance. By utilizing multiple study methods we can better understand the population dynamics of this species.

The high rate of migration we have documented in the Penobscot River is evidence that this population is part of a regional population. Shortnose sturgeon are currently managed as river-specific distinct population segments, and most studies of this species have focused on individual rivers, under the assumption that populations were closed to migration. In addition to the documentation of coastal migration in the Gulf of Maine, recently documented coastal movements between the Ogeechee and Altamaha Rivers in Georgia (Peterson, personal communication) indicate that regional interactions of populations is not restricted to the northern extent of the range. Given that even systems now known to have exchange between rivers, such as the Kennebec River where studies as recent as 2000 did not detect these movements (Squires 2003), study designs should begin to incorporate methods that could detect coastal movements. Failing to account for these movements could limit researchers' abilities to identify processes such as range expansion, or population changes which are critically important to the management of imperiled species. Individuals in each river system should continue to be protected since we do not yet have a good understanding of the nature of interactions between populations. At the same time, where appropriate, managing populations regionally for research purposes would enable detection of coastal movements of shortnose sturgeon where they occur. This in turn will help to provide a higher degree of biological reality to data provided to managers.

REFERENCES

Caroffino, D.C., Sutton, T. M., and Lindberg, M. S. 2009. Abundance and movement patterns of age-0 juvenile lake sturgeon in the Peshtigo River, Wisconsin. Environmental Biology of Fishes 86: 411-422.

Cooch, E., and White, G. 2010. Program MARK: "a gentle introduction". Pages 5-1 to 5-40 Chapter 15: Goodness of fit testing….

Cooch, E., and White, G. 2010. Program MARK: "a gentle introduction". Pages 14-1 to 14-38 *in* Paul Lukacs, editor. Chapter 14: Closed population capture-recapture models.

Cooch, E., and White, G. 2010. Program MARK: "a gentle introduction". Pages 15-1 to 15-50 *in* William Kendall, editor. Chapter 15: The 'robust design'.

Dadswell, M. J., Taubert, B. D., Squiers, T. S., Marchette, D., and Buckley, J. 1984. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818. Washington D.C., National Oceanic and Atmospheric Administration.

Dinsmore, S. J., White, G. C., and Knopf, F. L. 2003. Annual survival and population estimates of mountain plovers in southern Phillips County, Montana. Ecological Applications 13: 1013-1026.

Fernandes, S. J. 2008. Population demography, distribution, and movement patterns of Atlantic and shortnose sturgeons in the Penobscot River estuary, Maine. M.Sc. thesis, Department of Ecology and Environmental Sciences, The University of Maine, Orono, ME.

Fernandes, S. J., Zydlewski, G. B., Zydlewski, J. D., Wippelhauser, G., Kinnison, M. T. 2010. Seasonal Distribution and Movements of Shortnose and Atlantic Sturgeon in the Penobscot River Estuary, Maine. Transactions of the American Fisheries Society 139: 1436-1439.

Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of closure assumptions. Ecology 80: 2517-2525.

Kendall, W. L., Nichols, J. D., and Hines, J. E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78: 563-578.

Pine, W. E., Pollock, K. H., Hightower, J. E., Kwak, T. J., and Rice, J. A. 2003.A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28:10-23.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of captures. The Journal of Wildlife Management 46: 752-757.

Powell, L. A., Conroy, M. J., Hines, J. E., Nichols, J. D., and Krementz, D. G. 2000. Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. Journal of Wildlife Management 64: 302-313.

Squiers, T. S. 2003. Completion Report: Kennebec River shortnose sturgeon population study 1998-2001. Maine Department of Marine Resources.

Zehfuss, K. P., Hightower, J. E., and Pollock, K. H. 1999. Abundance of Gulf sturgeon in Apalachicola River, Florida. Transactions of the American Fisheries Society 128: 130-143.