

# Understanding the basis of shortnose sturgeon (*Acipenser brevirostrum*) partial migration in the Gulf of Maine

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**Abstract:** Movement of shortnose sturgeon (*Acipenser brevirostrum*) among major river systems in the Gulf of Maine is common and has implications for the management of this endangered species. Directed movements of 61 telemetered individuals monitored between 2010 and 2013 were associated with the river of tagging and individual characteristics. While a small proportion of fish tagged in the Kennebec River moved to the Penobscot River (5%), a much higher proportion of fish tagged in the Penobscot River moved to the Kennebec River (66%), during probable spawning windows. This suggests that Penobscot River fish derive from a migratory contingent within a larger Kennebec River population. Despite this connectivity, fish captured in the Penobscot River were larger (~100 mm fork length) and had higher condition factors (median Fulton's *K*: 0.76) than those captured in the Kennebec River (median Fulton's *K*: 0.61). Increased abundance and resource limitation in the Kennebec River may be constraining growth and promoting migration to the Penobscot River by individuals with sufficient initial size and condition. Migrants could experience an adaptive reproductive advantage relative to nonmigratory individuals.

**Résumé :** Les déplacements d'esturgeons à museau court (*Acipenser brevirostrum*) entre les grands réseaux hydrographiques du golfe du Maine sont répandus et ont des répercussions sur la gestion de cette espèce en voie de disparition. Les déplacements dirigés de 61 individus dotés d'étiquettes téléométriques suivis de 2010 à 2013 ont été associés au fleuve où a eu lieu l'étiquetage et à des caractéristiques individuelles. Si une petite proportion des poissons étiquetés dans le fleuve Kennebec est passée au fleuve Penobscot (5%), une proportion beaucoup plus importante de poissons étiquetés dans le fleuve Penobscot est passée dans le fleuve Kennebec (66%) durant de vraisemblables fenêtres de frai. Cela donne à penser que les poissons du fleuve Penobscot sont issus d'un contingent migrateur d'une plus grande population du fleuve Kennebec. Malgré cette connectivité, les poissons pris dans le fleuve Penobscot étaient plus grands (longueur à la fourche : ~100 mm) et présentaient des facteurs d'embonpoint plus élevés (*K* de Fulton médian : 0,76) que les poissons capturés dans le fleuve Kennebec (*K* de Fulton médian : 0,61). Une abondance accrue et la limitation des ressources dans le fleuve Kennebec pourraient restreindre la croissance et promouvoir la migration vers le fleuve Penobscot d'individus de taille et d'embonpoint initiaux suffisants. Les migrants pourraient en tirer un avantage adaptatif sur le plan de la reproduction par rapport aux individus non migrants. [Traduit par la Rédaction]

## Introduction

Migratory behaviors displayed by fishes facilitate the tracking and use of transient resources over a lifetime (Dingle and Drake 2007). In many cases, migratory behaviors vary widely among individuals within populations, reflecting a “mixed” or “partial” migratory condition (Jonsson and Jonsson 1993; Dodson et al. 2013). While such partial migration patterns might arise from a degree of chance wandering of individuals within and among habitats, such patterns are more often thought to reflect a plastic, or “conditional”, life history strategy cued by individual (e.g., size, sex) or environmental (e.g., productivity) conditions (Jonsson and Jonsson 1993; Gross and Repka 1998; Thorpe et al. 1998). Implicit in this view is that partial migration has implications for the subsequent performance and fitness of individuals. The option to migrate or not often results in a change in “ecological status” of that subgroup within the population, resulting in differences in their relative growth, survivorship, and reproduction (Secor 2015).

As such, migratory and nonmigratory contingents may have differential contributions to overall population performance. In the present study, we consider the conditional basis of partial migration in an endangered sturgeon and what role migrants might contribute to overall population performance.

The “conditional” context of partial migration suggests that there are costs and benefits underlying both the propensity to remain resident or the propensity to migrate. While residency might be less energetically demanding and risky with respect to predator exposure (Bernatchez and Dodson 1987; Kusnierz et al. 2014; Secor 2015), migratory individuals may mitigate these costs by accessing more productive alternate habitats that facilitate greater growth (Naslund et al. 1993) and fecundity (Morita and Takashima 1998; Klemetsen et al. 2003). Such trade-offs within a conditional strategy suggest that both migratory and resident life histories can be adaptive, even where the individuals adopting these different life histories appreciate very different survival and fecundity outcomes. Ultimately, whether or not individuals adopting a strategy

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realize higher fitness than the alternative, these individuals must make the best of the situation defined by variable conditions. It is even possible for individuals to switch between migratory or resident behavior as conditions change (Bond et al. 2015).

While both migration and residency can be adaptive within a population, these life histories may contribute to population growth and stability in different ways. In partially migratory species where migrants access superior habitats and experience greater growth, they can realize much higher fecundity and contribute disproportionately to recruitment relative to residents (Kerr et al. 2009). On the other hand, in cases where migrants experience higher mortality or are forced into marginal habitats, they might play a comparatively minor role in population performance (Chapman et al. 2011). Reproductive contributions of different migratory life history types may also facilitate population stability in the face of variable environmental conditions (Kerr et al. 2010). Hence, the identification of residents or migrants is also important for anticipating how changing conditions and habitat availability (both local and distant) influence population outcomes.

Shortnose sturgeon (*Acipenser brevirostrum*) are known to move extensively within both rivers and estuaries (McCleave et al. 1977; Bain 1997; Kynard 1997). Shortnose sturgeon may range widely using upriver locations for spawning and much of the available freshwater and even brackish portions (where accessible) of the river during the remainder of the year (Kieffer and Kynard 1993; Bain 1997). However, these fish were not thought to leave their natal rivers. More recent work demonstrates that some individuals in some populations undertake extensive movements through marine environments to visit other coastal river systems (Fernandes et al. 2010; Peterson and Farrae 2011; Zydlewski et al. 2011, Dionne et al. 2013; Wippelhauser et al. 2015). In both the northern and southern extents of their range, these movements have been linked to spawning activities (Peterson and Farrae 2011; Dionne et al. 2013; Wippelhauser et al. 2015). In the northern part of the species' range, successful reproduction occurs in the Kennebec River (Wippelhauser and Squiers 2015). Conspicuously, no reproduction has been observed in the adjacent Penobscot River, despite an annual overwintering population of nearly 1000 adults (Lachapelle 2013). Acoustic telemetry of shortnose sturgeon captured in the Penobscot River clearly demonstrates that many adults including mature (bearing late-stage eggs) females move to the Kennebec River during the presumptive spawning period (Dionne et al. 2013; Wippelhauser et al. 2015; Johnston 2016).

These observations, combined with repeated failures to find sturgeon eggs or larvae in the Penobscot River (G. Zydlewski, unpublished data) and the absence of detectable genetic divergence between these two rivers (King et al. 2014), have led to the hypothesis that most, if not all, shortnose sturgeon captured in the Penobscot River originate from a Kennebec River source. Based on this hypothesis, we assessed sturgeon movements, demographic attributes, and condition factor to infer (1) whether partial migration is random or conditional, (2) the adaptive advantage (if any) in a lengthy movement through the marine environment, and (3) what role Penobscot River migrants play in the recovery of this endangered species.

To accomplish this, we used telemetry to monitor movements between the Kennebec and Penobscot rivers and compared multiple demographic parameters (length, age, proportion of mature females, growth, and Fulton's condition factor) for shortnose sturgeon from the two rivers. We apply these data to probable scenarios that underlie the propensity for some Kennebec River origin fish to migrate while others remain resident.

## Methods

### Capture and handling

Gillnetting protocols in the Kennebec River followed that of Wippelhauser and Squiers (2015). Briefly, long (90 m long, 1.8 or 2.4 m high, 30 m panels of 152, 178, and 203 mm mesh, all mesh stretch measure) and short (one or two 30 m panels of 152, 178, or 203 mm mesh, all mesh stretch measure) bottom-set experimental gill nets were used to capture adult shortnose sturgeon between 1977 and 2013. In the Penobscot River, bottom-set multifilament gill nets (50 or 100 m long, 2.4 m high, 152 or 305 mm mesh, all mesh stretch measure) were used to sample shortnose sturgeon between 2006 and 2013. Very few individuals were caught in 305 mm nets and only catch information from 152 mm nets was analyzed for comparative purposes with the Kennebec River.

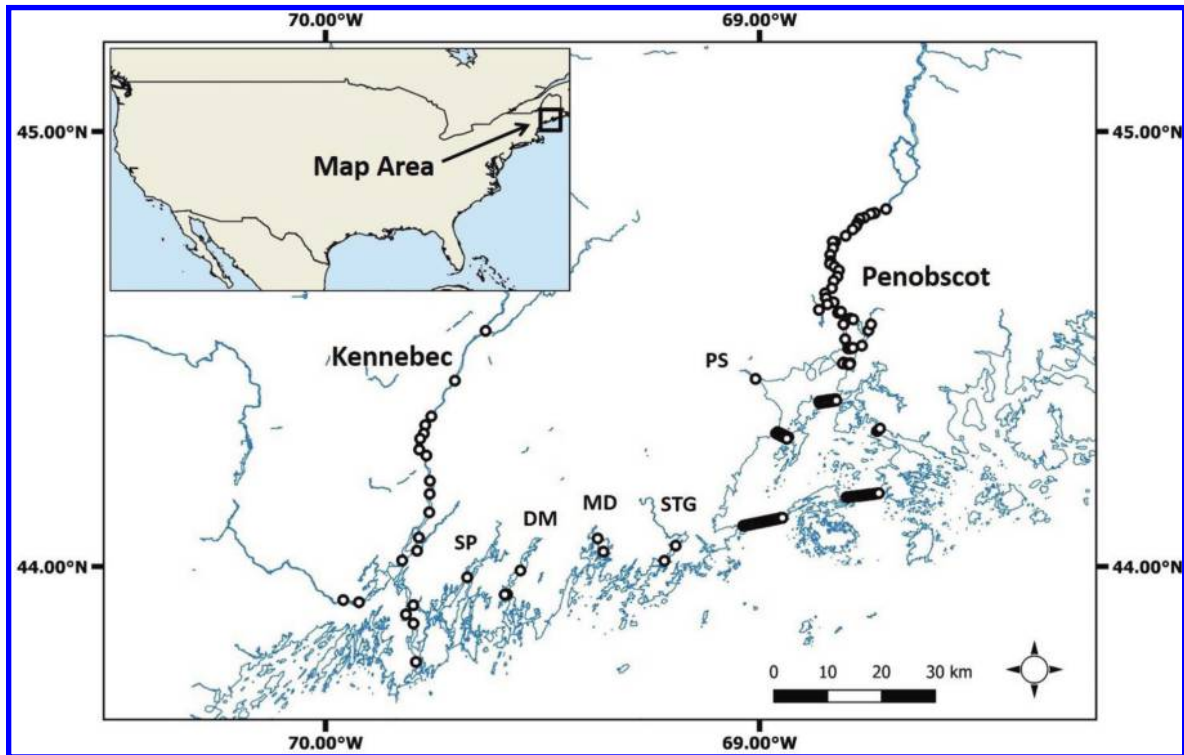
All fish captured from each river were measured for total length, fork length, mass (kilograms) and tagged externally (i.e., Carlin or Floy tag) and internally (passive integrated transponder (PIT)) if not previously marked. Sex was characterized in fish caught in the Penobscot River using a borescope (Kynard and Kieffer 2002) and classified as either mature female (when eggs were visible) or unknown (including males, post-spawn females, or immature females). Pectoral fin spine sections used for ageing purposes were removed from a subset of individuals captured in the Penobscot River in 2012 ( $n = 27$ ) and in both rivers in 2013 (Penobscot River  $n = 30$ , Kennebec River  $n = 33$ ). As suggested in Kahn and Mohead (2010), fin spine sections were taken as close to the point of articulation as possible (within 0.5 mm) while avoiding an artery at this location. A section no greater than 1 cm in length was removed from the leading pectoral fin spine on the left pectoral fin using a bonesaw and scalpel (Kahn and Mohead 2010). The removal site was disinfected with chlorohexidine (2.0%) upon procedure completion. All shortnose sturgeon were released at the location of capture immediately after handling was complete.

### Telemetry

Concurrent monitoring for shortnose sturgeon migrations between the Kennebec and Penobscot rivers was conducted from 2010 to 2013. Subsets of captured shortnose sturgeon were surgically implanted with acoustic transmitters in the Penobscot River ( $n = 36$ ) and Kennebec River ( $n = 25$ ) (Wippelhauser et al. 2015). Transmitters included Vemco coded models V13TP-1L, V13-1x, V16TP-4x, and V16-4x and had battery life expectancies of 723, 1006, 1825, and 2993 days, respectively. Individuals selected for surgical implantation with acoustic transmitters in the Kennebec River were greater than 55 cm total length and assumed to be adults (Wippelhauser et al. 2015). Transmitter implantation in fish caught in the Penobscot River targeted pre-spawning females based on borescopic examination. The surgical implantation method followed that in Dionne et al. (2013). Briefly, surgery was only performed on individuals that appeared in good condition, when water temperature was between 7 and 25 °C, and when dissolved oxygen was greater than 5.0 mg·L<sup>-1</sup>. All individuals undergoing surgery were anesthetized with MS-222 (buffered tricainemethanesulfonate). A 3–4 cm ventral incision allowed for transmitter insertion and was closed with internal and external sutures (Penobscot River) or just external sutures (Kennebec River). After surgery, individuals recovered for at least 15 min and were released at the location of capture.

Frequency of movement by tagged shortnose sturgeon was defined for individuals inhabiting or moving into the Kennebec River, Penobscot River, and four small coastal rivers in-between (i.e., Passagassawakeag River, Medomak River, St. George River, and Damariscotta River) (Fig. 1). In the Kennebec River, an array of 18–20 stationary Vemco acoustic receivers was maintained annually by the Maine Department of Marine Resources between 2012 and 2013 and covered river kilometres (rkm) 4.5–102 (Wippelhauser et al. 2015) (Fig. 1). Sturgeon considered to be leaving or entering

**Fig. 1.** Map of Gulf of Maine river systems where acoustic receivers were maintained to monitor movements of shortnose sturgeon (*Acipenser brevirostrum*). Bordered circles represent receiver locations. Small coastal rivers include the Sheepscot (SP), Damariscotta (DM), Medomak (MD), St. George (STG), and Passagassawakeag (PS). Map data: Quantum GIS Development Team (2017). QGIS Geographic Information System. Open Source Geospatial Foundation <http://qgis.osgeo.org>. [Colour online.]



the Kennebec River were able to do so at three locations, the mouth of the Kennebec River (rkm 4.5), at the confluence with the Back River (rkm 16), or at the confluence with the Sasanoa River (rkm 21). Acoustic receivers were positioned at all three of these potential exit/entrance points. For the Penobscot River and the four smaller coastal rivers, we used a framework similar to that outlined in Dionne et al. (2013) to characterize movements of shortnose sturgeon between 2010 and 2013. During this time, arrays of 121–122 stationary acoustic receivers (Vemco models VR2 and VR2W) were deployed in the Penobscot River and Penobscot Bay, while eight were deployed in the smaller coastal rivers: Passagassawakeag River ( $n = 1$ ), St. George River ( $n = 2$ ), Medomak River ( $n = 2$ ), and Damariscotta River ( $n = 3$ ) (Fig. 1). All receivers were deployed and cooperatively maintained by the University of Maine, the U.S. Geological Survey Maine Cooperative Fish and Wildlife Research Unit, and the National Oceanic and Atmospheric Administration (NOAA). The receiver array in the Penobscot River/Bay spanned from rkm 47 to 0 in the river between 2010 and 2013, from rkm 0 to –45 in the bay between 2010 and 2012, and from rkm 0 to –15 in 2013. An impassable dam (Veazie Dam) limited upriver movements of shortnose sturgeon in the Penobscot River to rkm 47 during this study.

Following the protocol described in Dionne et al. (2013), guidelines were used to delineate individuals and movements used in later analyses. Detections of an individual in any river system were considered valid if composed of multiple detections on a single receiver with no other detections recorded on any other receiver at the same time. Any tags found to be stationary for a period greater than 8 weeks between March and November were excluded from further analyses. Additional criteria were applied for assessing movements in the Kennebec River or Penobscot River. In the Kennebec River, individuals were considered migrants if they passed downstream of rkm 21, 16, or 4.5 and were subsequently detected on another receiver outside the Kennebec

River (e.g., in the Penobscot River or other river/bay system). Individuals were not considered Kennebec migrants if subsequently detected by any receiver upstream of rkm 4.5, 16, or 21 within 2 weeks of moving downstream of these points. Returning individuals were defined as those returning to the Kennebec River and moving upstream of rkm 4.5, 16, or 21 after previous designation as a mover. In the Penobscot River, only individuals that moved downstream of rkm 5 and were later detected outside Penobscot Bay (e.g., in the Kennebec River or other coastal river/bay system) (Zydlewski et al. 2011) were considered migrants for this analysis. Fish were not considered migrants from the Penobscot if detected upstream of rkm 5 within 2 weeks of initially moving downstream of that point. Returning fish were those moving upstream of rkm 5 in the Penobscot River after previously fulfilling the movement requirement above. Additional filtering criteria for Penobscot and Kennebec River detections (based on Dionne et al. 2013) excluded single detections greater than 20 rkm from a previous legitimate detection and tags not detected on three or more occasions within 10 rkm and 24 h.

#### Demographic correspondence

We compared the length–frequency distributions, mass at length, age, and growth between shortnose sturgeon captured in the Kennebec River and Penobscot River as metrics of demographic correspondence. With the exceptions of age and growth (which was calculated using individuals caught in multiple mesh sizes), we based comparisons on individuals captured in 152 mm mesh sizes at a specific location in each river system during the months of August through November in 2012 and 2013. This facilitated inter-system contrasts and controlled for effects of gear selectivity, environmental conditions, season, and reproductive status on size structure. The two sites, rkm 65 in the Kennebec River and rkm 36.5 in the Penobscot River, were chosen because they were adjacent to annual overwintering locations (Lachapelle 2013;



G. Wipfelhauser, unpublished data). Kolmogorov–Smirnov two-sample tests were used to test for differences in length–frequency distributions between rivers.

Mass at length relationships were developed for both the Kennebec and Penobscot rivers using  $\log_{10}$ -transformed mass and fork length (FL) to describe the allometric relationship

$$(1) \quad \text{Mass} = a(\text{FL})^b$$

where  $a$  is a constant and  $b$  is the allometric growth parameter. Analysis of covariance (ANCOVA) was used to examine differences in mass at length regression coefficients between rivers.

Pectoral fin spines were air-dried in the laboratory for at least 1 month prior to sectioning. Multiple thin sections (approximately 0.5 mm thick) were taken from each fin spine using an Isomet low-speed saw (Buehler, Lake Bluff, Illinois, USA) and diamond wafering blade. Fin spine annuli were enumerated visually with a compound microscope (SZ60, Olympus) using transmitted or reflected light under 30 $\times$  magnification. Glycerin was applied to increase the clarity of the annuli. Annuli were identified as a pair of translucent and opaque zones as observed in previous studies (Brennan and Cailliet 1989; Jackson et al. 2007). Two readers aged samples using the double-blind procedure described by Everett et al. (2003). This approach resulted in the exclusion of three of 57 fin spines from the Penobscot River and 2 of 33 from the Kennebec River when readers were unable to establish an agreed upon age after three attempts.

An initial comparison of growth between rivers used recapture of marked fish to calculate change in fork length over time (Hamel et al. 2014). Recapture data from 1977–2013 and 2006–2013 were used for the Kennebec and Penobscot rivers, respectively. A more contemporary comparison using this method was not possible because of the low number of recaptures that occurred in the Kennebec River between 2009 and 2013. To control for differences in initial size at tagging and gear selectivity, individuals were binned according to fork length at tagging (50 mm fork length bins) using only fish initially caught in 152 mm mesh nets.

Growth comparisons between rivers were also carried out based on von Bertalanffy growth curves. Although a von Bertalanffy growth curve for shortnose sturgeon caught in the Kennebec River was previously developed ( $L_\infty = 938$  mm,  $k = 0.098$ ,  $t_0 = -3.89$ ) (Squiers and Smith 1979; Dadswell et al. 1984), none was available for the Penobscot River. Therefore, we developed von Bertalanffy curves for both rivers based on fin spine age at length data from individuals caught in 2012 and 2013. Due to low sample sizes, and an inability to sample shortnose sturgeon younger than 6 years of age in either river system, we combined fin spine age at length data from both rivers and only included year-classes with multiple observations (7–8 and 10–19 years). We then estimated a “global” von Bertalanffy model using an iterative solving procedure that minimized the residual sum of squares (SOLVER Microsoft Excel) based on the equation

$$(2) \quad L_{t+1} = L_\infty(1 - e^{-k(t-t_0)})$$

Using the fixed global  $t_0$  (or the theoretical time when length equals 0) value, we optimized estimates of  $L_\infty$  (theoretical maximum fork length) and  $k$  (Brody growth coefficient) for both rivers separately.

Additionally, we developed a second von Bertalanffy growth curve for the Penobscot River using the mark–recapture-based change in length approach of Fabens (1965). Individuals used in the model had been at large for at least one winter or 180 days (Nitschke et al. 2001) and displayed positive growth. Fork length at marking ( $M_i$ ), recapture ( $R_i$ ), and the time at large ( $\Delta t_i$ ) of the  $i$ th individual were collated for shortnose sturgeon caught between

2006 and 2013 in the Penobscot River and used to estimate the von Bertalanffy parameters  $L_\infty$  and  $k$ . We utilized the iterative solving procedure that minimizes the residual sum of squares (SOLVER Microsoft Excel) to estimate  $L_\infty$  and  $k$  given the following equation:

$$(3) \quad R_i = M_i + (L_\infty - M_i)(1 - e^{-k\Delta t_i})$$

The theoretical time at which length would be zero ( $t_0$ ) is not estimated using this model. Therefore,  $t_0$  was estimated for the Fabens model (Hamel et al. 2014, 2015) using the formula in Pauly (1979):

$$(4) \quad \log(-t_0) = -0.3922 - 0.2752\log L_\infty - 1.038\log k$$

#### Fulton’s condition factor

Fulton’s condition factor ( $K$ ) was calculated for shortnose sturgeon captured using 152 mm mesh in the Kennebec River and Penobscot River using the equation

$$(5) \quad K = \left(\frac{M}{\text{FL}^3}\right) \times 10^5$$

where  $M$  is mass (grams) and FL is fork length (millimetres). Fulton’s condition factor was compared between rivers for fish captured when data temporally overlapped (2012 and 2013) and within rivers for longer-term comparisons (Kennebec River 1977–1981 and 2012–2013; Penobscot River, 2006–2009 and 2010–2013).

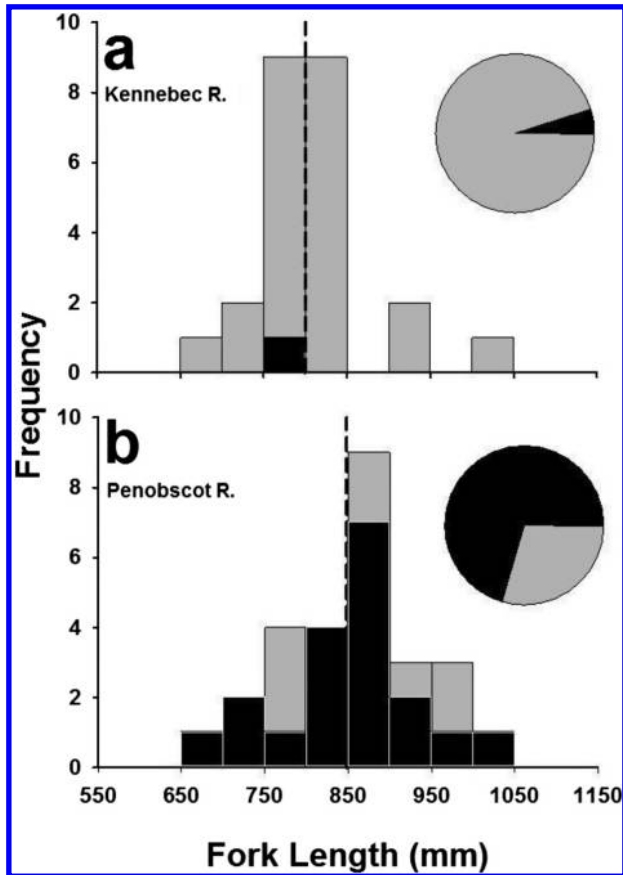
## Results

### Telemetry

Adult shortnose sturgeon tagged in the Kennebec and Penobscot rivers demonstrated different patterns of movement from the river of original capture. Between 2010 and 2013, only one tagged individual from the Kennebec River moved to a different river, while 19 individuals from the Penobscot River moved to another river. The single Kennebec River fish moved to the Damariscotta River and remained there for 23 days (25 May to 20 June 2012) and again for 42 days (25 May to 13 August 2013) the next year. When not in the Damariscotta River, this individual moved throughout the Kennebec River in both years. It is notable that only four additional Kennebec River fish were removed from the analysis based on our data criterion. Two moved downriver past rkm 16 but were not detected again. A third was solely detected 1 week after tagging, while the fourth had single detections in 2012 and 2013. Excluding these fish, only 5% of acoustically tagged individuals left the Kennebec River, i.e., frequency of emigration from the Kennebec River was low and consistent with additional physical recapture and PIT tag identification. Only seven out of 1089 shortnose sturgeon PIT tagged in the Kennebec River (1998–2000) were opportunistically recaptured in the Penobscot River between 2007 and 2013 (out of 1210 capture events); four were recaptured once in the Penobscot River, two were captured twice, and one was recaptured five times. In stark contrast, shortnose sturgeon tagged in the Penobscot River demonstrated a greater propensity to leave their system. Eighteen fish tagged in the Penobscot River moved into the Kennebec River. Two other fish left the Penobscot River and were detected exclusively in adjacent small coastal river systems (e.g., one only in the Sheepscot River and the other only in the Damariscotta River).

Individuals emigrated from the Penobscot River in the spring (March through May,  $n = 12$ ), the summer (June through August,  $n = 1$ ), and fall (September through November,  $n = 7$ ). However, the temporal pattern of movement was not always consistent among years for an individual. One tagged female left the Penobscot River in April 2011 for the Kennebec River and returned in May of

**Fig. 2.** Fifty millimetre length–frequency bin distributions for shortnose sturgeon (*Acipenser brevirostrum*) caught and tagged with acoustic transmitters in the (a) Kennebec River and (b) Penobscot River. Gray bars represent all tagged individuals and black bars represent tagged individuals documented leaving the river of tagging. Pie charts represent the proportion of tagged individuals that did (black) or did not (gray) leave the river of tagging.



the same year only to emigrate to the Kennebec River again in October of the following year (2012). This individual then subsequently returned to the Penobscot River in May 2013. In both years, this individual was detected at a known spawning location near Brunswick, Maine, on the Kennebec River.

Movements from the Penobscot River to the Kennebec River, a distance of approximately 150 km, on average took 12.0 days (range 8–18 days) in spring and 13.2 days (range 9–23 days) in fall. The single summer emigrant moved to the Damariscotta River over a period of 6 days in August. Regardless of movement timing or speed, all but one individual returned to the Penobscot River taking on average 15.1 days to do so (range 9–34 days). Return movements occurred in the spring ( $n = 6$ ) and summer ( $n = 6$ ) of the same year that individuals left the Penobscot River. Fall emigrants returned the following spring ( $n = 5$ ) or summer ( $n = 2$ ). The one individual that did not return was not subsequently observed in any of the monitored rivers after initially leaving the Penobscot River.

Sex was confirmed in only eight of 25 shortnose sturgeon tagged with acoustic transmitters in the Kennebec River. Six were identified as female and two were identified as male. In the Penobscot River, 16 of 29 individuals tagged with acoustic transmitters were identified as females. Although the length range of individuals with acoustic transmitters was similar between the two rivers, the mean length of acoustically tagged fish in the Kennebec River (mean = 800 mm) (Fig. 2a) was shorter than that in

the Penobscot River (mean = 848 mm) (Fig. 2b) ( $t$  test  $t = 2.49$ ,  $df = 59$ ,  $p = 0.025$ ).

### Demographic correspondence

Differences in length–frequency distributions were observed between shortnose sturgeon captured in the Kennebec River and Penobscot River. Between August and November in 2012 and 2013, 111 shortnose sturgeon were captured in the Kennebec River and 189 were captured in the Penobscot River. Although size ranges were similar, length–frequency distributions were found to differ (Kolmogorov–Smirnov  $D = 0.621$ ,  $p < 0.001$ ) with a smaller median fork length observed in the Kennebec River (median = 701 mm, range = 568–914 mm) (Fig. 3a) than in the Penobscot River (median = 811 mm, range = 625–1112 mm) (Fig. 3b).

Differences between mass at length relationships from both river systems were significant (Kennebec River:  $R^2 = 0.76$ ,  $p < 0.001$ ; Penobscot River:  $R^2 = 0.87$ ,  $p < 0.001$ ) and illustrate that shortnose sturgeon caught in the Kennebec River have a lower mass at a given fork length than individuals caught in the Penobscot River (Fig. 3c). No differences in mass at length allometric slopes were observed (ANCOVA  $p = 0.750$ ) but intercept values differed (ANCOVA  $p < 0.001$ ). On average, mass at a given fork length was 18.9% lower for individuals caught in the Kennebec River than those from the Penobscot River (Fig. 3c).

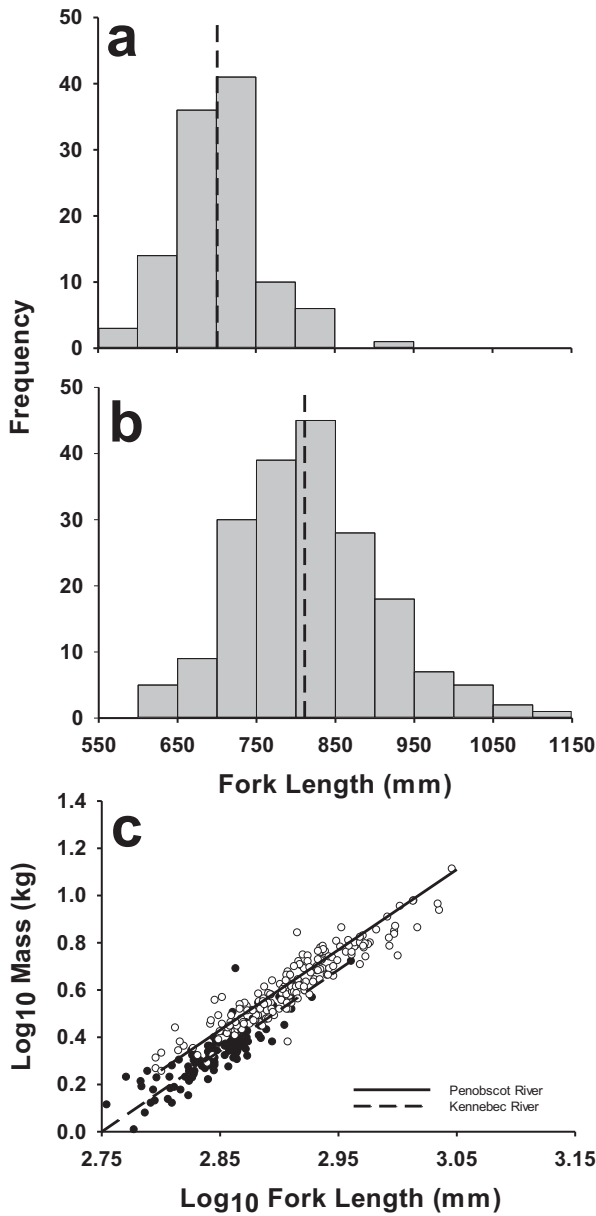
The estimated ages of sampled shortnose sturgeon were similar between rivers. Fin spine ages ranged from 7 to 20 years (mean =  $12.7 \pm 3.3$  years) for fish from the Kennebec River and from 6 to 22 years (mean =  $12.8 \pm 3.0$  years) for fish from the Penobscot River. Median age was 13 years in both rivers and a Mann–Whitney rank sum test revealed no significant difference in median age between the Kennebec and Penobscot rivers ( $T = 1435$ ,  $p = 0.884$ ). Within all length bins, shortnose sturgeon caught and recaptured in the Kennebec River grew slower than fish caught and recaptured in the Penobscot River (Fig. 4a).

The von Bertalanffy model including fin spine age at length data from both rivers resulted in a fixed  $t_0 = -7.741$  ( $L_\infty = 1152$  mm,  $k = 0.057$ ,  $t_0 = -7.741$ ). River-specific optimizations of  $L_\infty$  and  $k$  under the fixed  $t_0$  illustrated that Kennebec River shortnose sturgeon reached a lower asymptotic fork length and had a higher Brody growth coefficient ( $L_\infty = 877$  mm,  $k = 0.099$ ,  $t_0 = -7.741$ ) than fish in the Penobscot River ( $L_\infty = 1325$  mm,  $k = 0.046$ ,  $t_0 = -7.741$ ) (Fig. 4b). Application of the Fabens recapture method to a total of 183 recapture events (216 total recapture events minus 33 events with negative growth) recorded from the Penobscot River between 2006 and 2013 resulted in a von Bertalanffy growth relationship parameterized as  $L_\infty = 990$  mm,  $k = 0.128$ ,  $t_0 = -0.51$ ;  $R^2 = 0.43$ ,  $p < 0.001$  (Fig. 4c).

### Fulton's condition factor

Shortnose sturgeon caught in the Kennebec River were more slender than those caught in the Penobscot River when fish in both rivers were captured from 2012 to 2013. The condition factor of Kennebec River fish was markedly lower (median  $K = 0.61$ ) than in the Penobscot River (median  $K = 0.76$ ; Mann–Whitney  $U = 2473.0$ ,  $p < 0.001$ ) (Fig. 5a). However, condition changed over time in the Kennebec River, with fish being more plump between 1977 and 1981 (median  $K = 0.82$ ) and more slender decades later (2012–2013) when median condition factor was 0.61 (Mann–Whitney  $U = 1446$ ,  $p < 0.001$ ) (Fig. 5a). Although on a shorter time scale, condition of shortnose sturgeon caught in the Penobscot River also decreased over the periods sampled that approximated decadal comparisons in this river (2006–2009 and 2010–2013) from a median of 0.80 to 0.76, respectively (Mann–Whitney  $U = 41263$ ,  $p = 0.002$ ). This general pattern was also observed when Fulton's condition factor was examined on an annual basis from 2006 to 2013 in the Penobscot River (Kruskal–Wallis  $p < 0.001$ ), although annual variability in the metric makes the results noisier (Fig. 5b). Nonetheless, the change in Fulton's condition factor in the Penob-

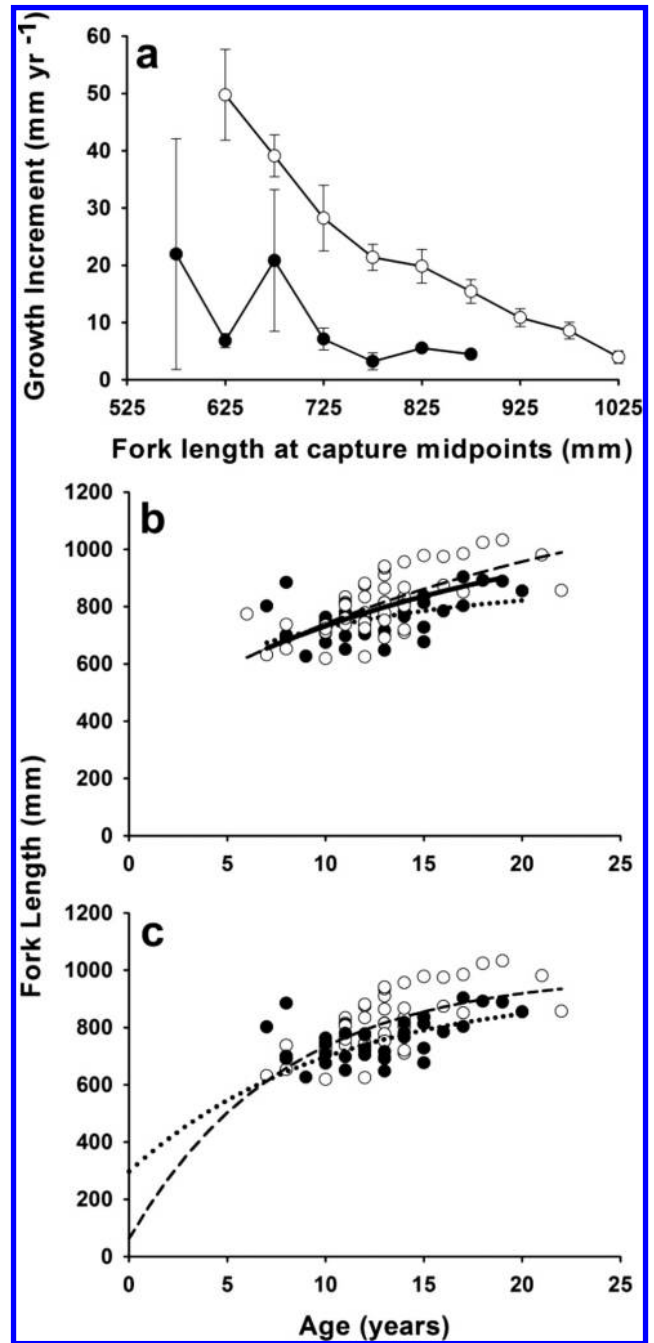
**Fig. 3.** Fifty millimetre fork length–frequency bin distributions for all shortnose sturgeon (*Acipenser brevirostrum*) caught in 152 mm mesh in the (a) Kennebec River and (b) Penobscot River between August and the end-of-year in 2012 and 2013. Median fork lengths (dashed vertical lines in Figs. 3a and 3b) were 701 and 811 mm for the Kennebec and Penobscot rivers, respectively. (c)  $\text{Log}_{10}$  mass at length relationship comparisons between rivers (Fig. 3c). A significant difference in regression y-intercepts was observed but not in slope.



scot River represents a much smaller decrease (2.5%) than the decline observed over the longer period in the Kennebec River (25.6%).

While only one shortnose sturgeon acoustically tagged in the Kennebec River was detected outside the Kennebec River between 2010 and 2013, seven shortnose sturgeon originally PIT tagged in the Kennebec River in 1998 ( $n = 1$ ), 1999 ( $n = 2$ ), and 2000 ( $n = 4$ ) were recaptured in the Penobscot River between 2007 and 2013. Three of these were recaptured in the Penobscot River during 2012 and 2013 (one fish was captured twice), facilitating a concurrent comparison (admittedly with low sample size) of condition with fish in the Kennebec River. These three fish had higher condition (me-

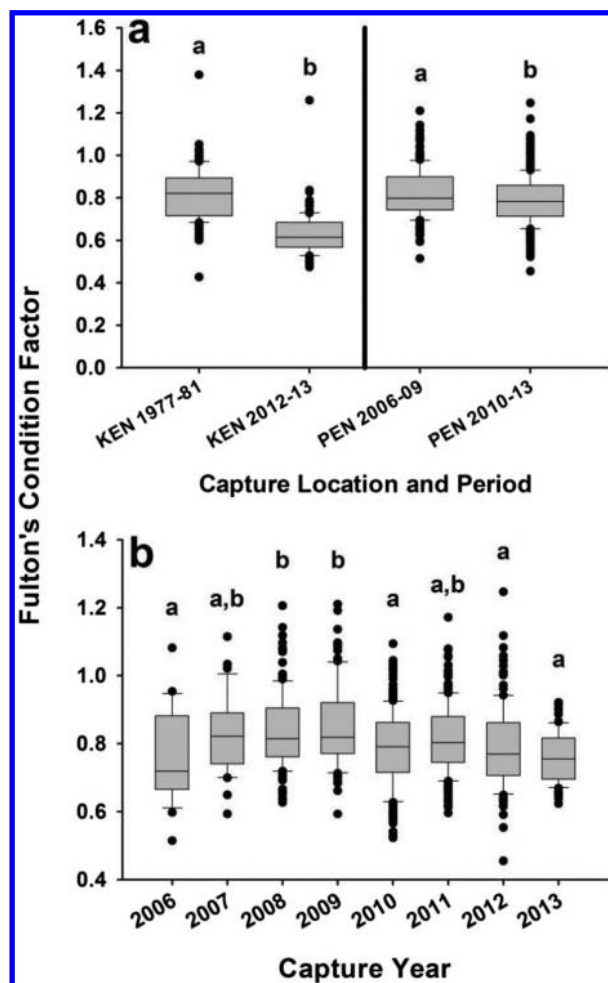
**Fig. 4.** (a) Shortnose sturgeon (*Acipenser brevirostrum*) growth (mean  $\pm$  SE) formatted as change in fork length bins over time in the Kennebec River (1977–2013 solid circles) and the Penobscot River (2006–2013, open circles). (b) von Bertalanffy growth curves parameterized using fin spine length at age data from 2012 to 2013 in both rivers (solid line), the Kennebec River (solid circles, dotted line), and the Penobscot River (open circles, dashed line). (c) Additional von Bertalanffy models for the Kennebec River based on estimates by Squiers and Smith (1979) (dotted line) and for the Penobscot River based on the recapture-based Fabens approach (dashed line). Models overlay fin spine age at length data for both rivers.



median  $K = 0.91$ ) than fish in the Kennebec River in 2012–2013 (median  $K = 0.61$ ; Mann–Whitney  $U = 52.0$ ,  $p = 0.002$ ). The four other visitors to the Penobscot River (recaptured from 2007 to 2011) also had higher condition factors at the time of recapture (median



**Fig. 5.** (a) Median Fulton's condition factor for individual shortnose sturgeon (*Acipenser brevirostrum*) caught in the Kennebec River (KEN) between 1977 and 1981 and between 2012 and 2013 and the Penobscot River (PEN) between 2006 and 2013. (b) Annual median Fulton's condition factor for fish caught in the Penobscot River between 2006 and 2013. Each box delimits the 25th and 75th percentiles with the median line falling in the middle. Error bars denote the 10th and 90th percentiles and circles represent outliers. Letters (a and b) denote significant differences between or among median values of Fulton's condition factor within each comparative analysis pair (separated by a vertical line).



$K = 0.89$ ) than observed in Kennebec River fish from 2012 to 2013 (Mann-Whitney  $U = 336.5$ ,  $p < 0.001$ ).

## Discussion

Given the potential risks and energetic costs of an extensive marine migration, repeated movements of shortnose raises questions concerning individual and population consequences. Recent (2010–2013) telemetry and recapture analyses indicate that movement patterns between the Kennebec and Penobscot rivers are an ongoing feature of this system. Furthermore, the tendency for individuals in the Penobscot River to be larger (~100 mm), grow faster (e.g., greater change in fork length over time), and have higher condition factors (25%) than those in the Kennebec River implies a growth benefit to undertaking this migration. This benefit may offset the costs of migration for at least some shortnose sturgeon migrating through the Gulf of Maine. Moreover, the greater growth and size of these fish are expected to result in higher fecundity (Dadswell 1979). As such, these migrants may

contribute more to population productivity than indicated by their relatively low representation in the population.

Between 2010 and 2013, 66% of all individuals tagged with acoustic transmitters in the Penobscot River emigrated and were detected in the Kennebec River. This is similar to the estimate of 70% noted by Dionne et al. (2013) several years earlier. In addition, females with late-stage eggs had much higher odds of emigrating from the Penobscot River than other individuals (Dionne et al. 2013) and were frequently detected in the vicinity of spawning grounds in the Kennebec River (Wippelhauser et al. 2015). This circumstantial evidence suggests that these movements to the Kennebec River are associated with spawning. However, that high movement rate is not mirrored, proportionally speaking, by movements from the Kennebec River to the Penobscot River. This is evidenced by the documentation of only one of 25 individuals originally acoustically tagged in the Kennebec River being detected outside this river, although this individual never entered the Penobscot River. McCleave et al. (1977) also documented extensive in-estuary movements, but no fully marine excursions, of 14 shortnose sturgeon (total length range 70–116 cm) tagged with acoustic transmitters in Montsweag Bay, an estuary directly connected to the Kennebec River. While it is possible that the targeted tagging of female shortnose sturgeon in the Penobscot River contributed to relatively high observed rates of emigration, it is most likely an underestimate. A lack of evidence for spawning in the Penobscot River would indicate that mature males in that system most likely also emigrate to successfully reproduce. Males, unlike females, however, could not be classified using the boreoscopic techniques applied in this study. Because males have a greater spawning frequency than females (Dadswell et al. 1984), any estimate of emigration based primarily on female movements would likely be an underestimate.

Several lines of evidence underpin the assertion that the movements of sturgeon were highly directed and conditional rather than the random (i.e., product of indiscriminate wandering). First, fish that moved between these river systems spent a very small proportion of their time in the marine environment (days to weeks) relative to the time spent in the river systems themselves (months to years) (Zydlowski et al. 2011; Dionne et al. 2013). Moreover, this movement is extensive (150 km), and although swimming performance has not been directly assessed in adult shortnose sturgeon, swimming performance (i.e., speed and endurance) does appear to be conditional based on size in lake sturgeon (Peake et al. 1997). Second, Penobscot River emigrants did not wander to other river systems but consistently moved to the Kennebec system. And third, and perhaps most importantly, these movements were typically round trips (i.e., not random) and, within the limits of our data set, repeated. The majority of shortnose sturgeon that departed the Penobscot River for the Kennebec River returned to the Penobscot River within weeks to months and one sturgeon repeated this round trip in more than one year.

But what of the partial nature of partial migration, in the sense that not all individuals undertake a migration? While we do know that a very modest proportion of PIT-tagged individuals (seven recaptures out of approximately 1089) moved from the Kennebec River to the Penobscot River, such movements are clearly not a regular part of the life histories of all Kennebec River individuals. Given the asymmetry in estimated abundances of shortnose sturgeon inhabiting these two rivers (approximately 9436 versus 1277) (Wippelhauser and Squiers 2015; Dionne 2010), only a modest proportion of the shortnose sturgeon moving from the Kennebec River would be able to account for most (or all) of the fish observed in the Penobscot River. The same might be said of fish moving from the Kennebec River to other rivers in the Gulf of Maine (e.g., Saco and Merrimack rivers) (Wippelhauser et al. 2015). Empirically, we know that most shortnose tagged in the Kennebec system are tracked and recaptured within that same river. Thus, it seems likely that the Kennebec River population consists of a

dominant contingent of resident fish and a lesser contingent of migrant individuals.

The relative dominance of migrant and resident individuals in different river systems presents an opportunity to examine demographic differences in fish size and condition. Full demographic correspondence represents a null expectation consistent with nonconditional and pervasive movements (Koizumi 2011). Taking into account the directed movements, the lack of demographic correspondence that we observed might be expected if (i) the two systems afford different ecological opportunities for growth and conditioning or (ii) movement is conditional with respect to some attribute of the individuals that migrate. This brings us to considering the potential causes and consequences of partial migration in these rivers.

Fishes depend on many different cues that might elicit migration or residency, but most theory suggests that cues tied to growth opportunities are important (Chapman et al. 2011; Gillanders et al. 2015). For many populations, the local density of conspecifics and associated intensity of intraspecific competition is a major determinant of growth potential (Olsson and Greenberg 2004). This is a plausible scenario for shortnose sturgeon when considering historical changes in abundance and the physical environment in the Kennebec River. Mean abundance estimates for shortnose sturgeon in the Kennebec River have increased dramatically over recent decades, from 5177 individuals (95% CI 4206–6279) between 1977 and 1981 to 9436 individuals (95% CI 7542–11 888) between 1998 and 2000 (Wippelhauser and Squiers 2015). In 1999, the removal of the Edwards Dam on the main stem of the Kennebec River opened up an additional 29 km of habitat that resulted in a new spawning area and possibly facilitated even further recruitment into this river (Wippelhauser et al. 2015). This change did not, however, increase the effective amount of preferred estuarine foraging habitat, as the Edwards Dam was located at the tidal limit of the upper Kennebec River estuary (Wippelhauser and Squiers 2015). Coincident with increases in abundance, our examination of historical trends illustrates a substantial decline in condition factor (25.6%), a surrogate for nutritional status, over the last three decades (Fig. 5). Such trade-offs between density and condition are very common in both marine and freshwater systems (Rose et al. 2001).

With changes in competitive environments, there would of course be greater opportunities for some individuals to benefit from seeking resources elsewhere and perhaps gain an adaptive advantage. An association between competition for food resources and propensity for partial migration is well known for other fishes. For example, in brown trout (*Salmo trutta*), both relatively high fish density (Olsson and Greenberg 2004) and low food availability (O'Neal and Stanford 2011) are correlated with higher rates of migratory behavior. If migration is similarly influenced in shortnose sturgeon, then a conditional migratory strategy would be an adaptive means to make the “best of a bad situation.” Because the Penobscot River has a lower abundance of shortnose sturgeon than the Kennebec River, it is likely that greater feeding opportunities are available there. Shortnose sturgeon abundance in the Penobscot River was recently estimated at 1277 (95% CI: 992–1562) (Dionne 2010) between 2008 and 2011. This is only 14% of the estimated abundance in the Kennebec River. Thus, even though the Penobscot River estuary (by river kilometres) is shorter (35%) than the Kennebec River estuary (Fernandes et al. 2010; Wippelhauser et al. 2015), more habitat may be available per capita in the Penobscot River. Very few shortnose sturgeon were captured or observed in the Penobscot River prior to the initiation of University of Maine surveys in the last decade (Dadswell et al. 1984). These observations lead to the hypothesis that the Penobscot River environment imposes less intraspecific competition and greater scope for growth. This idea is supported by the higher condition factor observed in fish captured in the Penobscot River versus the Kennebec River (median 0.76 versus 0.61) (Fig. 5). However, the greater growth

opportunities in new habitats are not without bounds, and recent condition factor data suggest that the advantages in the Penobscot River may be declining. Condition factors have decreased slightly (0.80 to 0.78) from the 2000s (2006–2009) to the 2010s (2010–2013). Nonetheless, Fernandes et al. (2010) demonstrated that shortnose sturgeon spend approximately 3 months in an area of the river known to support exceptionally high densities of infaunal invertebrates dominated by spionid polychaete worms (mean density = 3075–4150 individuals·m<sup>-2</sup>) (M. Dzaugis and G. Zydlewski, unpublished data). These polychaetes dominate shortnose sturgeon diets in this area (G. Zydlewski, unpublished data). Improved quantitative information on the diets and prey availability for shortnose sturgeon in both the Kennebec River and Penobscot River would be instructive in more rigorously assessing this hypothesis of competition-linked migration.

While the use of larger-mesh gill nets (178 and 203 mm) in the Kennebec River could have influenced our analysis by biasing the growth curve “down” via selection of older, slower-growing individuals (e.g., the Lee’s phenomenon) (Lee 1912; Ricker 1969), differences in length–frequency, mass at length, and recapture-based changes in length indicate that this did not influence the results. Median fork length, mass at length, and recapture-based growth were all lower in fish caught in the Kennebec River than those caught in the Penobscot River when using equivalent gear (152 mm mesh). Thus, potential growth differences anticipated by the von Bertalanffy growth models derived for the Kennebec River (Squiers and Smith 1979; Dadswell et al. 1984) and Penobscot River (Fabens based) were substantiated by catch data standardized by mesh size.

Migration to the Penobscot River could possibly be an adaptive advantage for individuals able to make the trip if growth increases result in increased reproductive potential. Greater growth strongly influences mass at length relationships, which in turn are tied to greater fecundity and potentially greater relative fitness (Dodson et al. 2013). Importantly, both von Bertalanffy growth curves for Kennebec River shortnose sturgeon indicate that these fish achieve a lower asymptotic fork length than those in the Penobscot River. Growth differences between the two rivers could result in substantial divergence in gonadal investment, particularly for females in each river. Considering the growth models (above), and assuming a constant fecundity–mass relationship for shortnose sturgeon (i.e., 11 585 eggs/kg body mass) (Dadswell et al. 1984), a 20 year old female migrating to the Penobscot River could realize a 31% increase in fecundity.

Although migrants to the Penobscot River may be a small proportion of the Kennebec River population, they could disproportionately contribute to regional recruitment and facilitate population resilience to disturbance. For example, simulated intrapopulation resilience of white perch (*Morone americana*) in the Patuxent River increased with increasing representation of the more productive dispersive contingent (Kerr et al. 2010). The authors postulated that while successful recruitment by the dispersive contingent was periodic, the increased productivity of this contingent relative to the resident contingent facilitated greater population resilience (Kerr et al. 2010). This mechanism may also be relevant to shortnose sturgeon of the Kennebec River population considering the likelihood of differential reproductive contributions based on physical size differences. Further biological data from known female shortnose sturgeon inhabiting the Kennebec River, and potential genetic assignment of larval production to parents, might provide further means to assess the relative recruitment contributions of fish based on movement patterns.

While our data do not directly assess how fish size or condition factor influences the odds that shortnose sturgeon will adopt a migratory life history in the first place, we do know that sturgeon movements at other life stages are tied to fish characteristics (Trested et al. 2011; Dionne et al. 2013). Specifically, Dionne et al. (2013) demonstrated that larger female shortnose sturgeon were



more likely to emigrate from the Penobscot River to the Kennebec River within the first year after capture than smaller individuals of unknown sex. Likewise, there are reasons to suspect that larger size and higher condition factor would be beneficial to enabling marine migrations by shortnose sturgeon. Shortnose sturgeon do not tolerate full-strength seawater as juveniles (Jenkins et al. 1993; Jarvis and Ballantyne 2003) and salinity tolerance of sturgeon is linked to larger body size (Zydlewski and Wilkie 2013). Larger fish are also expected to be more efficient at swimming longer distances and face lower risks from predators. Indeed, sturgeon species that are more commonly considered marine migrants, such as the Atlantic sturgeon (*Acipenser oxyrinchus*), are comparatively large and range more widely in marine habitats as they grow (Bain 1997). The minimum distance traversed by shortnose sturgeon between the Penobscot River and the Kennebec River is estimated at 150 km, a movement that takes between 8 and 34 days in marine environments, depending on the season of movement.

We do not know the actual energetic cost of such a movement, but behaviors during this migration are consistent with mechanisms to help offset energetic costs. These fish intermittently move into small coastal estuaries between the major rivers (Zydlewski et al. 2011) in a fashion that might facilitate feeding opportunities. Indeed, marine migrations have not been documented in parts of the species' range where large rivers are further separated and small estuaries are less common. The predation risks to shortnose sturgeon in marine environments are largely unknown, but one known predator, the gray seal (*Halichoerus grypus*) (Fernandes 2008), is most common in coastal areas.

Our research currently operates under the tentative assumption that reproduction does not occur in the Penobscot River. Nearly a decade of effort to capture early life stage shortnose sturgeon in the Penobscot River has been unsuccessful and the proportion of tracked Penobscot River fish that return to the Kennebec River is high. Nonetheless, absence of data is not proof of absence and we must allow that spawning might occur at low levels or intermittently in this system. New capacity to discriminate natal origins based on chemical proxies in dorsal scutes could help to resolve this possibility (Altenritter et al. 2015). Even if such reproduction does not presently occur, it might someday be initiated by the types of conditional migrants that we have described, thereby facilitating population recovery of this species in the Gulf of Maine. The combination of greater growth opportunities in the Penobscot River and the ability of shortnose sturgeon to access those resources without migration might be expected to quickly facilitate the establishment of such a population. Recent success in restoring access to potential historic spawning habitat in the Penobscot River (Opperman et al. 2011; Trinko Lake et al. 2012) greatly increases potential for such an outcome.

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