

Past and Future Habitat Suitability for the Hudson River Population of Shortnose Sturgeon: A Bioenergetic Approach to Modeling Habitat Suitability for an Endangered Species

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Abstract.—Diadromous species encounter highly variable water quality as they traverse freshwater, estuarine, and marine environments. The U.S. federally endangered shortnose sturgeon *Acipenser brevirostrum* is a diadromous estuarine resident species that relies heavily on tidal freshwater regions of estuaries as spawning, nursery, and foraging habitat. A recent recovery in abundance in the Hudson River shortnose sturgeon population coincided with an ecosystem shift in the tidal freshwater estuary from hypoxia to normoxia (dissolved oxygen > 4 mg/L) during the summer juvenile rearing period. Decades of persistent summertime hypoxia encompassing as much as 40% of shortnose sturgeon nursery habitat was followed by a sudden shift to normoxia (1970 to 1978) due to the U.S. Clean Water Act legislation. Here, we evaluate how past and present water quality in the tidal freshwater Hudson River affects nursery habitat suitability. Habitat suitability, as indexed by potential instantaneous growth rate, was estimated with an empirically derived bioenergetic growth model before (pre-1978: 20% and 40% dissolved oxygen [DO] saturation) and after (1988: 85% DO saturation) the shift in seasonal ecosystem oxygenation. Habitat suitability was then forecast in the context of regional climate change and potential zebra mussel *Dreissena polymorpha* oxygen demand. Results from this simulation study indicated that even moderate reductions in water quality can significantly lower habitat suitability, supporting the circumstantial association between improved water quality and shortnose sturgeon recovery. Although presently occurring at high abundance levels, Hudson River shortnose sturgeon in the future may encounter diminished nursery habitat due to warming temperatures and increased benthic oxygen demand by zebra mussels.

Introduction

Globally, most sturgeon species (Acipenseridae) are listed as either threatened or endangered (Birstein 1993). Sturgeons are particularly sensitive to anthropogenic habitat alteration (e.g., water quality, flow regulation) during early life phases (Secor and Gunderson 1998; Jager et al. 2002; Campbell and Goodman 2004; Coutant 2004; McAdam et al.

2005). Habitat degradation has been implicated as both a primary (NMFS 1998; McAdam et al. 2005; Paragamian et al. 2005) and contributing (Birstein 1993; NMFS 1998; Collins et al. 2000; Niklitschek and Secor 2005) factor to recruitment failure among sturgeon species. Lethal and sublethal environmental conditions are particularly important during the first year of life when recruitment bottlenecks can occur in restricted spawning and nursery habitats. By the same token, life table analysis demonstrated that positive population growth is expected to be

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most sensitive to improvements in larval and juvenile habitats (Gross et al. 2002).

Despite the range-wide endangered status of shortnose sturgeon *Acipenser brevirostrum* along the east coast of North America, recent research on the Hudson River (New York, USA) population of shortnose sturgeon indicated that the population increased from c. 13,000 adults in 1979–1980 (Dovel et al. 1992) to 57,000 in 1997 (Bain et al. 2007). This corresponds to a fourfold increase over an 18-year period. There is corroborating evidence that year-class strength built during the 1980s and peaked at 31,000–52,000 yearling recruits during the late 1980s and early 1990s (Woodland and Secor 2007). Therefore, the Hudson River is a unique case study: an example of robust population growth that can be examined in the context of promoting sturgeon recovery elsewhere.

Suitable nursery habitat is a useful index of the recruitment process because it integrates complex and interacting environmental factors that affect first-year growth and survival. A common means for modeling suitable habitat is empirical, based upon intensively surveyed regions. Abundances can be linked to multiple environmental factors through statistical models, providing prediction of responses under simulated environmental conditions (Crance 1986; Jager et al. 2002; Jensen et al. 2005; Austin 2007). Such methods are less feasible for highly mobile or rare species. Another principal approach uses ecophysiological responses to environmental conditions determined experimentally to predict the distribution and production of fish (Neill et al. 1994; Boisclair 2001; Niklitschek and Secor 2005). This method is intuitively appealing in that it incorporates fundamental biology into a predictive framework rather than applying a purely empirical approach. Still, it is subject to the assumption that fish can locate all suitable habitats. Therefore, such terms as potential growth, potential production, and potential habitat volume are commonly associated with this approach (Logerwell et al. 2001; Luo et al. 2001; Niklitschek and Secor 2005).

Here, we apply an ecophysiological bioenergetic modeling approach to examine the predicted suitability of nursery habitat for the upper Hudson River estuary. Historical water quality data indicate that prior to the 1970s, dissolved oxygen (DO) concentrations in a heavily polluted segment of the Hudson River estuary downstream of the Troy–Al-

bany area (river kilometer [rkm] 235–175, Figure 1) dropped precipitously from springtime normoxia (6–7 mg/L) to c. 2 mg/L at the onset of summer (Figure 2) (20–25% DO saturation) before reaching a nadir in the early fall (<1 mg/L; Leslie et al. 1988). This c. 60-km segment, dubbed the “Albany Pool” (Boyle 1969), coincides with approximately 40% of the estimated nursery habitat for Hudson River age-0 shortnose sturgeon (Dovel et al. 1992; Haley 1999) and occurs directly downstream of spawning habitats. April–May spawning is believed to occur predominantly in the uppermost segment of the tidal freshwater Hudson River, below the Federal Dam in Troy (hereafter Troy dam) and 246 rkm from the river mouth (Dadswell et al. 1984). Larval and young-of-the-year juvenile nursery habitat in the Hudson River extends downstream from the spawning grounds and encompasses much of the tidal freshwater portion of the estuary (Bain 1997; Figure 1). Thus, the hypoxic zone below Albany may have functioned as a recruitment bottleneck, rendering much of the summertime nursery habitat unsuitable for juvenile shortnose sturgeon. The system recovered to summertime normoxia (>4 mg/L) between 1970 and 1978 (Figure 2) following national legislation that stipulated more stringent controls on pollutant discharge.

Although water quality in the tidal freshwater Hudson has improved substantially since the passage of the Federal Water Pollution Control Act Amendments of 1972 and 1977, future nursery conditions could be affected by more recent ecosystem changes. There is evidence that the invasive zebra mussel *Dreissena polymorpha* has already precipitated a 10% decline in DO saturation in bottom waters extending c. 40 km downstream of rkm 184 (Caraco et al. 2000). Caraco et al.’s analysis of water quality data (1986–1998) from this stretch of the Hudson River found that summertime (June–September) DO saturation declined from 95% to 85% following the colonization of the river by zebra mussels. This shift in water quality could not be explained through fluctuations in temperature, summer flow, organic loading, or wind stress (Caraco et al. 2000). Further, warming temperatures associated with global climate change could result in superoptimal water temperatures for shortnose sturgeon juveniles.

We used a bioenergetics model to both hind-cast and forecast the effects of temperature and DO

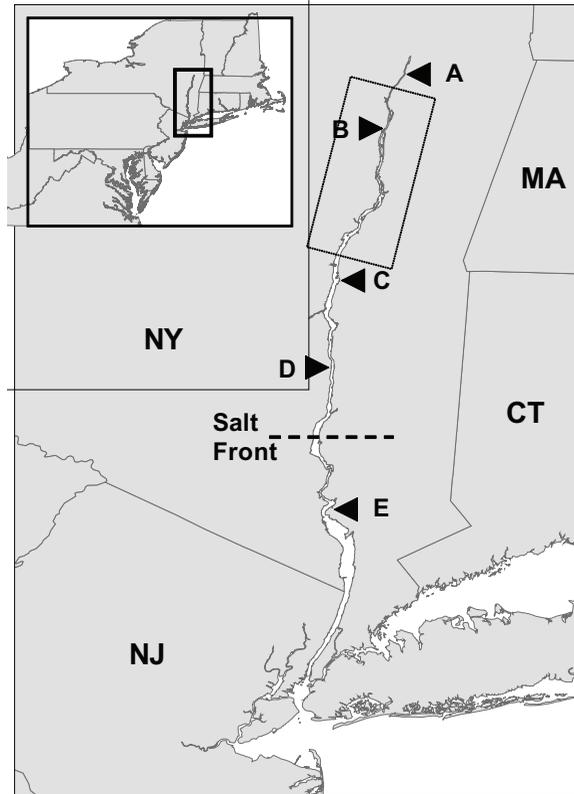


Figure 1.—Map of the tidal freshwater portion (river kilometer [rkm] 245–63) of the Hudson River, New York. The historical location of a large zone of summer hypoxia (Albany Pool), as indicated by a dotted rectangle, overlapped c. 40% of the tidal freshwater reach in this system. Letters mark the approximate locations of sampling stations used to generate long-term mean temperature estimates for the bioenergetics model: A—Green Island (rkm 248), B—Glenmont (rkm 215), C—Tivoli Bay (rkm 160), D—Poughkeepsie (rkm 120), and E—Haverstraw Bay (rkm 63).

on habitat suitability and availability. Habitat suitability was indexed by the potential instantaneous individual growth rate predicted for young-of-the-year shortnose sturgeon entering the system. Predictions of negative instantaneous growth rates for a given area were interpreted as dysfunctional nursery habitat. In our historical simulation, we investigated potential loss of nursery habitat in the presence of moderate (40% DO saturation) to severe (20% DO saturation) hypoxia during the summer months in the Albany Pool area. In the future simulation, we assumed moderate increases in temperature and decreases in DO due to the influence of global warming and zebra mussels, respectively. We evaluated the amplitude of nursery habitat degradation associated with an increase of temperature by 1–3°C and/or a

decrease in DO (to 70% saturation) throughout the entire nursery region.

Methods

Habitat Data

Historical water temperature data were obtained for five independent sampling stations (Table 1) evenly spaced along the tidal freshwater portion of the Hudson River (Figure 1). Data were downloaded from the U.S. Geological Survey (Green Island station #1358000) and National Estuarine Research Reserve System Web sites (Tivoli Bay South), collected from the literature (Haverstraw Bay, Drisco et al. 2003), and obtained through individual cor-

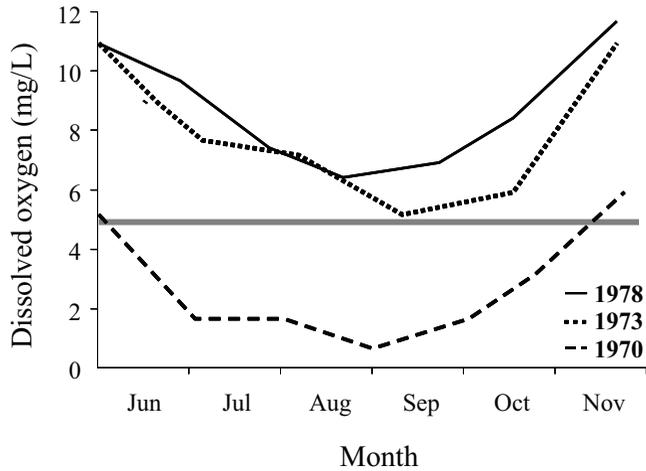


Figure 2.—Time series of spring–fall dissolved oxygen conditions in the Hudson River during the 1970s at Glenmont, New York (directly downstream of the Albany, New York). The horizontal thickened line (c. 5 mg/L) indicates an approximate threshold for negative growth in juvenile sturgeons under summer conditions (Secor and Niklitschek 2001). Data from Leslie et al. 1988 (Figure 72).

responsiveness (R. J. Alstadt, Poughkeepsie water treatment facility, personal communication; New York Department of Environmental Conservation, Glenmont station #13010142). Available data from 1987 to 2005 were used to generate single point-estimates of average summer temperature at the five primary water quality stations (Table 2). Data collection methods vary between stations: temperature

data at Green Island is collected at 3 m (mid-depth), Glenmont data reflected surface conditions, Poughkeepsie data are collected just inside an intake pipe c. 2.4 m above the riverbed, and Haverstraw Bay (<3 m depth) and Tivoli Bay (0.7–2.1 m depth) data are collected using a handheld multiparameter probe in shallow areas. Ordinary least-squares linear regression was used to generate point-estimates

Table 1.—Sampling station site name, location (river kilometer), data attributes (datum collection frequency, total data included, data range [years]), and source of historical water temperature data from the Hudson River. Sources include the U.S. Geological Survey (USGS, www.usgs.gov), New York Department of Environmental Conservation (NYDEC), National Estuarine Research Reserve System (NERRS, www.nerrs.gov), Poughkeepsie water treatment facility (PWTF), and SUNY Marine Science Research Center (MSRC, Drisco et al. 2003).

Site	River km	Temperature data			
		Sampling frequency	Total data (<i>N</i>)	Data range	Source
Green Island	248	~monthly	73	1970–1985, 1988–1994	USGS
Glenmont	215	monthly	18	1993–2002	NYDEC
Tivoli Bay	160	0.5 h	7,616	1995–2000	NERRS
Poughkeepsie	120	daily	1,448	1987–2005	PWTF
Haverstraw Bay	37–63	biweekly	52 ^a	1985–2002	MSRC

^a Each Haverstraw Bay datum used in this analysis represents a biweekly mean calculated from 25 individual temperature measurements collected from the Haverstraw–Tappan Zee region of the Hudson River (see Drisco et al. 2003).

Table 2.—Nineteen-year time-series of observed and reconstructed (*) river temperature data from five sampling stations along the upper Hudson River estuary (river kilometer 248–63).

Year	Site				
	Green Island	Glenmont	Tivoli South	Poughkeepsie	Haverstraw
1987	20.8	21.2*	22.5*	21.7	22.6
1988	24.7	21.9*	23.2*	22.4	22.3
1989	14.7	21.4*	22.7*	21.9	22.7
1990	23.0	22.1*	23.3*	22.6	23.2
1991	23.0	22.3*	23.5*	22.8	21.5
1992	21.5	20.9*	22.3*	21.4	20.4
1993	21.4	21.3	23.1*	22.4	22.7
1994	22.6	21.8	23.0*	22.3	23.5
1995	21.6*	18.6	21.3	22.5	23.8
1996	20.7*	18.6	21.3	21.6	21.4
1997	21.6*	21.8	21.0	22.5	22.2
1998	22.2*	19.3	21.7	23.1	23.2
1999	21.6*	14.1	21.5	22.4	22.9
2000	20.2*	16.7	20.3	21.1	20.7
2001	22.2*	20.3	23.8*	23.1	23.1
2002	22.2*	19.4	23.7*	23.1	23.9
2003	21.4*	21.8*	23*	22.3	24.3*
2004	20.8*	21.1*	22.5*	21.7	23.7*
2005	22.9*	23.3*	24.3*	23.7	25.7*

of missing temperature data at some stations based on the continuous temperature data available from the Poughkeepsie water treatment facility (explanatory variable). The Poughkeepsie versus Green Island, Glenmont, and Tavoli Bay regressions ($R^2 > 0.62$, F -stat = 144.2, $p \leq 0.01$) were restricted to data collected concurrently at a daily resolution to avoid the effect of short-term weather variability on temperature relationships between stations. The Poughkeepsie versus Haverstraw Bay temperature regression was based upon biweekly mean values; therefore, the relationship was less precise, $R^2 = 0.5$, although highly significant at $\alpha = 0.05$ (F -stat = 14.2, $p = 0.002$).

Observed and estimated temperature data from each station were averaged across months from July to September with summer water temperature calculated as the mean of the monthly averages. Incremental change in water temperature between sampling stations was assumed to follow a linear relationship with distance and was interpolated at c. 10-km intervals between stations. Each interpolated point was considered representative of the river conditions occurring in an entire river

segment. The final result of these regressions was a spatially explicit reconstruction of average summer water temperature at 21 individual points and for 20 river segments along the upper Hudson River estuary. This reconstructed temperature record (Table 3) extended 185 km from an upstream boundary at Green Island (directly upstream of Troy dam, rkm 248) downstream to the salt front at Haverstraw Bay (rkm 63). The highly fragmented historical DO data precluded any attempt to reconstruct a spatially representative model of dissolved oxygen. Instead, we chose to simulate historical and future conditions through proscribed reductions in % DO in the area(s) of interest.

Habitat Availability and Suitability Index

Estimates of individual potential instantaneous daily growth rate for each river segment were generated using a bioenergetics model (Appendix 1) derived by Niklitschek (2001) through extensive laboratory and mesocosm studies. The model is parameterized with temperature, DO saturation, salinity, and fish weight, reflecting the observed and/or modeled de-

Table 3.—Nineteen year time-series of observed, reconstructed (*) and linearly interpolated river temperature data along the upper Hudson River estuary (river kilometer [rkm] 248–63). River km indicates the down-estuary boundary of each segment (excluding rkm 248, which represents the upstream boundary of the data set). Code identifiers indicate sampling stations (see key at bottom of table).

River km	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
A 248	20.8	24.7	14.7	23.0	23.0	21.5	21.4	22.6	21.6*	20.7*	21.6*	22.2*	21.6*	20.2*	22.2*	22.2*	21.4*	20.8*	22.9*
239.8	20.9	24.0	16.4	22.8	22.8	21.3	21.4	22.4	20.9	20.2	21.6	21.5	19.7	19.4	21.8	21.5	21.5	20.8	23.0
231.3	21.0	23.3	18.0	22.5	22.6	21.2	21.4	22.2	20.1	19.7	21.7	20.7	17.8	18.5	21.3	20.8	21.6	20.9	23.1
222.6	21.1	22.6	19.7	22.3	22.5	21.0	21.3	22.0	19.3	19.1	21.7	20.0	15.9	17.6	20.8	20.1	21.7	21.0	23.2
B 215	21.2*	21.9*	21.4*	22.1*	22.3*	20.9*	21.3	21.8	18.6	18.6	21.8	19.3	14.1	16.7	20.3	19.4	21.8*	21.1*	23.3*
205.8	21.4	22.1	21.6	22.3	22.5	21.1	21.6	22.0	19.0	19.0	21.6	19.7	15.3	17.3	20.9	20.1	22.0	21.4	23.4
196.7	21.6	22.3	21.8	22.5	22.7	21.3	21.9	22.2	19.5	19.5	21.5	20.1	16.5	17.9	21.5	20.8	22.2	21.6	23.6
187.5	21.9	22.6	22.0	22.7	22.9	21.6	22.2	22.4	19.9	19.9	21.4	20.5	17.8	18.5	22.1	21.6	22.4	21.8	23.8
178.3	22.1	22.8	22.3	22.9	23.1	21.8	22.5	22.6	20.4	20.4	21.2	20.9	19.0	19.1	22.6	22.3	22.6	22.0	24.0
169.2	22.3	23.0	22.5	23.1	23.3	22.0	22.8	22.8	20.9	20.8	21.1	21.3	20.3	19.7	23.2	23.0	22.8	22.3	24.2
C 160	22.5*	23.2*	22.7*	23.3*	23.5*	22.3*	23.1*	23.0*	21.3	21.3	21.0	21.7	21.5	20.3	23.8*	23.7*	23.0*	22.5*	24.3*
150	22.3	23	22.5	23.1	23.3	22.1	22.9	22.9	21.6	21.4	21.4	22.1	21.7	20.5	23.6	23.6	22.9	22.3	24.2
140	22.1	22.8	22.3	22.9	23.1	21.8	22.8	22.7	21.9	21.5	21.7	22.4	22.0	20.7	23.4	23.4	22.7	22.1	24.0
130	21.9	22.6	22.1	22.7	22.9	21.6	22.6	22.5	22.2	21.5	22.1	22.7	22.2	20.9	23.3	23.2	22.5	21.9	23.9
D 120	21.7	22.4	21.9	22.6	22.8	21.4	22.4	22.3	22.5	21.6	22.5	23.1	22.4	21.1	23.1	23.1	22.3	21.7	23.7
110.5	21.9	22.4	22	22.7	22.6	21.3	22.4	22.5	22.7	21.6	22.4	23.1	22.5	21.1	23.1	23.2	22.6	22.0	24.1
101	22.0	22.4	22.2	22.8	22.4	21.1	22.5	22.7	22.9	21.6	22.4	23.1	22.6	21.0	23.1	23.4	23.0	22.3	24.4
91.5	22.2	22.4	22.3	22.9	22.1	20.9	22.5	22.9	23.1	21.5	22.3	23.1	22.6	20.9	23.1	23.5	23.3	22.7	24.7
82	22.3	22.3	22.4	23.0	21.9	20.8	22.6	23.1	23.3	21.5	22.3	23.1	22.7	20.8	23.1	23.6	23.6	23.0	25.0
72.5	22.5	22.3	22.6	23.1	21.7	20.6	22.6	23.3	23.5	21.4	22.2	23.2	22.8	20.8	23.1	23.8	24.0	23.4	25.3
E 63	22.6	22.3	22.7	23.2	21.5	20.4	22.7	23.5	23.8	21.4	22.2	23.2	22.9	20.7	23.1	23.9	24.3*	23.7*	25.7*

A—Green Island, B—Glenmont, C—Tivoli Bay, D—Poughkeepsie, E—Haverstraw Bay.

pendence of consumption, metabolism (routine and active), and excretion rates on these four parameters. Postprandial and egestion rates are modeled solely on temperature and DO saturation values in accordance with laboratory observations (Niklitschek 2001). The model was developed under maximum consumption conditions; therefore, growth estimates represent maximum potential rates. For the purposes of these simulations, we chose to predict \dot{g} for a 5-g young-of-year shortnose sturgeon (hereafter “juvenile”), a size that approximates the weight of a 4–6 month old fish (Dadswell et al. 1984; Carson 1987). In all model runs, salinity was restricted to zero in accordance with observed low-salinity preferences of age-0 fish (Dadswell et al. 1984). We considered estimates of instantaneous growth rate at each river segment as an index of habitat suitability (HSI); therefore, increases or decreases in instantaneous growth rate estimates for each river segment were interpreted as an increase or decrease in HSI. It is important to note that there are several other definitions of HSI in the literature (e.g., Crance 1986; Bray 1996; Vadas and Orth 2001); for the purposes of this study, it is defined strictly as the modeled potential instantaneous growth rate for a particular river segment. The total available summertime nursery habitat (138 km) was calculated as the distance between Troy dam (rkm 246) and the mean seasonal location of the salt front (rkm 108, de Vries

and Weiss 2001). The percent of available nursery habitat was calculated as the fraction of the total nursery habitat in which HSI values were predicted to be positive under a given scenario. Nursery habitats that did not support positive HSI values were considered unavailable to juveniles.

Scenario 1: Historical Perspective—Legacy of the Albany Pool

This scenario simulated the impact of the historically polluted Albany Pool area on the availability and suitability of nursery habitat (Table 4). A baseline model was populated with mean summer temperatures observed or reconstructed from 1987 to 2005 for each river segment. Dissolved oxygen saturation was fixed at 85% commensurate with recent summer (June–September) monitoring data (Caraco et al. 2000). For hindcast simulations, DO saturation was decremented for the area corresponding to the historical extent of the Albany Pool. Dissolved oxygen saturation was reduced to 40% under the moderate hypoxia scenario and 20% under the severe hypoxia scenario for all river segments between rkm 231 and 178 (DO remained fixed at 85% up- and downstream of the Albany Pool area). Temperatures used in the hindcast simulations were the same as those used in the baseline model. The model was run and the effect on HSI within the Albany Pool

Table 4.—Summary table of bioenergetic modeling simulations of habitat suitability for a 5-g juvenile shortnose sturgeon in the upper Hudson River estuary. Temperature indicates range of years used for simulation and simulated change (e.g., +1°C). Salinity was held constant at 0 for all model runs. DO = dissolved oxygen.

Simulation	Scenario	Model input	
		DO (% sat)	Temperature
Historical: Albany Pool	Baseline run (current conditions)	85	1987–2005
	Moderate hypoxia	40	1987–2005
	Severe hypoxia	20	1987–2005
Forecast: Climate change	Baseline run (85% DO)	85	1988
	1°C increase	85	1988 + 1°C
	3°C increase	85	1988 + 3°C
	Baseline run (70% DO)	70	1988
	1°C increase	70	1988 + 1°C
	3°C increase	70	1988 + 3°C

area was compared among the baseline and historical scenarios. We then examined the change (if any) in nursery habitat availability between scenarios.

Scenario 2: Future Perspective— Temperature and Dissolved Oxygen

We simulated the impact of future regional climate change due to a combination of increased temperature and decreased dissolved oxygen saturation (Table 4). Mean summer temperature from 1988 was selected as a baseline temperature regime and DO was fixed at 85%. This year was representative of the period 1987–2005: temperatures at Tivoli Bay, Poughkeepsie, and Haverstraw Bay deviated less than $\pm 1^\circ\text{C}$ from the 19-year average while the Green Island and Glenmont sites were within ± 1.5 SD of the mean site-specific temperature. Also, 1988 produced the strongest year-class on record from 1980 to 1999 as hindcast from the 2004–2005 extant population (Woodland and Secor 2007) and is therefore assumed to represent appropriate physical conditions for juvenile shortnose sturgeon survival and growth.

In the first simulation series, temperature was increased by 1°C and then by 3°C for all river segments (DO fixed at 85%). Each increase was followed by a model run, the result of which was compared to baseline (1988) HSI values. We then simulated a concurrent decrease in dissolved oxygen saturation of 15%, representing increased oxygen demand from zebra mussels. Under this reduced oxygen simulation, DO saturation was fixed at 70% basin-wide while temperatures were again raised by 1°C and 3°C increments for each river segment. Patterns in estimated habitat suitability for all model runs were analyzed in a manner similar to the historical analysis.

Results

Habitat Suitability

Present-day summertime nursery habitat in the Hudson River appears to exceed the thermal growth optima for shortnose sturgeon by $2\text{--}3^\circ\text{C}$ (Figure 3). The shape of the temperature-growth response is conserved under 85% and 70% DO conditions; yet, thermal conditions corresponding to maximum HSI differs between the two DO levels. At 85%

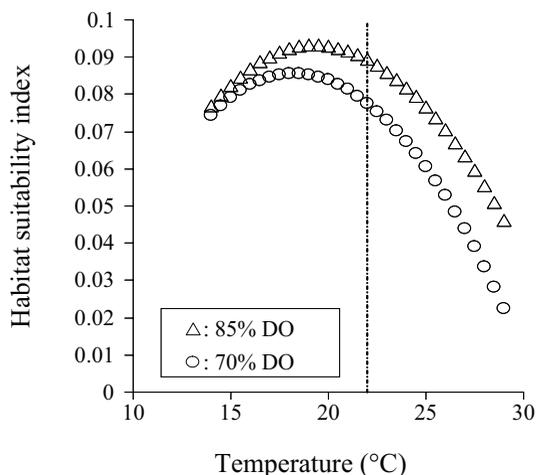


Figure 3.—Habitat suitability as indexed by modeled potential instantaneous growth rates for a 5-g juvenile shortnose sturgeon under the full spectrum of summer (July–September) water temperatures recorded from the tidal freshwater portion (river kilometer 248–63) of the Hudson River between 1987 and 2005. Mean water temp (21.9°C) over this period is denoted by the dashed line.

DO saturation HSI_{max} (0.093/d) occurs at 19.5°C while HSI_{max} (0.086/d) occurs at 18°C under 70% DO conditions (Figure 3). The average summer temperature of the upper Hudson River estuary from 1987 to 2005, 21.9°C , indicates a nursery-wide mean HSI of 0.089/d and 0.078/d under 85% and 70% DO saturation conditions, respectively. This corresponds to HSI values that are c. 9% less than optimal HSI values for either dissolved oxygen value (Figure 3).

Scenarios

Simulation 1: historical perspective—legacy of the Albany Pool.—The model predicted substantially reduced habitat suitability under moderate to severe hypoxia scenarios (Figure 4). The baseline model (85% DO) indicated a threefold higher average HSI value ($0.091/\text{d} \pm 0.0003$ [± 1 SD]) than that estimated under moderately hypoxic conditions (40% DO, HSI = $0.028/\text{d} \pm 0.016$) in the Albany Pool area. Overall habitat availability did not change under the moderate hypoxia scenario because HSI values remained positive throughout the river segments. The severe hypoxic stress scenario (20% DO) resulted in

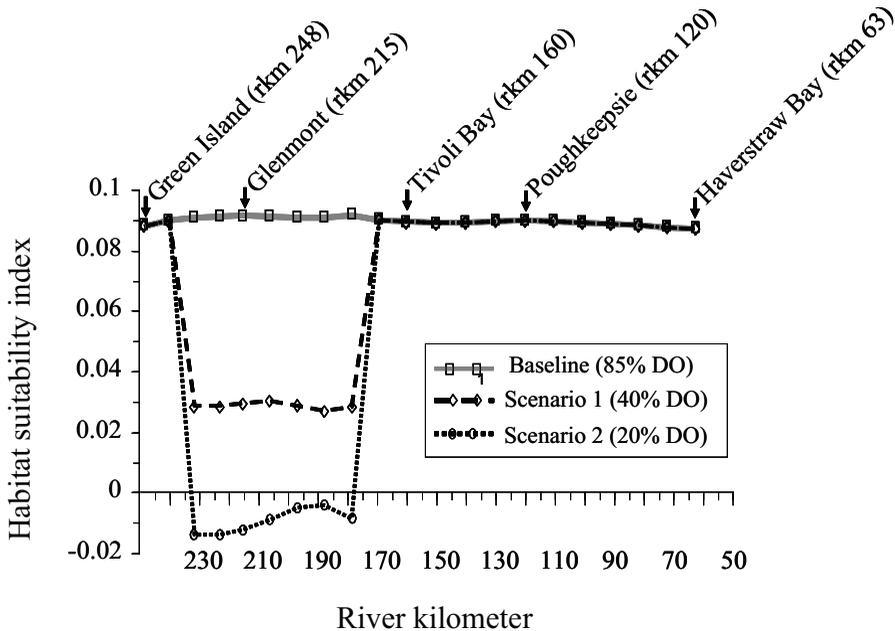


Figure 4.—Predicted habitat suitability is plotted against river kilometer (rkm) for a 5-g juvenile shortnose sturgeon under recent (baseline) and historical water quality simulations in the upper Hudson River estuary (tidal freshwater). Baseline conditions were modeled by fixing dissolved oxygen (DO) saturation at 85% for the entire estuary. Historical water quality scenarios were modeled by imposing moderate (40% DO) to severe (20% DO) seasonal summer hypoxia conditions on 53 km of the river downstream of Albany, New York (rkm 231–148).

a severe reduction in nursery habitat suitability with HSI declining to negative values in the Albany Pool area ($-0.010/d \pm 0.033$). Under the severe hypoxia scenario, total habitat availability (185 km) was reduced to 55% of available habitats (Figure 4).

Simulation 2: Future scenarios—temperature and dissolved oxygen.—Habitat suitability index values declined in the presence of a 1°C increase in water temperature (Figure 5; % DO saturation was maintained at 85% across river segments). Mean HSI across all river segments was reduced to $0.086/d \pm 0.0008$, a 4% decline from average habitat suitability under baseline conditions ($0.090/d \pm 0.007$). Raising water temperatures by a total of 3°C substantially reduced the average HSI, lowering the basin-wide mean suitability index to $0.077/d \pm 0.011$. Overall, the 3°C warming scenario reduced the average HSI by 14% from current temperature conditions. Habitat availability was unaltered.

When combined with a 15% decline in DO saturation, increasing water temperatures resulted in

a significant decline in HSI values, both within and between climate change scenarios (Figure 5). The 70% DO scenario result was qualitatively similar to the 85% scenario: baseline HSI $> 1^{\circ}\text{C}$ HSI $> 3^{\circ}\text{C}$ HSI. In the 70% DO scenario, increasing temperature by 1°C reduced HSI to an average of $0.073/d \pm 0.010$, 6% lower than from average baseline conditions ($0.078/d \pm 0.009$). When temperature was increased by 3°C in concert with 70% DO, average HSI declined to $0.061/d \pm 0.014$. This represents a 22% reduction in average habitat suitability from the baseline 70% DO run. Habitat availability was unaltered. These results indicate that, over all river segments, habitat suitability is substantially less at 70% DO with a 1°C increase than under 85% DO and a 3°C increase.

Discussion

Assessing the current and future status of freshwater and estuarine nursery habitats is particularly impor-

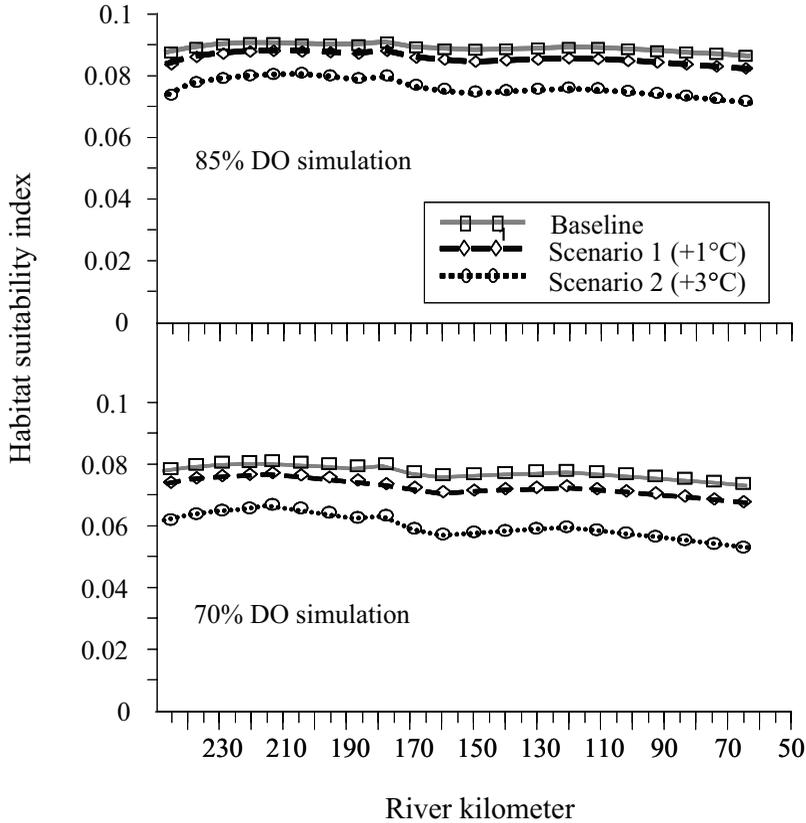


Figure 5.—Predicted habitat suitability is plotted against river kilometer for a 5-g juvenile shortnose sturgeon under a series of climate simulations on the Hudson River. Two baseline runs predict habitat suitability under average summer water temperatures (1988 data) and dissolved oxygen saturation conditions fixed at 85% (upper panel) and 70% (lower panel). The effect of two regional warming scenarios (+1°C and +3°C above baseline temperatures) on habitat suitability are modeled under 85% (upper panel) and 70% (lower panel) dissolved oxygen saturation conditions.

tant to the management of diadromous species. A recent synthesis of available data concluded that 18 North American diadromous species (excluding Pacific salmonids) are at risk of extinction from habitat destruction or degradation (Musick et al. 2000). Risks to diadromous fishes arise in part from the influence of fixed migration corridors (e.g., riverine habitat) that can serve as natural constrictions and may force species to traverse or remain within a compromised environment. Human development of riverine and estuarine areas can directly influence local water quality (e.g., DO, temperature), hydrography, and sedimentation rates, processes that can substantially alter the physical and chemical habitat of diadromous fishes. In the case

of anadromous species, this can limit the accessibility and availability of suitable spawning and nursery habitat (Maurice et al. 1987; Collins et al. 2000, Niklitschek and Secor 2005). Conversely, this suggests that these populations may respond favorably to restoration of these critical movement and nursery habitats. The potential benefit of nursery habitat restoration depends on the survival elasticity of the affected life stage(s) (Schaaf et al. 1987; Gross et al. 2002), the total area and potential contribution of the habitat to the parental stock (Beck et al. 2001; Dahlgren et al. 2006), and the emergent effects of habitat expansion on population resiliency (Kraus and Secor 2005). Nursery habitats may be limited to suitable patches within a single estuary-river sys-

tem (i.e., distinct population segments) or it may include multiple estuarine systems in the case of a panmictic stock (Ray 1997). The life history of shortnose sturgeon relegates populations to specific estuaries wherein changes in habitat suitability affect local population dynamics, making this species a tractable choice for this type of analysis.

Habitat degradation is listed as a principal factor in the decline of shortnose sturgeon populations range-wide (NMFS 1998), a conclusion corroborated by results from this modeling exercise. Our analysis suggests nursery habitat degrades rapidly under realistic historical and future water quality scenarios. Laboratory studies have shown that juvenile and yearling shortnose sturgeon are unusually sensitive to hypoxia and demonstrate decreased routine metabolism, consumption, feeding metabolism, growth, and survival at DO levels less than 40% saturation (Jenkins et al. 1993; Niklitschek 2001; Secor and Niklitschek 2001; Campbell and Goodman 2004). Prolonged exposure to the level of pervasive hypoxia (<30% DO saturation) observed prior to the late 1970s would have been lethal to juveniles (Niklitschek 2001; Campbell and Goodman 2004). Also, there is evidence that larval dispersal downstream is extensive in northern populations (Kynard and Horgan 2002), a behavioral trait that would effectively increase the likelihood of exposure to summer hypoxia for late-spring spawned fish dispersing downriver (Figure 1).

In addition to losses from direct asphyxiation, reduced production associated with increased metabolic costs (Secor and Gunderson 1998) or synergistic interactions among stressors (i.e., "habitat squeeze" sensu Coutant 1985) may lead to indirect mortality. The potential impact of a temperature-hypoxia squeeze is apparent from the future scenario modeling (Figure 5) in which there was a greater net decline in suitability when increased temperature was coupled with a 15% reduction in DO (Figure 5). In the Hudson River, larvae and age-0 juveniles have been collected along channels and deeper habitats (3–23 m, Hoff et al. 1988), areas prone to hypoxia. A study of Atlantic croaker *Micropogonias undulatus* in the Neuse River estuary (North Carolina, USA) found that intermittent hypoxia restricted fish to resource-limited shallow habitats led to crowding that may have reduced growth rates and drastically reduced prey densities in preferred deeper habitats (Eby et al. 2005). Therefore, the return

of normoxia during the critical summer growth and development period may have eliminated a substantial recruitment bottleneck to the Hudson River population. Further, improved habitat quality may be beneficial to all age-classes and stimulate population growth through increased production across life stages (Gross et al. 2002).

Our modeling efforts suggest that nursery habitat suitability for shortnose sturgeon is very responsive to changes in water quality. While empirical evidence is lacking to conclusively identify the factor or suite of factors that led to fourfold population growth in c. 20 years, nursery habitat suitability increased 62–111% and a potentially lethal dispersal barrier (Albany Pool) was eliminated just prior to the species' recovery. Results from the 20% DO scenario (historical simulation) suggest that shortnose sturgeon may have recovered 45% of the preindustrial total nursery habitat availability with the recovery of summertime normoxia. While hypoxia levels of 20% DO saturation have been reported in the Albany Pool area (Boyle 1969; Leslie et al. 1988), the actual magnitude of summertime hypoxia would have fluctuated seasonally and interannually due to variability in precipitation, wind stress, river depth, and anthropogenic inputs. Interestingly, the Albany Pool area, which was once the site of pervasive seasonal hypoxia, is predicted, based upon temperature and DO conditions, to be one of the most productive nursery areas ($HSI = 0.089/d \pm 0.001$ [rkm 231–178]) in the river. Increasing habitat availability would increase potential recruitment and overall carrying capacity (Schaaf et al. 1993; Gallaway et al. 1999; Luo et al. 2001; Niklitschek and Secor 2005). In fact, the recent fourfold increase in abundance of adult shortnose sturgeon (Bain et al. 2007) may reflect a reversion in Hudson River carrying capacity to preindustrial conditions.

The accuracy of the simulations is necessarily dependent on the quality of the data available to the model and the parameterization of the model. Specific attributes of the temperature data that we used to reconstruct historical conditions in the Hudson River have the potential to bias our hindcast estimates of habitat suitability. These data were collected for a variety of water quality monitoring purposes and, as such, may not be truly representative of benthic conditions as experienced by shortnose sturgeon. Heterogeneity in the physical features of estuaries (e.g., width, depth, flow rate, bathymetry)

can result in substantial spatial variability in vertical mixing, solar heating, and thermal stratification. Such issues are ameliorated in the freshwater Hudson River estuary, which shows little stratification in comparison to partially mixed estuaries like the Chesapeake Bay. Either over- or underestimating historical temperatures would bias our growth predictions; the directionality of the bias in this case would be an underestimation of potential growth rate in the face of exaggerated water temperatures. This is an important caveat that accompanies bioenergetic-based habitat modeling and must be taken into consideration when attempting to infer causality from model output. Second, the bioenergetic model applied in this analysis was parameterized through an extensive laboratory-based rearing study that utilized Savannah broodstock. Research has shown that shortnose sturgeon display latitude-dependent growth trajectories in which fish from southern estuaries (e.g., Pee-Dee, Altamaha, Savannah) grow at an accelerated rate and reach a lower asymptotic size than northern fish (Dadswell et al. 1984 and references therein). Therefore, the bioenergetics of the Hudson River population may be sufficiently different from the Savannah River population. Still, we would expect Savannah progeny to be better adapted to warm conditions, suggesting a conservative response to increased temperature relative to northern stocks. In terms of dissolved oxygen tolerances, there is little reason to expect that Hudson River progeny shortnose sturgeon would be less sensitive to hypoxia than Savannah River progeny.

A change in weight-at-age of juvenile Hudson River shortnose sturgeon over time could introduce bias into our modeling results due to the sensitivity of the bioenergetic model to sturgeon weight. Similarly, if the historical bottleneck on juvenile survival occurred earlier or later in the year, our selection of 5 g as an appropriate size-at-age would be inaccurate. Changing the weight parameter in the model alters the specific values of individual estimates; yet the patterns of habitat suitability described here for a 5 g individual are qualitatively similar to those obtained for fish up to 18.3 g. Unfortunately, we do not have sufficient data on fish less than 5 g to evaluate scenario sensitivity to a smaller size-class.

This shortnose sturgeon case study indicates that efforts directed at recovering water quality can

substantially increase the suitability and availability of spatially restricted nursery habitats. In light of the highly elastic survivorship rates during the young-of-the-year period (Gross et al. 2002), we believe that we have provided an important piece of circumstantial evidence linking the recovery of Hudson River shortnose sturgeon to the restoration of summertime normoxia. A similar situation occurred in the Delaware River (Delaware, USA), in which recent studies have linked restored water quality to the reproductive success of anadromous species. One study found the abundance of age-0 American shad *Alosa sapidissima* and striped bass *Morone saxatilis* increased 1,000-fold in a decade (1980s–1990s) following the return of normoxic conditions to a 40-km stretch of the river (Weisberg et al. 1996). In another study (Maurice et al. 1987), evidence of increased American shad egg and larvae abundance was attributed to the removal of a seasonal hypoxic zone that had prevented spawning aggregations of anadromous shad to reach the upstream nontidal spawning habitat. Interestingly, our simulation study indicated nonlinear bioenergetic responses due to the interaction of temperature and DO, suggesting that current regulations aimed at maintaining water quality standards may be insufficient to protect sensitive species or life stages under future climate changes. This uncertainty provides further incentive for fisheries managers to adopt a precautionary approach when considering proposals that develop or somehow alter known or potential habitat.

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Appendix I: Survival and Bioenergetics Model for Juvenile Shortnose Sturgeon (Modified from Niklitschek 2001)

Notes

1. Coefficient values from Niklitschek (2001) have been incorporated into the original equations, which have been simplified whenever possible.
2. Some coefficients of $f(\text{DO}, \text{Sal})_{\text{FC}}$ were re-estimated and formulas re-arranged to allow extrapolation down to 0% DO saturation.

Symbols Common to All Equations

W = fish weight (g); T = temperature ($^{\circ}\text{C}$); DO = dissolved oxygen saturation (%); and Sal = salinity.

Growth

$$G = \text{FC} - (\text{RM} + \text{SDA} + \text{ACT}) - (F + U) \quad (\text{Kj/g/d})$$

Food Consumption (FC)

$$\text{FC} = 1.23 \times W^{0.20} \times f(T)_{\text{FC}} \times f(\text{DO}, \text{Sal})_{\text{FC}} \quad (\text{Kj/g/d})$$

$$f(T)_{\text{FC}} = \frac{0.28 \times \exp[0.24 \times (T - 6)]}{1 + 0.28 \times \{\exp[0.24 \times (T - 6)] - 1\}}$$

$$f(\text{DO}, \text{Sal})_{\text{FC}} = \begin{cases} \text{COK} + \frac{[1 - \text{COK}] \times \text{KO}_i}{\text{KO}_{\text{max}}}, & \text{for } \text{DO} < \text{CDO}_{\text{crit}} \\ 1, & \text{otherwise} \end{cases}$$

$$c_{\text{FC}} = \frac{1}{\text{CDO}_{\text{crit}} - 30}$$

$$c_{\text{FC}} = \frac{1}{\text{CDO}_{\text{crit}} - 30}$$

$$\text{KO}_{\text{max}} = (\text{DO}_{\text{crit}} - 30) \times e^{-c_{\text{FC}} \times (\text{DO}_{\text{crit}} - 30)}$$

$$\text{CDO}_{\text{crit}} = 110.1 \times f(T)_{\text{FC}}$$

$$\text{COK} = 1 - 1.98 \times [f(\text{Sal})_{\text{RM}} \times f(T)_{\text{RM}}]$$

Routine Metabolism

$$RM = 0.42 \times W^{-0.196} \times f(T)_{RM} \times f(DO)_{RM} \times f(Sal)_{RM} \quad (\text{Kj/g/d})$$

$$f(T)_{RM} = e^{-0.085 \times (T-6)}$$

$$f(DO)_{RM} = \begin{cases} \text{COK}_{RM} + \frac{(1 - \text{COK}_{RM}) \times \text{KO}_i}{\text{KO}_{\max}}, & \text{for } DO < \text{RDO}_{\text{crit}} \\ 1, & \text{otherwise} \end{cases}$$

$$\text{KO}_i = (\text{DO}_i - 25) \times e^{[-c_{RM} \times (\text{DO}_i - 25)]}$$

$$\text{KO}_{\max} = \text{KO}_i \text{ at } \text{RDO}_{\text{crit}}$$

$$\text{COK}_{RM} = e^{(-0.027 \times T)}$$

$$\text{RDO}_{\text{crit}} = \frac{\log_e(T)}{0.051} + 25$$

$$c_{RM} = \frac{1}{\text{RDO}_{\text{crit}} - 25}$$

$$f(Sal)_{RM} = \frac{K_{sa} + K_{sb}}{1 + e^{2.52 \times W^{-0.158}}}$$

$$K_{sa} = e^{0.09 \times (29 - \text{Sal}) \times W^{-0.158}}$$

$$K_{sb} = e^{0.11 \times (\text{Sal} - 1) \times W^{-0.158}}$$

Postprandial Metabolism (SDA)

$$\text{SDA} = [0.12 + 0.00099 \times (\text{DO} - 79.6)] \times \text{FC} \quad (\text{Kj/g/d})$$

Active Metabolism (ACT)

$$\text{ACT} = 0.35 \times \text{FC} \quad (\text{Kj/g/d})$$

Egestion (F)

$$F = 0.075 \times \text{FC} \times (T - 18)^{-0.55} \times e^{\text{CRO}} \quad (\text{Kj/g/d})$$

$$\text{CRO} = -0.26 \times p_{\text{FC}} + 2.6 \times p_{\text{FC}}^2 - 0.011 \times (\text{DO} - 76.7)$$

p_{FC} = actual proportion of FC consumed by the fish

Excretion (U)

$$U = \text{RNE} + \text{XNE} \quad (\text{Kj/g/d})$$

$$\text{RNE} = 0.062 \times W^{-0.29} \times \text{RM}$$

$$\text{XNE} = 0.039 \times \text{FC}$$