A Population Model to Assess Influences on the Viability of the Shortnose Sturgeon Population in the Ogeechee River, Georgia

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Published online: 09 Apr 2013.

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Abstract

Southern populations of the federally endangered Shortnose Sturgeon *Acipenser brevirostrum* are considered to be at greater risk of extirpation than northern populations. Our study focused on the Ogeechee River, Georgia, a small, undeveloped, coastal river that supports a population with fewer than 300 Shortnose Sturgeon. We designed a population viability analysis (PVA) model to represent and quantify the demographic influences of three factors (poor water quality, intrusion of saline water via rice canals, and incidental harvest) on the viability of this population. As an isolated population, only 75% of simulated populations persisted beyond a 20-year time horizon with all factors simulated. However, immigration from the Altamaha River may help to support the population. We quantified population persistence with and without simulating each factor and found that (1) incidental harvest had no effect on simulated persistence, (2) poor water quality decreased simulated persistence by 29%, primarily due to low oxygen conditions in summer, and (3) roughly one-third of this effect was attributed to rice canals (premature exposure of juveniles to high salinities). Simulated recruitment to age 1 was limited by a habitat squeeze between density-dependent starvation upstream near the spawning grounds and premature exposure to salinity downstream. These results highlight a need for research on availability of summer refuge and freshwater rearing habitat. As these results derived from a PVA model, which required many assumptions, they should be considered preliminary. Further field research is needed to confirm those results where it is possible to test intermediate predictions. We conclude by suggesting that efforts to maintain or increase the number of viable populations of Shortnose Sturgeon in southern U.S. rivers will probably require an understanding of (1) source-sink dynamics between populations in rivers with access to adequate freshwater rearing habitat and those without, and (2) the effects of climate change.

Diadromous fishes, including sturgeons, are considered at particular risk of extirpation for several reasons. As long-distance migrants, they require access to multiple habitats: rivers, estuaries, and oceans. Degradation of any of these habitats or barriers that prevent movement between habitats poses a significant threat (Limburg and Waldman 2009). In addition,

life history traits, especially large size and infrequent breeding events, correlated with migration of capital-breeding fishes further increase risk (Jager et al. 2008).

Populations of the species of concern here, Shortnose Sturgeon *Acipenser brevirostrum* inhabit large coastal rivers from the Saint John River, New Brunswick, to the St. Johns River, Florida (Cooke and Leach 2004). In contrast to the Atlantic Sturgeon *A. oxyrhinchus* this species does not travel far into the marine environment. Adults spawn in their natal rivers and juveniles remain in freshwater for 1 or 2 years before moving downstream to the estuary. The saltwater–freshwater interface seems to be a preferred area for feeding (Kynard 1997).

Protection for the Shortnose Sturgeon was initiated in 1966, and for 19 population segments in 25 U.S. rivers (SSRT 1998). Populations in southern rivers are considered at higher risk of extirpation than those farther north (5 of 11 southern rivers had fewer than 1,000 adults, Kynard 1997). Although efforts have been made to delist northern populations that show signs of recovery (see Bain et al. 2007), at the time of this writing, all populations remain subject to special protection under the U.S. Endangered Species Act (1973).

Our study focuses on the Shortnose Sturgeon population in the Ogeechee River, Georgia, a 425-km-long, black-water, coastal river in the southeastern United States. Because of its small size, the Ogeechee River is not impounded or used for navigation, and dredging is restricted to its estuary. Two tributaries, the Canoochee River and Black Creek, enter the Ogeechee River at river kilometers (rkms) 50 and 83, respectively, measured from the Intracoastal Canal. Rice canals below the Canoochee River confluence (rkms 44 and 50) connect the Ogeechee River to a point on the Little Ogeechee River that is closer to the ocean and therefore more saline. During normal flood tides the rice canals inject higher salinity water into the Ogeechee River.

The Shortnose Sturgeon population in the Ogeechee River is smaller than those in the neighboring Savannah and Altamaha rivers, and is most closely related genetically to the Altamaha population (Quattro et al. 2002; Wirgin et al. 2005). Mark–recapture estimates were between 25 and 275 individuals in the early 1990s (Rogers and Weber 1994), around 150 individuals in year 2000 (Fleming et al. 2005), and between 200 and 450 individuals in 2007–2009 (Peterson and Farrae 2011).

When seeking to protect an endangered species, like the Shortnose Sturgeon, it is important to assess factors that might prevent population persistence and recovery. Resources designated for population recovery efforts can be prioritized and focused when these threats can be ranked and when key uncertainties are identified and used to guide research. Because it is impossible or expensive to test the future influences of alternative factors in the field, we are left with two scientific approaches: (1) comparative, range-wide studies, and (2) simulation studies that represent mechanistic linkages between putative threats and population response. This study takes the latter approach. We identified three factors that may be preventing recovery of this population: (1) poor water quality (especially in summer and under conditions of elevated future temperatures),

(2) rice canals that cause premature exposure of juveniles to high salinity, and (3) harvest as bycatch in the commercial shad fishery. These are described below as they relate to broader hypotheses.

One hypothesis is that southern populations of Shortnose Sturgeon, like the Ogeechee population, are limited by high temperatures and low dissolved oxygen in summer (Collins et al. 2000a, 2000b; Campbell and Goodman 2004). As a corollary to this, we hypothesize that elevated temperatures associated with climate change would make summer habitat quality worse and thereby further reduce the viability of the population. A second hypothesis is that small rivers, like the Ogeechee River, have limited freshwater rearing habitat. The river's relatively low flow and small size may limit the distance upstream where spawning may occur. A corollary is that the presence of rice canals (a factor that we simulate) exacerbates the lack of upstream access by introducing saline water higher in the system. In his range-wide assessment of the species, Kynard (1997) noted that larger populations tended to occur in rivers with access to freshwater inland to the fall line, a natural geologic division separating sedimentary substrates (coastal plain) from harder, crystalline, basement rock. Based on his research on larval behavior, Kynard (1997) hypothesized that shorter distances between spawning habitat and the estuary expose early life stages of sturgeon to saline water before they develop saltwater tolerance. A third hypothesis is that harvest is limiting population recovery. There remains a small commercial shad fishery, which can intercept adult sturgeon during their spawning migration.

The goal of this study was to design and use a population viability analysis (PVA) model to quantify factors that may threaten the future viability of the Ogeechee River Shortnose Sturgeon population. With this purpose in mind, we designed an individual-based and spatially explicit PVA model to represent mechanistic linkages between each of the factors listed above and sturgeon activities (movement, growth, reproduction, development, survival). Our hope is that results of these virtual experiments will help to prioritize further research and recovery efforts for this population and others like it.

METHODS

Physical Habitat

To support the PVA modeling effort, we required models of physical habitat. We opted to use simple empirical models, which are more affordable and computationally efficient than complex numerical models, while matching their accuracy (Marshall et al. 2011). These simple empirical models were developed using data collected during field surveys and by simulated data from a two-dimensional (2D) hydrodynamic model.

One of us (D.F.) measured surface and bottom temperature, salinity, and dissolved oxygen (DO) from a boat at 5-km intervals between rkms 20 and 80 in the Ogeechee River biweekly between the spring of 2007 and late summer of 2009. In addition, we measured bathymetry and fixed elevations for use in hydrodynamic modeling.

To characterize seasonal changes in stage and water quality, staff from Dynamic Solutions, Inc. (Knoxville, Tennessee) implemented a 2D hydrodynamic model, Environmental Fluid Dynamics Code (EFDC), for the lower Ogeechee River. We refrained from linking EFDC dynamically with the PVA model, instead using it in a supporting role to represent spatial variation in depth and to simulate the effect of rice canals on salinity. Dynamic maps of EFDC-simulated salinities in the lower Ogeechee River with and without rice canals are available online at the following sites (last accessed 5 Oct 2012): http://www.esd.ornl.gov/∼zij/projects/SERDP/wcanalsd200-204.AVI (with rice canals) and http://www.esd.ornl.gov/∼zij/projects/SERDP/wocanalsd200-204.AVI (without rice canals).

We divided river habitat in the PVA model into 0.5-km longitudinal segments beginning below Fort McAllister and ending at the confluence with Black Creek at rkm 83. In the PVA model, we represented three cells across in each longitudinal segment. River habitat was described in terms of depth and three water quality attributes: temperature, dissolved oxygen, and salinity. Below we describe empirical models that we developed for the three water quality variables.

Simulated Habitat Quality

We developed a general modeling framework for habitat quality that distinguishes static and dynamic aspects of habitat quality and describe how this framework was implemented for Shortnose Sturgeon in the Ogeechee River. All model parameters related to habitat modeling and Shortnose Sturgeon movement are defined and assigned values in Table 1.

Static Habitat Quality

Sturgeons are benthic feeders that generally prefer deep pools and channel habitat (Crance 1986; Kynard et al. 2009). To define static habitat quality for Shortnose Sturgeon, we used the EFDC model grid and initial conditions for the lower Ogeechee River to assign an average cell depth. The midchannel cells were generally deeper than the marginal cells. This depth index was treated as static and did not vary with tides or flow, as depth varied little in this broad, unconstrained river.

Dynamic Habitat Quality

Our Shortnose Sturgeon PVA model required three water quality variables: temperature, salinity, and dissolved oxygen. We specified tolerances for high temperatures, high salinities, and low dissolved oxygen that, when exceeded, were assumed to cause mortality after 1 d of exposure. Habitat choice was influenced by water quality in poor and marginal ranges, as described in the section on "Movement."

We defined relationships for each of the three variables (water temperature, dissolved oxygen, salinity) described below. To represent environmental stochasticity, we added normally distributed residual error, ε, with zero mean and SD, and root-mean

square error of residuals (RMSE) to each fitted relationship used to simulate water quality equations (1–4). The RMSE is a reasonable approximation of the prediction error when sample size is large.

Equation (1) describes a relationship fitted to salinity data collected in the Ogeechee River below the influence of rice canals and reported in graphs by Sheldon and Alber (2005). In the equations below, $x =$ rkm and $Q =$ river flow below the Black Creek and Ogeechee River confluence in m^3/s.

$$S(x, Q) = Ssw\left(1 - \frac{x}{x + e^{\left(\frac{Salina + Salinc\,Q}{Salinb + Salind\,Q}\right)}}\right) + \varepsilon_2. \quad (1)$$

We used a simple approach to simulate salinity influences of rice canals. The area of influence occurred between rkms $Rice\_low$ and $Rice\_hi$. Salinities simulated using the EFDC with rice canals showed that salinities in the area of influence were uniform and highly correlated with those downstream from Seven Mile Bend (see website given under "Physical Habitat"). We developed a simple model linking salinities in the area of saltwater intrusion from Little Ogeechee River through the rice canals with that below the bend at rkm $Rice\_loc$.

Seasonal variation in water temperature is modeled from air temperature, T_{air}, and day of year, day, based on data at the Eden gauge on the Ogeechee River (equation 2). We simulated air temperature using equation (3) fitted to over 50 years of National Climate Data Center data measured at the Savannah International Airport (Table 1).

$$T_w(day) = w_0 + w_t T_{air}(day) + \varepsilon_1, \quad (2)$$

$$T_{air}(day) = T_{avg} + (T_{max} - T_{avg})\sin\left(\frac{2\pi}{365}[day - J_0]\right) \quad (3)$$

Water temperatures, T_w, were estimated from air temperature and day of the year (Figure 1).

We used our water quality survey data for the Ogeechee River to evaluate seasonal and longitudinal variation. Because bottom and surface measurements were not significantly different, we used an average of the two, if both were available, and the single available measurement, if not. Longitudinal variation in temperature was not significant, but season explained at least 94% of variation in water temperatures (sine term in equation 3) measured by Jager et al. (2011) in 2007–2009. In the Ogeechee River, water temperature also showed a significant decrease in response to increased total flow.

Lower DO levels occurred at high temperatures during summer and fall. Values below 4 mg/L were observed between July and September in the lower Canoochee River, in the lower Ogeechee River basin (Figure 1). We fitted multiple linear regression models for DO (Table 1). In the Ogeechee River, salinity, log-transformed total flow, water temperature, T_w, rkm, X, and the percentage of upstream flow from the Canoochee River,

TABLE 1. Habitat simulation and movement parameter values used in simulations of Shortnose Sturgeon in the Ogeechee River. Abbreviations are as follows: DO = dissolved oxygen; USGS = U.S. Geological Survey; and DD = density dependent.

| Model parameter name	Value	Description and source
$Cell\_dl\_km$	0.5	Length of one side of a cell (km), specified
$Cell\_dw\_km$	0.05	Width of one side of a cell (km), specified
$Nreach$	3	Number of reaches, defined by significant tributary inputs, specified
$Reach\_km$	56, 82.6	Canoochee River, Black Creek confluences (rkm)
$NumHabVars$	3	Number of dynamic habitat variables (temperature, salinity, DO)
$Rice\_lo$	44.0	Downstream rkm where rice canal influence begins
$Rice\_hi$	50.0	Upstream river km where rice canal influence ends
$Rice\_ptr$	13.4	Pointer to downstream r km where salinity is comparable to that between $Rice\_lo$ and $Rice\_hi$ rice canals
Ssw	27.1043	Salinity at zero distance from ocean (‰), fitted to salinity data in Sheldon and Alber (2005)
$Salina$	36.4226	Logit intercept controls inflection point (distance km), fitted to salinity data in Sheldon and Alber (2005)
$Salinb$	2.1192	Logit denominator intercept controls slope, fitted to salinity data in Sheldon and Alber (2005)
$Salinc$	0.1255	Coefficient of flow in determining inflection, fitted to salinity data in Sheldon and Alber (2005)
$Salind$	0.1405	Coefficient of flow in determining slope, fitted to salinity data in Sheldon and Alber (2005)
$\varepsilon_1, \varepsilon_2, \varepsilon_3$	0.2, 0.5, 0.2	RMSE of salinity, water temperature, DO; results of analyses above
T_{air}	19.3218	Average air temperature (°C; Savannah airport)
T_{max}	28.3772	Maximum air temperature (°C; Savannah airport)
T_{wgt}	0.5	Weighting between air and water temperature (°C), fitted
J_0	106.7	Day of year at which air temperature first reaches its average
w_0	1.71702	Intercept in equation (2) for water temperature(°C)
w_T	0.89068	Coefficient of air temperature (°C) in equation (2), fitted
v_0	13.937	Intercept of DO relationship (mg/L), equation (4), fitted
v_S	−0.0556	Coefficient of salinity (‰) in DO equation (4), fitted
v_Q	−0.20856	Coefficient of log upstream flow (m³/s) at relevant upstream USGS gauge(s) (Eden plus Blichton) in DO equation (4), fitted
v_{rkm}	−0.0219	Coefficient of rkm in DO equation (4), fitted
v_{pQ}	−0.0055	Coefficient of percent flow from Canoochee in DO equation (4), fitted
v_T	−0.2394	Coefficient of water temperature (°C) in DO equation (4), fitted
$Birth\_rkm$	83	Spawning migration destination in rkm, Hook (2011)
$Qavoid$	0.5	Avoid moving to cells when their quality is below this threshold during daily within-range movements, fixed
$MinTerrQual$	0.5	Threshold average quality required in forming a home range, fixed
$InRangeDist$	2.0	Average distance moved within home range (km)
$AvgDisp$	1.8, 2.2, 2.4	Average number of cells moved during migration or to find a new home range for three life stages, fixed
$MinDensHSI$	0.25	Minimum density-related habitat quality, fixed
$Memory$	0.5	Memory factor in decision to leave current cell, fixed
$MinTerrQual$	0.5	Minimum average quality of home range, fixed
$MinTerr$	5.0	Minimum home range size (km) all seasons and both genders
$MaxTerr$	8.0	Maximum home range size (km) all seasons and both genders, fixed
$good\_density$	1,1,1	Cell density at which DD quality is 1; primary, breeding, and winter seasons, mixed gender, fixed
$bad\_density$	20,20,20	Cell density at which DD quality is 0; primary, breeding, and winter seasons, mixed gender, fixed
$Clone\_size$	20,000	Population size at which cloning begins for new offspring, fixed
$nclone$	50	Number of "clones" represented by each simulated fish until reaching adulthood or until population size decreases below $Clone\_size$, fixed
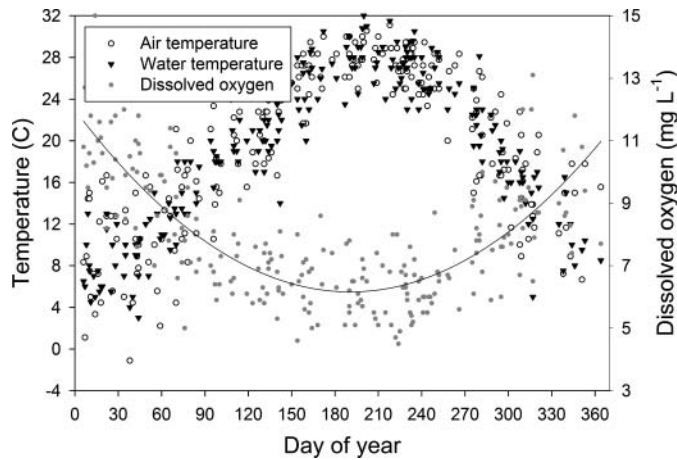
FIGURE 1.   Water temperature and dissolved oxygen in the in the Ogeechee River and air temperature measured at the U.S. Geological Survey gauge at Eden, Georgia.

night (Mulholland et al. 2005).

$$
\begin{aligned}
DO = {} & v_{0,Og} + v_{S,Og}S + v_{Qt}Q_{tot} + v_{T,Og}T_w + v_x X \\
& + v_p pQ + \varepsilon_3.
\end{aligned} \tag{4}
$$

Effects of Habitat on Sturgeon

Our framework simulates the effects of habitat on Shortnose Sturgeon through a series of context-specific suitability criteria that influence movement and survival. Habitat suitability is calculated daily for each cell of the Ogeechee River. Suitability is defined by a combination of static habitat quality (depth) and dynamic habitat quality, which is defined by water temperature, salinity, and DO.

We identified quality thresholds to distinguish cells with optimal, marginal, and poor habitat (Figure 2). Separate thresholds can be provided for each life stage and for each period (primary, breeding, and winter). Tolerance limits separating marginal from poor habitat mark a transition where simulated mortality begins to occur. Optimal versus marginal ranges control simulated sturgeon movements as individuals can move to avoid suboptimal conditions. Below, we describe literature sources for thresholds.
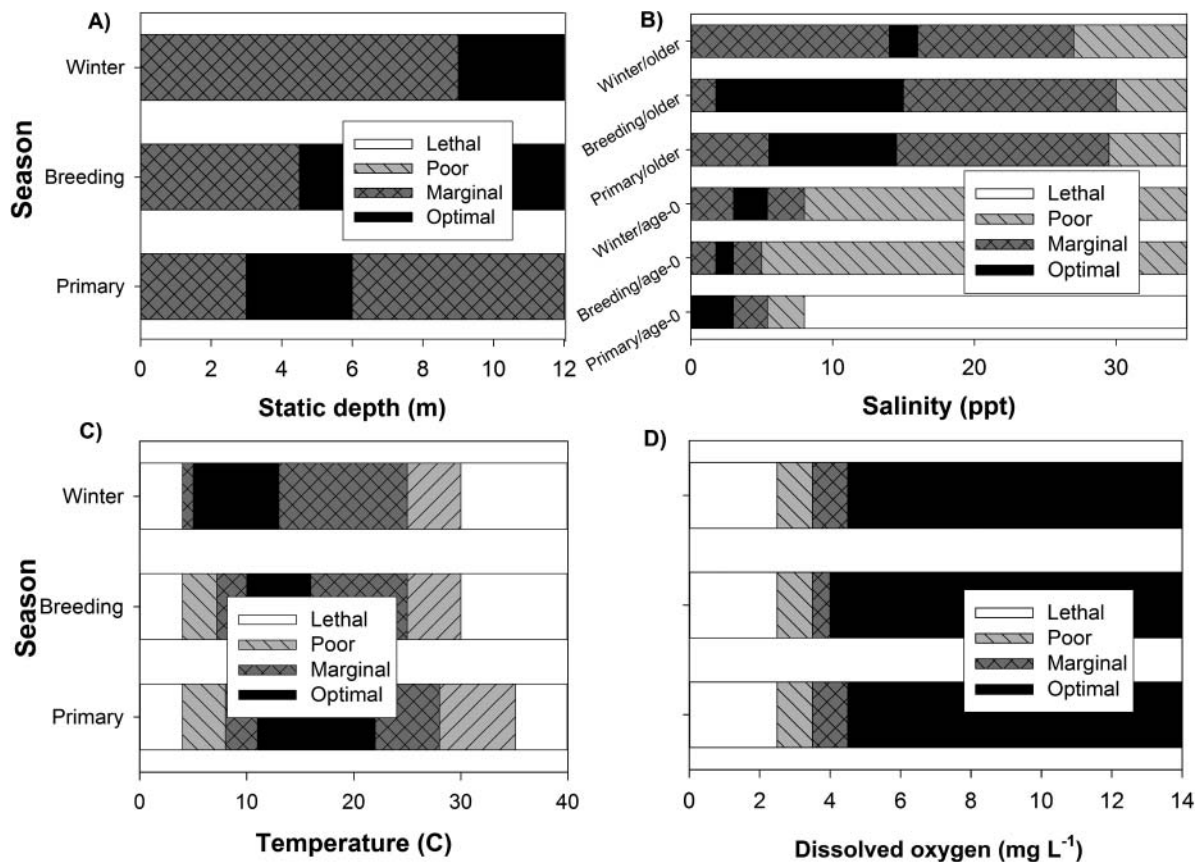
%Qc, explained 79% of variation in DO in the Ogeechee River (equation 4). We subtracted 0.3 mg/L from the intercept to account for the fact that measurements were taken during the day, based on an average difference of 0.6 mg/L between day and

FIGURE 2.   Ranges of (**A**) depth, (**B**) water temperature, (**C**) salinity, and (**D**) dissolved oxygen that influence movement (poor and marginal) and survival (lethal) of Shortnose Sturgeon. Tolerances differ among seasons for all variables and salinity tolerances differ for age-0 and older sturgeon.

Depth.—We did not simulate mortality related to depths unless the cell's overall quality was zero. We simulated different depth preferences for the primary feeding period (summer), breeding season, and fall–winter based on Crance (1986). Shortnose Sturgeon preferred shallower habitat during the feeding period than in the winter (Figure 2).

Temperature.—Temperature criteria were different for the primary feeding period (summer), breeding season, and fall–winter. Season-specific limits can thereby account for higher acclimation temperatures in summer, and lower ones in winter. Ziegeweid et al. (2008a) reported upper safe temperatures between 28.7°C and 31.1°C, and thermal maxima between 33.7°C and 36.1°C for Shortnose Sturgeon. Based on this, we simulated a decrease in daily survival from a value of 1 to 0 for a 24-h exposure to temperatures between 28.0°C and 35.1°C. During the breeding and fall–winter seasons, we lowered the upper safe limit to 24°C and the upper critical temperature to 30°C. Survival effects on early life stages are described in the section on "Reproduction." We set an optimal range from 10°C to 16°C to influence movement of adult spawners during breeding. Collins et al. (2000a) reported that upstream movement by juveniles was stimulated at temperatures above 22°C, and we used this as the upper optimal temperature in summer. We adopted Crance's (1986) lower safe limit of 7.2°C during spawning and incubation. Lower temperature limits during winter were assumed not to be an important source of mortality.

Salinity.—We specified upper tolerances to salinity that differed by life stage and season. Early life stages were least tolerant (upper lethal salinity of 5‰, based on Holland and Yelverton 1973) during the breeding season, and had an optimal range set between 1.75‰ and 3‰ (Crance 1986; Collins et al. 2000a; Campbell and Goodman 2004). For the feeding period, we raised the upper limit to 8‰ for early life stages (Collins et al. 2000a) and to 20‰ for older life stages (Crance 1986; Hall et al. 1991; Collins et al. 2000a; Ziegeweid et al. 2008b). Because salinity tolerance is higher during colder periods, we raised the upper threshold for adults in winter to that of seawater. Optimal ranges were calibrated to produce observed movement patterns, specifically to segregate adults downstream and juveniles upstream in winter. The range for early life stages was between 3‰ and 5.4‰ and the range for older life stages was between 22‰ and 26‰.

Dissolved oxygen.—Tolerances to low DO have been studied for early life stages of Shortnose Sturgeon (Niklitschek 2001; Secor and Niklitschek 2001), but not for adults. According to Secor and Niklitschek (2001), age-0 Shortnose Sturgeon began to exhibit physiological and behavioral changes to DO levels below 4.5 mg/L when temperatures are in the range of 22–27°C (Niklitschek and Secor 2005). This was caused by increased respiration. Campbell and Goodman (2004) found LC50 values (i.e., concentrations lethal to 50% of test fish) varied from 2.2 to 3.1 mg/L depending on the age of age-0 sturgeon and the temperature. We simulated a linear decrease in sturgeon survival for all periods and life stages for DO levels between 3.5 and 2.5 mg/L and considered values above 4.5 mg/L to be optimal (Figure 2).

Movement

Shortnose Sturgeon use different habitats at different times of year and for different activities. Our PVA model simulated daily sturgeon movements in response to environmental gradients as well as spawning migrations and dispersal events. We initialized Shortnose Sturgeon locations in the PVA model in winter at the mouth of the estuary. According to Dadswell et al. (1984), Shortnose Sturgeon begin migratory behavior as adults, moving upstream as temperatures rise in spring and downstream as temperatures cool in fall. Similar migratory behavior has been observed in juveniles. Our PVA model simulated longer migrations prior to spawning and during the transition from larva to juvenile. In addition, individuals dispersed whenever average water quality in their home range deteriorated below *MinTerrQual* or growth fell below its expectations. For each individual a running average of its past growth was kept that served as its expectation for growth (see Jager et al. 1993).

Initially and after a dispersal event, each individual formed a home range consisting of a list of contiguous stream cells. Cells below a quality threshold, *Qavoid*, at the time of its formation were excluded. As Shortnose Sturgeon is a gregarious species, we permitted home ranges of individual sturgeon to overlap with those of other individuals. However, we simulated the effects of sturgeon density on habitat quality, following Sullivan et al. (2003). We specified density preferences (*good_density*, *bad_density*) to be the same for the three seasons: primary (summer, fall), breeding (spring), and secondary (winter), defined by parameters *breed_start*, *breed_end* and *winter_start*, *winter_end* (Table 2).

Once formed, each individual was restricted to its home range, as described in Jager et al. (2006). New locations were selected daily from the list of cells belonging to the home range. Closer locations were more likely to be selected. Daily distance moved was drawn from an exponential distribution with mean, *AvgDist*.

Biological Processes

Below, we describe methods for simulating reproduction, growth, and survival in the PVA model. All model parameters are defined and assigned values in Table 2.

Reproduction

In our simulations, females migrate to spawn once (1) they are mature, (2) they have waited longer than the spawning interval, and (3) their relative weight exceeds the threshold, R_f_breed. We used length as the criterion for maturation (*Mat_avg_fem* and *Mat_avg_mal* in Table 2). Values for length were based on observations in the Altamaha River, where first spawning occurred after fish reached 58.6 cm fork length (FL) (age 2–3) for males and 72.2 cm (age 6) for females (Heidt and Gilbert 1979). We assumed a minimum spawning interval of

2 years for males (*Breed_intv_mal*) and 3 years for females (*Breed_intv_fem*). Longer intervals may be expected in large populations due to density-dependent effects (e.g., 5 years in Altamaha River; Heidt and Gilbert 1979).

The spawning migration of Shortnose Sturgeon begins in late winter, but seems to follow different patterns in different rivers. In some rivers (e.g., the Hudson River), adults that are ready to spawn congregate downstream and migrate upstream together (Dovel 1981), and in other rivers, individuals migrate separately (Peterson and Farrae 2011). When the congregation option is simulated, all spawners join a group near a specified downstream location at the start of the breeding season. Members of each simulated group follow a "bellweather" individual that chooses a migration destination. Here, we simulated independent upstream movements by individuals during the 10-d spawning period. The birth location for the initial population was set to *Birth_rkm*, at the confluence with Black Creek. This is one of a handful of locations identified by a sediment survey as potentially suitable for spawning (Hook 2011). After migrating, simulated adults identified suitable spawning locations and formed aggregations based on proximity. The model tracked the birth location for each new individual to facilitate later simulation of homing behavior.

Once a female joined a spawning aggregation, the number of eggs released depended on her size according to the relationship

$$\text{Eggs} = feca \; W^{fecb}, \quad (5)$$

where W = female weight in kilograms and *feca* and *fecb* represent fecundity values (Table 2; Dadswell 1979). Each female was assigned a "nest" that tracks how many eggs she has produced and their development to hatch and to become free-feeding juveniles. Eggs were exposed to three sources of mortality: (1) a baseline survival, *Sbirth*, which includes factors such as fertilization success; (2) density-dependent survival, which decreased as the ratio of optimal to actual density once the density of eggs deposited in a river cell exceeds an optimum density, *Degg*; and (3) temperature-related survival. Density-dependent survival has been demonstrated for this species (Kynard et al. 2011) and other sturgeons (Mohler 2003). Temperature-related survival was applied to both the egg and larval life stages. These three contributing factors were multiplied, as described for White Sturgeon *A. transmontanus* by Jager et al. (2002).

Developmental progression from egg to larva to juvenile was determined by accumulated fractional development, as in Jager et al. (2002). We used equations for time-to-hatch (equation 6) and yolk-sac absorption (equation 7) as a function of temperature, T, provided by Wang et al. (1985) as follows:

$$\text{Hatch } (d) = \frac{1}{24} h_0 \, e^{h_1 \, T}, \quad (6)$$

and

$$\text{Fledge } (d) = \frac{1}{24} y_0 \, e^{y_1 \, T}. \quad (7)$$

Timing predicted by these relationships, which were developed for White Sturgeon and Lake Sturgeon *A. fulvescens*, was consistent with data reported for Shortnose Sturgeon, including the accumulated thermal units to hatch (Parker and Kynard 2004) and duration of the larval life interval (Hardy and Litvak 2004), and showed them to be consistent. For eggs, each day contributed "1/Hatch" to a sum that reaches one at hatching. For larvae, each day contributed "1/Fledge" toward becoming free-feeding juveniles.

Survival from egg to hatch and survival of larvae were both simulated daily as a function of temperature. We represented temperature-related egg survival by specifying an ideal range (*Tegg_min1*, *Tegg_max1*) and lethal limits (*Tegg_min0*, *Tegg_max0*). Because no relationship between egg survival and temperature has been reported for Shortnose Sturgeon, we relied on information from the closely related Atlantic Sturgeon. Ideal incubation temperatures for Atlantic Sturgeon eggs are between 20°C and 21°C; incubation at temperatures below 18°C is prolonged, which can lead to increased mortality due to fungus (Mohler 2000; Mohler et al. 2003). Among Gulf Sturgeon *A. oxyrinchus desotoi*, incubation survival decreases linearly from a maximum at 15°C, by 33% for each 5°C up to 25°C (Chapman and Carr 1995). For larvae, we adopted the same lower limit as for eggs (*Tlarva_min0*, *Tlarva_min1* in Table 2). Hardy and Litvak (2004) found that survival of larval Shortnose Sturgeon decreased linearly from a value of 1 to a value of 0 as temperature increased from *Tlarva_max1* = 20°C to *Tlarva_max0* = 35°C for larvae acclimated at 18°C.

Our individual-based model began to track postlarval individuals once the yolk sac was absorbed and juveniles began feeding. If, in a given year, population size exceeded a specified threshold at this time, the model tracked one individual juvenile to represent a number of its siblings as "clones." All model statistics reported as output were subsequently weighted by the number of clones. In addition, density-dependent functions used the expanded population size. Once these individuals survived to adulthood, clones were tracked individually.

Growth

Once individuals became juveniles (after yolk absorption), we assigned individual Shortnose Sturgeon an initial FL of 1.8 cm (Hardy and Litvak 2004). We simulated the effects of water quality (temperature, salinity, DO) on daily growth and tracked starvation as a source of mortality. Our bioenergetics model used equations (8) and (9) to track growth, where growth (ΔG, kg/d), depends on consumption (C) and energy costs; these costs include egestion (F) and excretion (U), total respiration (R), and, for females on the date of spawning, total weight of eggs, which depends on egg weight, *Ew*. Parameter values listed in Table 2 were calibrated in a Stella version of the bioenergetics model based on an earlier model for White Sturgeon (Bevelhimer 2002).

$$G_t = G_{t-1} + \Delta G,$$
$$\Delta G = C \cdot (1 - F - U) - R - Ew \cdot \text{Eggs}. \quad (8)$$

TABLE 2. Demographic parameter values used in simulations of Ogeechee River Shortnose Sturgeon.

Model parameter name	Value	Description and source
winter_start	Sep 16	Marchette and Smiley (1982, cited by Dadswell et al. 1984)
breed_start	Feb 10	End of winter, start of breeding and rearing period Altamaha River; Heidt and Gilbert (1979)
breed_end	Mar 15	End of breeding and rearing period, Altamaha River; Heidt and Gilbert (1979)
avg_age	18.0	Average age of initial population, Collins et al. (1996)
max_age	67	Maximum age (years), Dadswell et al. (1984:19)
pmale	0.667	Ratio of males to females initially and at each birth, Dadswell et al. (1984)
nstage	3	Number of life stages (age-0 postlarvae, juvenile, adult)
Reproduction		
breed_period	10	Length of breeding period (d), Heidt and Gilbert (1979)
guard_dist	10.0	Average distance moved by spawners during breeding period (km), no actual guarding, fixed
h_0	1185.03	Coefficient of hatching time relationship with temperature, Wang et al. (1985)
h_1	−0.127	Exponent of hatching time relationship with temperature, Wang et al. (1985)
y_0	1535.62	Coefficient of yolk sac absorption time with temperature, Wang et al. (1985)
y_1	−0.071	Exponent of yolk sac absorption time with temperature, Wang et al. (1985)
mat_avg_fem	72.2	Maturation length threshold (cm), females, Altamaha River, Heidt and Gilbert (1979)
mat_avg_mal	58.6	Maturation length threshold (cm), males, Altamaha River, Heidt and Gilbert (1979)
breed_intv_mal	730	Minimum interval (d) between breeding events for males, Heidt and Gilbert (1979)
breed_intv_fem	1,095	Minimum interval (d) between breeding events for females, Heidt and Gilbert (1979)
R_f_breed	0.6	Relative weight factor for breeding
feca	9.026	Fecundity versus weight (kg), Saint John River, New Brunswick, Dadswell (1979, cited by Dadswell et al. 1984)
fecb	1.14	Fecundity versus weight (kg), exponent, Saint John River, New Brunswick, Dadswell (1979, cited by Dadswell et al. 1984)
Tegg_min0	10.0	Minimum critical temperature (°C), Mohler (2003)
Tegg_min1	15.0	Minimum optimal temperature (°C), Mohler (2003); Chapman and Carr (1995)
Tegg_max1	21.0	Maximum optimal temperature (°C), Mohler (2003)
Tegg_max0	30.0	Maximum critical temperature (°C), Chapman and Carr (1995)
Tlarva_min0	10.0	Minimum critical temperature (°C), Mohler (2003)
Tlarva_min1	15.0	Minimum optimal temperature (°C), Mohler (2003)
Tlarva_max1	20.0	Maximum optimal temperature (°C), Hardy and Litvak (2004)
Tlarva_max0	35.0	Maximum critical temperature (°C), Hardy and Litvak (2004)
Sbirth	0.193	Baseline incubation survival, not including density or temperature effects, Buckley and Kynard (1981)
Degg	1.0×10^6	Optimal egg density per square kilometer, Dadswell et al. (1984); Mohler (2003); Kynard et al. (2011)
Growth		
max_age	67	Maximum age (years), Dadswell (1979:19)
L_∞	97.0	Von Bertalanffy length (cm) versus age (years); maximum length; Altamaha River, Heidt and Gilbert (1979)
k	0.149	Von Bertalanffy length (cm) versus age (years); growth rate; Altamaha River, Heidt and Gilbert (1979)
t_0	−3.15	Von Bertalanffy length (cm) versus age (years); initial size; Altamaha River, (Heidt and Gilbert 1979)
a	11.536	Allometric length–weight relationship, intercept 5.01/0.4343; Altamaha River, Heidt and Gilbert (1979)
b	2.95	Allometric length–weight relationship, exponent; Altamaha River, Heidt and Gilbert (1979)
F	0.09	Egestion as a proportion of consumption, Niklitschek (2001)
U	0.03	Excretion as a proportion of consumption, Niklitschek (2001)

TABLE 2. Continued.

Model parameter name	Value	Description and source
SDA	0.13	Specific dynamic action, cost of processing food as proportion of consumption, from Niklitschek (2001)
Ew	0.0175	Weight per egg (g), Dadswell et al. (1984)
c_a	1.12×10^{-4}	Allometric portion of C_{max} (g), exp(0.9)·21,900 KJ^{-1}·kg^{-1} pellet feed (Niklitschek 2001)
c_b	0.80	Exponent of weight in C_{max}, Niklitschek (2001)
c_x	0.007	Exponential decrease in C_{max} with age (years), calibrated
T_{max}	32.0	Maximum feeding temperature in $f(T)$ relationship, Ziegeweid et al. (2008a)
T_{opt}	28.0	Optimal feeding temperature in $f(T)$ relationship (above maximum of 27.9°C used by Niklitschek 2001)
θ	$\log_e(2.4)$	Q_{10} derived from data in Niklitschek (2001)
K	0.005	Prey carrying capacity (g dry weight/m^2), calibrated
r	1.2	Prey daily turnover rate, P/B, calibrated
P_{min}	1.5×10^{-5}	Minimum prey density (g dry weight/m^2), calibrated
r_a	4.91×10^{-6}	Respiration coefficient in allometric relationship, Niklitschek (2001)
A_r	1.1	Activity multiplier, calibrated in STELLA version
r_b	0.809	Respiration exponent in allometric relationship (based on data from Niklitschek 2001, calibrated in STELLA version)
r_c	0.0807	Respiration temperature coefficient (based on data from Niklitschek 2001, calibrated in STELLA version)
r_{act}	1.1	Respiration, activity multipier = 1.1 $\times$ 4.69 cal·9.5 $\times$ 10^{-7} cal^{-1}·kg^{-1} fish calibrated to match 0.2–0.5% loss/d in STELLA version
stage_female	45.0, 72.0	Female size thresholds for life intervals (cm): (1) salt tolerance, (2) spawning size, in Altamaha River (Dadswell et al. 1984)
stage_male	45.0, 58.6	Male size thresholds for life intervals (cm): (1) salt tolerance, (2) spawning size, in Altamaha River (Dadswell et al. 1984)
Survival		
Harv_start	Jan 1	Legal start date of commercial shad harvest in Ogeechee River
Harv_end	Mar 31	Legal end date of commercial shad harvest in Ogeechee River
P_{cap}	0.143	Probability of capture in shad net = 2/7 d $\times$ 0.5 of river cross section spanned by net
P_{rel}	0.10	Probability of release or escape, given encountering net, Collins et al. (1996) and Bahn et al. (2012)
Netlist	53, 54	locations of two nets, rkm (this study)
R_f_starve	0.5	Relative weight below which starvation occurs, fixed
P_{inf}	0.5	Inflection point, fraction of maximum length, L_∞, natural survival, fixed
SQ_{min}	1.0	Minimum depth-related survival, (1 = none)
S_{min}	0.15	Minimum annual natural survival, for smallest fish, fixed
S_{max}	0.85	Maximum annual natural survival, for largest fish (Peterson and Farrae 2011)

The sturgeon's maximum possible intake, C_{max}, is a function of fish age x, weight, and temperature, T, calibrated to match observed growth (equation 9). The temperature dependence of feeding, $f(T)$, was modeled using the Kitchell et al. (1977) expression. Parameters for $f(T)$ were taken from a laboratory study of juvenile Shortnose Sturgeon (Niklitschek 2001) and from Ziegeweid et al. (2008a) (Table 2). Actual daily consumption, C, is always less than C_{max} (equation 9).

$$C = pC_{max},$$
$$C_{max} = c_a\, W^{c_b}\, f(T)\, e^{-c_x\, x},$$

$$X = \left(\frac{\theta\,(T_{max} - T_{opt})}{20} \left[1 + \sqrt{1 + \frac{40}{\theta\,(T_{max} - T_{opt} + 2)}} \right] \right)^2$$
$$f(T) = \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^X e^{X\left(\frac{T - T_{opt}}{T_{max} - T_{opt}} \right)}. \tag{9}$$

Rather than setting consumption to a fixed proportion, p, of maximum consumption, we allowed consumption to vary by simulating local prey population dynamics. This enabled us to simulate density-dependent feedback that occurs when

too many Shortnose Sturgeon individuals forage in one cell and deplete prey resources. Crustaceans and mollusks are the primary food items of this species (Carlson and Simpson 1987). *Corbicula*, which is a favorite prey item of Shortnose Sturgeon in northern rivers, has notably low densities in the Ogeechee River, possibly because of the low alkalinity of this blackwater river (Stites et al. 1995). We focused on amphipods because this was the main component of the diet in the nearby Savannah River (M. Collins, South Carolina Department of Natural Resources, personal communication).

Following DeAngelis et al. (1991) and Jager et al. (1993), we simulated prey density at location x and day t, $P_{t,x}$, using a simple Lotka–Volterra model with harvest that requires a minimum prey density, P_{min}, to remain in each cell (equation 10). Prey growth rate, r, estimated by the ratio of production to biomass and the site-specific carrying capacity, K_x, was initially set to the maximum observed biomass of amphipods in the lower Ogeechee River and then calibrated to observed Shortnose Sturgeon growth rates. Amphipod biomass in a shallow Georgia salt marsh was 0.047 g/m (Covi and Kneib 1995).

$$P_{t+1,x} = \max\left\{ P_{t,x} \cdot r \cdot f(T_x)\left(\frac{K_x - P_{t,x}}{K_x}\right) - \sum_{i=1}^{N_x} C_{i,t},\ P_{min} \right\},$$

where $\quad C_{i,t} = \min(P_{t,x},\ C_{max}).$ (10)

The amount eaten, C, was summed over individuals i inhabiting cell x on day t and depended on the cell's water temperature, $T_{t,x}$, and the individual's weight, W_i. This amount was removed from the cell, which could lead to depletion of prey and, ultimately, starvation mortality.

Total respiration includes both standard and active components. Standard respiration depends on fish weight, temperature, and specific dynamic action (*SDA*), which was modeled as a fraction of consumption (equation 11). In addition, we used an activity multiplier r_{act} to account for active respiration, calibrated to match a daily weight loss of 0.2–0.5%. Data supporting parameter choices (Table 2) were measured by Niklitschek (2001) for this species and unknown parameters were calibrated in a Stella version of the growth model to match the von Bertalanffy length–age relationship fitted by Heidt and Gilbert (1979) to Shortnose Sturgeon in the Altamaha River.

$$R_{i,x} = r_{act}\left(r_a W_i^{r_b}\right) e^{r_c T_x} + SDA \cdot C_i$$ (11)

If the sturgeon gained weight, then its length was incremented to the length expected for its new weight, based on the length–weight relationship for Shortnose Sturgeon in the Altamaha River (parameters a and b in Table 2). We verified the bioenergetic component of the PVA model by evaluating how well growth simulated using the bioenergetics model tracked expected growth as a function of age equation (12).

$$L_{exp} = L_\infty\left(1 - e^{-k(t-t_0)}\right)$$ (12)

Survival

Survival of various risks is simulated for Shortnose Sturgeon juveniles and adults. We tracked natural mortality, density-dependent starvation, habitat-related mortality (caused by each of three aspects of poor water quality), and harvest as bycatch in the shad fishery. We tracked mortalities due to each cause separately. We randomized the order in which individuals were exposed to competing risks each day (when more than one factor contribute to death, randomizing ensures that one risk does not always get credited because it is calculated first). Parameters associated with survival are listed in Table 2.

Natural mortality.—Catch-curve data from Shortnose Sturgeon captured in the Ogeechee River during 2007–2008 provided an upper bound on survival of $S_{max} = 0.74$ (SE $= 0.33$) (Peterson and Farrae 2011). We simulated natural survival as an increasing logistic function of sturgeon FL, L (cm) (equation 13).

$$S_{nat} = \left[1 - \frac{S_{max}}{S_{min}^{\left(L/L_{max}\right)P_{inf}}\left(S_{max} - S_{min}\right)^{1-\left(L/L_{max}\right)P_{inf}} + S_{min}}\right]^{\left(\frac{1}{365}\right)}.$$ (13)

In this equation, the inflection point and slope were defined by parameter P_{inf} (proportion of L_∞ at inflection), S_{min} (minimum annual survival, extrapolated to zero length), and S_{max} (maximum survival for large sturgeon). The result was converted from an annual to a daily value.

Starvation.—In simulations with bioenergetics, we simulated starvation by assuming that sturgeon with a weight less than half that expected based on their length will die (see DeAngelis et al. 1991; Jager et al. 1993). In other words, each day its relative weight, W_r, must exceed W_f_starve for a given individual sturgeon to survive.

Habitat.—Habitat-related mortality occurred when any of the three dynamic habitat variables represented by X (water temperature, salinity, or DO) fell outside the bounds tolerated by a given life stage. For water quality variable v, with an upper lethal threshold, v_{S0}, and another threshold, v_{S1}, below which survival is 1, daily survival due to poor habitat, S_{hab}, was calculated by equation (14), where SQ_{min} is a lower limit. Lower lethal limits (e.g., for DO) were simulated by reversing all the signs in equation (14).

$$S_{hab} = SQ_{min} + (1 - SQ_{min})\begin{cases} 1, & v \leq v_{S1} \\[2mm] \dfrac{v_{S0} - v}{v_{S0} - v_{S1}}, & v_{S1} < v \leq v_{S0} \\[2mm] 0, & v > v_{S0} \end{cases}.$$ (14)

Harvest.—Shortnose Sturgeon are caught incidentally in commercial fisheries targeting American Shad *Alosa sapidissima* (Heidt and Gilbert 1979; Collins et al. 1996, 2000b).

We simulated the capture of migrating spawners swimming upstream and harvest mortality (S_{harv}), which depended on effort, the probability of capture, release, and survival after release. In the Ogeechee River, shad nets are legally deployed 2 d/week from January through March and may span up to half the river's width. Fishing pressure has apparently declined. An informal survey by Georgia Department of Natural Resources counted ~15–20 nets with 3–4 nets at a site (Fleming et al. 2005). Fewer nets were observed during our weekly field surveys of shad nets during the 2008 shad-fishing season, which included both legal and illegal fishing days. A single fisher was consistently observed with two nets just upstream of the Canoochee River confluence on most legal survey dates, and illegal fishing was not observed. We provided the PVA model with a list of deployed net locations and simulated the risk of harvest for individuals moving upstream past each of these locations. For each net, we estimated effort and capture probability (P_{cap}) as the product of the fraction of legal days per week (2/7) and the proportion of cross-sectional area spanned by 30-m (100 ft) nets (~0.5), all of which were assumed to be in contact with the bottom. Collins et al. (1996) estimated that 10–15% of sturgeon caught in shad nets died. Subsequently, Bahn et al. (2012) conducted a study in the Altamaha River that found 98% of sturgeons captured were released unharmed. We adopted an intermediate probability of live release given capture, $P_{rel} = 0.90$, and calculated S_{harv} as follows:

$$S_{harv} = (1 - P_{cap}) + P_{cap} \cdot P_{rel}. \qquad (15)$$

Simulation Experiments

To quantify the potential effects of each factor, we simulated 500 replicate populations in the Ogeechee River with an initial population size of 225 individuals over the historical period of 20 years for which we had temperature and flow drivers. Response variables included the fraction of replicate populations that persisted (P = "persistence") and mortality statistics. We simulated six possible causes of mortality: length-based natural morality, lethal habitat conditions (exposure to high salinities, extreme temperatures, or low DO), harvest as bycatch, and starvation).

We simulated persistence for a baseline scenario with all three factors simulated, P_{all}, and one with no factors included, P_{none}. We then compared results with and without simulating the effects of each of the factors under examination: poor habitat (water quality), rice canals, and incidental harvest. The PVA model was designed to allow us to virtually remove these effects. For water quality and harvest, we could "switch off" simulated deaths that would otherwise occur. For rice canals, simulation of salinities (i.e., physical habitat) was altered, which led to indirect changes in simulated mortality.

We estimated the contributions of each factor by comparing simulated persistence in simulations without the factor to the difference in persistence between simulations with all factors and no factors included. If we define P_{all-x} as the simulated persistence with factor x removed, we estimated the effect of factor x as $100 \times (P_{all-x} - P_{all})/(P_{none} - P_{all})$. A similar approach was used by Jager et al. (2002) to evaluate limiting factors for White Sturgeon populations in the Snake River, Idaho.

Separating the contribution of summer water quality, dominated by temperature and DO, from those of salinity required accounting for the fact that deaths related to salinity were also precluded when "switching off" habitat mortality. To estimate the separate effects of water quality from those of rice canals, we compared the simulated persistence in simulations with all habitat mortality removed and simulations with rice canals removed, i.e., $100 \times (P_{habitat} - P_{rice\ canals})/(P_{habitat} - P_{all})$.

We conducted a separate follow-on simulation as a preliminary evaluation of the effects of future climate warming. Although future climate conditions in the southeast are among the least certain, the forecast under doubled atmospheric CO_2 suggested that mean air temperatures in this part of coastal Georgia will increase by ~4°C (Mearns et al. 2003). We therefore repeated the baseline simulation (including habitat, rice canals, and harvest) with an increase in average (T_{air}) and maximum (T_{max}) air temperatures of 4°C.

Seasonal Growth Patterns

To evaluate seasonal growth patterns, we took a closer look at simulation results for one replicate of the Ogeechee River Shortnose Sturgeon population using baseline conditions. We present seasonal patterns in growth, relative weight, and starvation.

RESULTS

Simulation Experiment

We compared results for simulations with and without each mortality factor of interest below. Not surprisingly, persistence was increased the most by simulating the removal of all three factors (Figure 3). Simulated persistence increased by 30% from $P_{all} = 0.75$ (SE = 0.02) to $P_{none} = 0.97$ (SE = 0.01).

Harvest as bycatch had no effect on persistence, which did not differ from persistence in simulations with none of the factors (Figure 3). Habitat-related mortality had the largest effect on persistence, and removing this factor produced the same change in persistence, 100%, as did removing all of the factors. Average persistence in simulations in which we virtually removed rice canals alone (0.82) produced a change in persistence that was 31.8% of the difference between persistence in simulations with all factors and those with no factors (Figure 3). We noted that removing habitat-related mortality also removed salinity-related mortality due to rice canals because mortalities related to salinity were prevented as well as those due to extreme temperature and low DO. From their effects on simulated persistence, we estimated that removing rice canals decreased persistence to 31.8% of that produced by removing all habitat-related mortality, leaving 68.2% as an upper estimate on the effect of habitat not associated with rice canals.
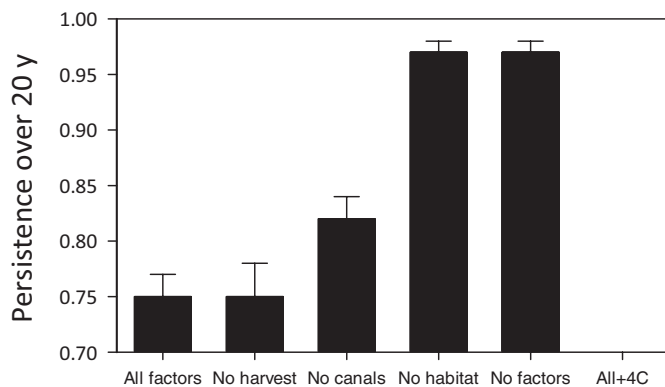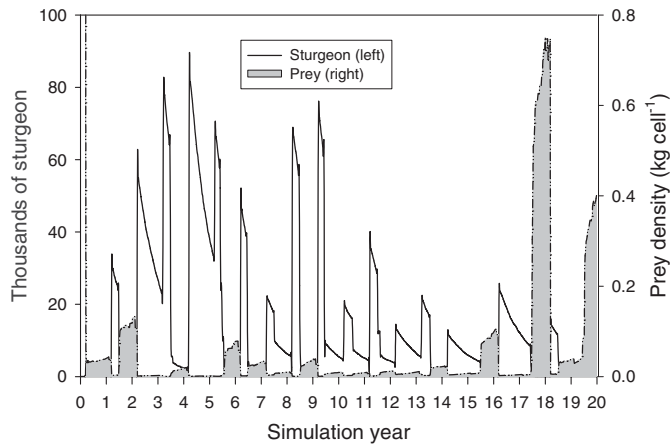
FIGURE 6. Model-simulated Shortnose Sturgeon population dynamics and prey dynamics over a 20-year simulation.

canals increased average persistence, but removal of incidental harvet did not.

Our modeling required assumptions about how each of these factors influences the population. For example, overall viability simulated by the PVA probably depended on our assumptions about natural mortality in the absence of other factors, which is difficult to estimate. A higher value would improve prospects for population persistence. Representation of habitat and inter-actions among water quality variables can also be refined in future. For example, we did not have the information needed to simulate thermal refuges, if any exist in this river. Prey deple-tion during summer, as postulated by Sulak and Randall (2002), may vary spatially. In theory, a more complex hydrodynamic water quality model could provide more spatial resolution in describing habitat. However, in our experience detailed habitat modeling provides a façade of engineering-like precision, when in fact, simulated persistence is far more sensitive to animal movement and avoidance behavior, which are poorly under-stood. In particular, more information is needed to understand where spawning occurs and age-0 sturgeon habitat exists, and how larvae and juveniles disperse prior to developing salinity tolerance. These are just a few of many aspects that may be refined in the future to improve our understanding of population dynamics and to guide future recovery efforts.

Effects of Summer Temperature and Dissolved Oxygen on Growth and Reproduction

Our modeling study supported the hypothesis that water qual-ity, particularly in summer, is probably a barrier to the recovery of this population. In addition to direct mortality caused by low DO and high temperatures, our simulations suggested that sum-mer temperatures become high enough in summer to reduce sturgeon growth. This result has not been confirmed by field data. In the nearby Altamaha River, Shortnose Sturgeon inhabit-ing deep pools with temperatures near 28°C lost weight between captures (Flournoy et al. 1992, cited in Campbell and Goodman

2004). Telemetry results have shown weight losses during sum-mer for the closely related Gulf Sturgeon (Wooley and Crateau 1985; Sulak and Randall 2002). Weaker evidence is provided by Bezold and Peterson (2008), who found that northern Lake Sturgeon transplanted into the Coosa River, Georgia–Alabama, had higher condition factors when captured in spring than when captured in fall.

Several hypotheses have been raised to explain slower growth rates among southern fish populations compared with their northern counterparts. One simple explanation is that southern populations experience suboptimal temperatures for growth dur-ing more of the year (Power and McKinley 1997; Garvey et al. 2003). High energetic costs, prey limitation during summer, or both may be proximate causes for slower growth (Kynard 1997; Mayfield and Cech 2004). Ultimate explanations posited for counter-gradient variation have to do with selective pressures on the reaction norm controlling growth. From a northern per-spective, Conover (1990) hypothesized overwinter mortality as the selective force favoring faster growth at high latitudes. From a southern perspective, Sulak and Randall (2002) suggested that fish, like sturgeons, that have high potential for growth use behavioral mechanisms (e.g., fasting) to maintain an optimal (smaller) body size. These explanations are not mutually exclu-sive, yet much remains to be learned about the proximate and ultimate factors that shape reaction norms in southern popula-tions of sturgeon, including the degree of local adaptation.

Small Coastal Rivers as Ecological Traps

Our study also supported the hypothesis that recruitment of Shortnose Sturgeon in the Ogeechee River is limited by lack of rearing habitat in the river, and the corollary that rice canals con-tribute to this influence. Kynard (1997) observed that healthy Shortnose Sturgeon populations tended to occur in undammed coastal rivers that provide spawning habitat at least 200 km inland. He hypothesized that premature exposure to brackish water during early life stages prevents recruitment in rivers lack-ing access to upstream freshwater habitat. In our simulations, we observed a trade-off between mortality of juveniles that en-countered elevated salinities prematurely in downstream areas and starvation for juveniles that remained farther upstream. This suggests a habitat squeeze for juveniles in smaller coastal rivers where access to freshwater spawning and rearing habitat is lim-ited. A longer freshwater area may prevent this habitat squeeze (1) by reducing the risk of premature exposure to brackish water, as hypothesized by Kynard (1997), and (2) by promoting spatial separation between spawning aggregations, which should re-duce density-dependent effects. Parker and Kynard (2004) also posited local adaptation in the behavior and timing of the age-0 sturgeon downstream migration. McAdam (2011) suggested that drift of larval sturgeon is delayed if the larvae hide in coarse substrates when it is available. These results suggest there are testable hypotheses that can be evaluated by studying habitat preferences of rearing sturgeon juveniles and comparing inland distances and amounts of spawning habitat in coastal rivers.

Locations used for spawning have not yet been confirmed in the Ogeechee River. Efforts to track three migrating adult females and 15 males were made during 1 year (Peterson and Farrae 2011). However, juveniles were occasionally sampled in earlier years (Fleming et al. 2005). We view the presence of juveniles as evidence of spawning in the Ogeechee River because high salinities pose a barrier to migration of juveniles from neighboring rivers. Concurrently with this study, Hook (2011) conducted a survey using side-scan sonar and identified habitat with adequate depths and substrate. That survey suggested that habitat with suitably hard substrates is rare in the Ogeechee River, where sandy substrate is typical (Hook 2011, summarized in Jager et al. 2011). Eight suitable locations were identified and all but one were > 130 km upstream and unlikely to be accessible at low flows. The first suitable site moving upstream occurred near the confluence of the Black River and Ogeechee River, near rkm 83, which is where we assumed that spawning would occur. Tributary confluences tend to collect coarse substrate deposits and are known to be used for spawning by sturgeon species including Shortnose Sturgeon (Collins et al. 2000a) and White Sturgeon (Perrin et al. 2003). Field research is needed to confirm both spawning locations and monitor movements of early life stages. This is hampered by difficulty in accessing areas farther upstream, which are not navigable at low summer flows. Together, these results lend credence to the idea that the Ogeechee River may not consistently provide adequate access to upstream spawning habitat during all years.

The results presented here have implications that lead us to be concerned about the future effects of climate change on Shortnose Sturgeon populations in southeastern U.S. rivers. A 4°C rise in temperature, such as we simulated, is now considered a conservative estimate for this region (Lettenmaier et al. 1999; Christensen et al. 2007). Our PVA results suggested that the outlook for this population would be bleak. In a metapopulation context, we would expect the larger Altamaha River, which probably helps to support the Ogeechee River population, to experience similar effects. This lends credence to the idea that warmer temperatures could have significant adverse effects on Shortnose Sturgeon populations in southern U.S. rivers.

In addition to the effects of rising air temperatures simulated in these preliminary runs, the predicted rise in sea level of 30–100 cm by the year 2100 (Meehl et al. 2007) would effectively shorten the freshwater portion of the river, which is critical for sturgeon spawning and rearing. In the Ogeechee River, a large oxbow in the river (Seven Mile Bend) is eroding (Hutchings 2010) and will probably result in much higher salinities as far as 50 rkm upstream, where the Canoochee River enters. Although erosion of oxbows is a natural process, this change, combined with the influx of saline water through the rice canals, will likely move the tidal portion of this river significantly farther upstream. This risk is one shared by Shortnose Sturgeon populations in other small, coastal rivers and those with dams far downstream (e.g., Kennebec, Androscoggin, and Merrimack rivers; Kynard 1997).

Future efforts to recover this species may best be advanced by understanding the source-sink dynamics between populations in rivers with access to adequate freshwater rearing habitat and populations in rivers lacking access or habitat. Our simulations suggest that this population, if isolated, is unlikely to persist for more than a few decades. However, genetic evidence indicates that the Ogeechee River population is closely related to that in the Altamaha River (Wirgin et al. 2005). The probability of emigration from the Ogeechee population was estimated to be 0.16 (SE = 0.275) and the probability of immigrating was 0.84 (Peterson and Farrae 2011). Thus, the PVA model presented here should be expanded to describe these systems in tandem to account for potential "rescue effects" (Brown and Kodric-Brown 1977) in which extirpated populations may be recolonized by their neighbors. We hypothesize that selection on adult saltwater tolerance controls straying rates and could determine whether this species can avoid the "ecological trap" (sensu Fletcher et al. 2012) of straying into rivers that are, or are in the process of becoming, demographic sinks.

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