

Year-Class Strength and Recovery of Endangered Shortnose Sturgeon in the Hudson River, New York

RYAN J. WOODLAND* AND DAVID H. SECOR

University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory,
Post Office Box 38, 1 Williams Street, Solomons, Maryland 20688, USA

Abstract.—Shortnose sturgeon *Acipenser brevirostrum*, a U.S. endangered species, has experienced a fourfold increase in abundance in the Hudson River in the past three decades. The age structure and trends in year-class strength of yearlings were investigated to evaluate the underlying pattern of annual recruitment that accompanied population recovery. Annuli in pectoral spine sections were used to estimate ages of specimens captured with gill nets bimonthly from November 2003 to November 2004. Age estimates (range = 5–30 years) were generated for 554 shortnose sturgeon ranging from 49 to 105 cm total length. Hindcast year-class strengths corrected for gear selectivity and cumulative mortality indicated high recruitments (31,000–52,000 yearlings) during 1986–1992. This interval was preceded and succeeded by approximately 5-year periods of lower recruitment (6,000–17,500 yearlings), suggesting 10-fold recruitment variability over the 20-year period. The pattern and relative magnitude of hindcast recruitment patterns were corroborated by shortnose sturgeon catch-per-unit-effort trends in an independent beam trawl survey. An analysis of hindcast year-class abundance and coincident environmental conditions indicated that flow volume and water temperature in the fall months preceding spawning were significantly correlated with subsequent year-class strength. Our results suggest that shortnose sturgeon of the Hudson River have experienced several strong year-classes concomitant with the observed population recovery during the 1980s and 1990s. The data indicate that population growth slowed during the late 1990s, as evidenced by a nearly constant recruitment pattern at depressed levels relative to the 1986–1992 year-classes.

Throughout their range, populations of shortnose sturgeon *Acipenser brevirostrum* have been negatively affected by anthropogenic changes to their habitats. Decreased water quality, habitat destruction, blockage of spawning runs, and incidental or intentional harvest (Kynard 1997; NMFS 1998; Collins et al. 2000; Secor and Niklitschek 2001; Root 2002) have caused reduced abundance or localized extirpations (e.g., Chesapeake Bay) in some instances (Secor et al. 2002). As a result, shortnose sturgeon was federally protected rangewide in 1973 pursuant to the Endangered Species Act in the United States and are considered a species of special concern under the Canadian Species at Risk Act.

Yet, while many shortnose sturgeon populations number less than 5,000 (Table 1), the total Hudson River population may be as high as 61,000 fish (Bain 2001). Results from mark–recapture studies indicate adult population growth from about 13,000 in 1980 (Dovel et al. 1992) to about 56,000 in 1998 (Bain 2001), a 400% increase over an 18-year period. In the case of the Hudson River, population growth can arise through increased adult survivorship, an increase in recruitment, or a combination of the two processes. An elasticity analysis conducted by Gross et al. (2002)

showed that rapid population growth of this and other sturgeon species is unlikely due to increased survival during the adult life stage. Rather, rapid population growth is most likely attributable to changes in first-year survival and the formation of strong year-classes. Their results are based on the premise that interannual mortality rate during the first year of life is highly variable relative to later stage mortality and fecundity rates, and thus exhibit the greatest scope for positive increase.

While a limited number of studies have directly addressed recruitment variability among sturgeon species (e.g., white sturgeon *A. transmontanus* [Paragamian et al. 2005]; lake sturgeon *A. fulvescens* [Nilo et al. 1997]), very little data are available on shortnose sturgeon recruitment dynamics (Dadswell et al. 1984; Kynard 1997; NMFS 1998). In the Hudson River, shortnose sturgeon mature at 3–8 years depending on sex (Bain 1997) and display a punctuated iteroparous spawning strategy in which adults of both sexes spawn intermittently (about every 2–11 years), substantially curtailing reproductive rates in comparison to annual spawners (Dadswell et al. 1984; Dovel et al. 1992; Boreman 1997). Within Acipenseridae, recruitment levels show similar magnitudes (3.5- to 7-fold), though causal mechanisms influencing the observed variability likely vary in importance by species and system. In a meta-analysis of recruitment variability among anad-

* Corresponding author: woodland@cbl.umces.edu

Received January 19, 2006; accepted September 1, 2006
Published online January 15, 2007

TABLE 1.—Estimated abundance of adult shortnose sturgeon in eight river systems along the Atlantic coast of Canada and the United States; CI = confidence interval.

River	Study period	Population estimate	95% CI	Source
Saint John	1973–1977	18,000	12,600–23,400	Dadswell (1979)
Kennebec	1977–1981	7,222	5,046–10,765	Dadswell et al. (1984)
Merrimack	1989–1990	33	18–89	NMFS (1998)
Connecticut	1976–1978	714	280–2,856	Dadswell et al. (1984)
Hudson	1998	56,708	50,862–64,072	Bain (2001)
Delaware	1981–1984	14,080	10,079–20,378	NMFS (1998)
Ogeechee	1993	361	326–400	NMFS (1998)
Altamaha	1988	2,862	1,069–4,226	NMFS (1998)

romous species, Rothschild and DiNardo (1987) found coefficient of variation of recruitment ($CV = 100\text{-SD}/\text{mean}$) values ranging from 25% to 284% among 25 stocks (four families, 11 species), with approximately two-thirds of the studies reporting recruitment variability between 50% and 150%.

Physical river conditions during spawning and young of the year (hereafter, age-0) rearing months have been shown to be important to year-class strength in anadromous species (Crecco and Savoy 1984; Maurice et al. 1987; Stevens et al. 1987). April–May spawning occurs in the uppermost segment of the tidal freshwater Hudson River, below the Federal Dam at Troy and approximately 246–190 km (rkm) from the river mouth (Bain 1997). Larval and age-0 juvenile nursery habitat in the Hudson River extends downstream from the spawning grounds and encompasses much of the tidal freshwater portion of the estuary (Figure 1; Bain 1997). In the Hudson River, adult shortnose sturgeon form dense overwintering aggregations in lower parts of the estuary (Dovel et al. 1992), suggesting that prespawning adults encounter similar environmental conditions. Annual fluctuation of environmental conditions could presumably affect either prespawning adult conditioning or early vital rates, thereby influencing subsequent year-class strength. A narrow range of preferred spawning conditions has been observed for water temperature and hydrological flow in previous studies (Dadswell et al. 1984; Kynard 1997), and may influence year-class strength through direct (e.g., age-0 survival) or indirect effects (e.g., spawning cues).

In this study we hypothesized that the rapid population growth of Hudson River shortnose sturgeon observed from 1980 to 1995 was facilitated by the presence of one or several very strong year-class(es) early in the period. Therefore, our goals were to (1) analyze the age structure of the extant population as a means of hindcasting the recruitment strength of those age-classes identified (ancillary steps included a partial age validation study and correlation with an independent record of abundance), (2) address our prediction

that recruitment would be higher after 1980 than before 1980 by comparing annual year-class strengths, testing for dominant cohorts, and investigating temporal trends, and (3) conduct an analysis examining the relationship between year-class strength and both water temperature and hydrological flow volume, potential factors influencing recruitment variability for Hudson River shortnose sturgeon.

Methods

Prior to sampling, protocols for capture and handling shortnose sturgeon were reviewed and approved by the National Marine Fisheries Service (NMFS) Protected Species Division (permit number 1360-01) and the New York State Department of Environmental Con-

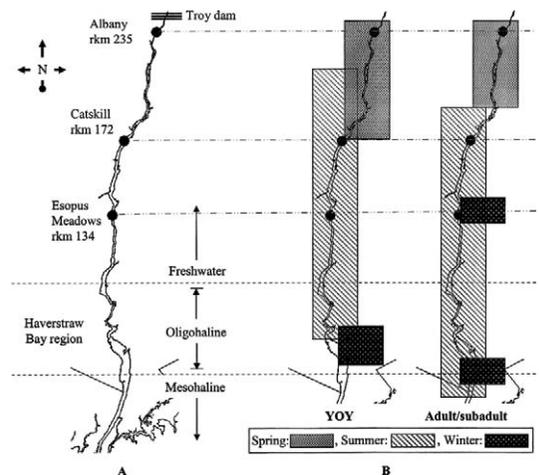


FIGURE 1.—Panel (A) shows a portion of the Hudson River, New York, indicating the spatial distribution of shortnose sturgeon sampling locations: Albany (April 2004), Catskill (June and August 2004), and Esopus Meadows (November 2003 and 2004 and March 2004). Panel (B) shows the seasonal habitat utilization for the age-0 (YOY), subadult, and adult stages with reference to the freshwater–brackish water interface (dashed lines) and primary sampling areas (alternating dashed and dotted lines). The figure was modified from Bain (1997).

ervation. Our methods adhered to the proscribed capture, care and handling protocols for shortnose sturgeon published by NMFS (Moser et al. 2000).

Shortnose sturgeon was sampled from November 2003 through November 2004 on a bimonthly basis. Sampling locations and gear deployments were chosen to maximize catch based upon the annual distribution of shortnose sturgeon in the system (Figure 1) (Dadswell 1979; Dovel 1979; Bain 1997). Fall and late winter sampling (November 2003, March and November 2004) was conducted near Esopus Meadows Point (rkm 134, measured from the terminus of the Hudson River), targeting an overwintering aggregation of primarily prespawning adults. Spring sampling (April) was carried out at the spawning grounds near Albany (rkm 235). Summer sampling (June–August) locations varied but were concentrated in the Catskill area (rkm 172). A total of 596 shortnose sturgeon was captured: 384 at Esopus Meadows, 129 near Albany, and 83 from the Catskill area.

Gill nets used for sampling were constructed of number 6 single-strand, clear monofilament rigged with a foam-core float line and lead-core line, and measured 1.83 m high \times 30.5 m long. Mesh sizes of 10.2, 15.2, and 17.8 cm (stretch measure) were selected based on previous research which reported all sizes of shortnose sturgeon larger than 48-cm fork length (FL) were susceptible to the meshes (Dadswell 1979). Multiple nets were deployed perpendicular to the river channel during slack tide and allowed to soak from 3 to 60 min, shorter soak times associated with very high catches during periods of winter aggregation. Captured shortnose sturgeon were extricated from the nets and immediately transferred to floating recovery pens. Each individual was measured to the nearest 10-g increment and to the nearest millimeter for FL and total length (TL). A 1-cm section of pectoral spine was removed from one of the pectoral fins approximately 1 cm distal from the point of articulation for age determination ($n = 580$; Rien and Beamesderfer 1994). All individuals were released alive and in apparently good condition following disinfection of the remaining spine with iodine.

Annuli were identified and enumerated on transverse sections approximately 1–2 mm thick with a dissecting scope under reflected light conditions. We defined an annulus as a bipartite structure of alternating opaque and translucent bands when viewed under reflected light (Stevenson and Secor 1999). Spine sections were aged twice without reference to individual size, date of capture, sampling location, or prior age estimate. Damaged or unreadable spines were removed from the sample and eliminated from further analyses. After eliminating damaged or unreadable spines ($n = 26$), age

estimates were generated from 554 spines. Spines were determined to be unreadable due to the presence of supernumerary annuli (division of a single prominent annulus into two or multiple lamellar structures), apparent resorption or deposition of calcareous material, and physical deterioration.

Aging precision was high as CV equaled 4.0% for the sample (Chang 1982). Nonparametric tests of means for CV values indicated a lack of both age (Kruskal–Wallace $\chi^2 = 5.8$; $df = 3$; $P = 0.12$) and temporal bias among estimates (Kruskal–Wallace $\chi^2 = 2.8$; $df = 3$; $P = 0.43$). The periodicity and timing of annulus formation was tested with a marginal increment analysis (MIA; Haas and Recksiek 1995; Campana 2001). Marginal increment ratios were calculated as the ratio of the width of the marginal increment to the mean width of the three previous, fully formed increments. The spring marginal increment ratio was 0.58 ± 0.08 (mean \pm SE), significantly less ($P < 0.05$) than both the summer (0.73 ± 0.09) and fall ratios (0.80 ± 0.09). Although the youngest (5–7 years) and oldest (19–26 years) shortnose sturgeon included in the MIA were not present in all months or seasons, there was no indication of bias in our results when the seasonal MIA was repeated using a subsample with a common age structure (10–17 years; Woodland 2005).

Age estimates from pectoral spines were used to construct mixed-sex growth models using the von Bertalanffy (1938) growth model. Attempts to fit gender-specific growth rates were not feasible because it was not possible to determine sex by external examination in the field. Only shortnose sturgeon of estimated age 5–23 years were included in the growth model because only these ages included multiple observations. Parameters for the growth model were derived through an iterative solving procedure that minimized the residual sum of squares between predicted and observed size at age (MS Excel, Solver).

Catch was adjusted for size selectivity based on mesh dimensions (10.2, 15.2, and 17.8 cm). Selectivity curves were generated and evaluated using catch data from sampling periods in which all nets were fished simultaneously with equal effort. The analysis was limited to 40–45 net-minute deployments at the Esopus Meadows (March) and Albany (April) sampling locations. This ensured physical river conditions were similarly affecting catchability among mesh sizes. Selectivity curves were modeled as Gaussian distributions with individual peaks corresponding to the observed l_o (optimal length captured) for each mesh size. Estimated means and standard deviations for all curves were generated using a maximum likelihood procedure applied to 25-mm-size bins and assuming a

normal error structure. We assumed that each mesh was equally efficient at capturing some optimal length of fish, l_o , dictated by the size of the mesh (Hamley 1975; Hovgård and Lassen 2000). Subsequently, selection curves were scaled to a common maximum value of 1 (Hamley 1975).

Following correction for gear selectivity, catch values for all age-classes across meshes were subjected to an effort modifier in which a ratio of the mesh-specific effort to total fishing effort was used to adjust the selectivity-corrected catches. Adjusted catches for each age-class were summed across meshes and the resultant age structure subjected to a catch-curve analysis (Ricker 1975). Analysis was limited to ages that had fully recruited to the gear (ages 7 and higher). The presence of anomalous year-class strength, indicated by the deviation of adjusted catch at age from the predicted catch, was analyzed by applying analysis of variance to the least-squares catch-curve residuals grouped into four successive stanzas composed of five year-classes each (e.g., group₁ = 1999–1995, etc).

The relative strength of each year-class at age 1 (yearlings) was predicted from the adjusted catch data and estimated annual mortality rate ($Z = 0.22$). Analysis was limited to age 5–26 years (1999–1979 year-classes) due to low sample size for the oldest age-classes. Age at capture was standardized to reflect a sampling date of November 2004. A recruitment strength index (RSI) was calculated by standardizing the resultant year-class strengths to a relative scale of 1. We estimated the historical abundance of yearlings from 1979 to 1999 by apportioning 61,000 (approximate Hudson River population estimate; Bain 2001) across observed (5–30 years) and estimated (1–4 years, from catch curve) age frequencies. The population fractions representing the 1979–1999 year-classes were then corrected for cumulative annual mortality to produce yearling abundance estimates.

As a method of corroborating hindcast year-class strength estimates, we compared trends in RSI with trends in shortnose sturgeon bycatch from a trawl survey. Data (1985–2003) from the Hudson River Utilities Fall Juvenile Survey were obtained from Normandeau Associates, which conducts the survey for a consortium of Hudson River Valley utility companies. Gear used is a benthic 3-m beam trawl of 3.8-cm body mesh with a cod end and cod end liner of 3.2 and 1.3 cm, respectively (Geoghegan et al. 1992). We used our growth model to estimate the age at which shortnose sturgeon recruit to the trawl gear based on the reported mean size at capture for the species (Bain et al. 1997). Trawl survey data were iteratively lagged in yearly time steps to verify that the highest regression

correlation coefficient was associated with the predicted age of capture.

Historical annual flow data (1979–1997) from the U.S. Geological Survey's (USGS) Green Island, New York, monitoring station (number 01358000) in Troy (rkm 246) was downloaded from the USGS website (USGS 2005). The data set contained one mean flow volume datum (ft³/s) per day per month, except for 1997, which only included January–September data. Historical daily water temperature data (°C, 1987–1999) was obtained from the Poughkeepsie Public Water Treatment (PPWT) facility in Poughkeepsie, New York (rkm 125) due to pervasive gaps in the archived data from the Green Island monitoring station. Regression analysis indicated water temperature at the downstream PPTW facility was offset by approximately 1°C and increased in a simple linear relationship ($b_1 = 1.02$, $b_0 = -1.2$; $r^2 = 0.97$) relative to water temperature at the Green Island monitoring site. Therefore, PPTW water temperature was used in analyses as a nonbiased (H_0 ; $b_1 = 1$; t -critical = 1.032; $df = 24$; $P > 0.25$) proxy of water temperature throughout the shortnose sturgeon spawning area. The correlation of both flow and temperature on RSI values of age-1 shortnose was evaluated using nonparametric correlation analysis (Spearman's rank correlation coefficient) due to persistent nonnormality of the data (Zar 1999). Mean monthly value, within-month variability (CV), and the daily rate of change of both parameters ($dFlow = m^3 \cdot s^{-1} \cdot d^{-1}$; $dTemp = °C/d$) were calculated for flow and temperature at the Green Island site. Analyses were constructed to identify correlations between the environmental parameters, and both early life history stages (April–December, during and after spawning) and adult prespawning conditioning (September–March, preceding spawning).

Results

The size distribution of captured shortnose was left-skewed, with an average weight of 2.78 ± 0.04 kg and TL of 783 ± 4 mm. The von Bertalanffy growth curve for TL was

$$TL = 1,045[1 - \exp^{-0.07(t+7.42)}],$$

TL_∞ being constrained to the maximum observed TL (1,045 mm; Figure 2). The relationship between FL and TL was described by a simple linear function (FL = TL × 0.88 – 12.19 [$r^2 = 0.95$]).

Selectivity curves for each mesh size had a unique l_o that followed a pattern of increasing l_o with increasing mesh size (Figure 3). Catch data, following correction for gear selectivity and effort, yielded an adjusted total catch of C_{adjust} equal to 1,238 shortnose sturgeon

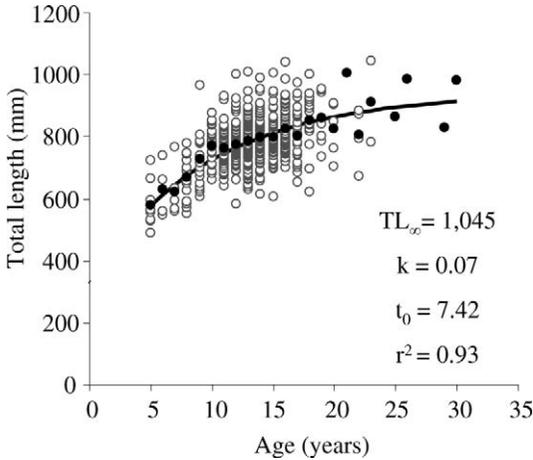


FIGURE 2.—Size-at-age data for Hudson River shortnose sturgeon (sexes combined). The length data for individual ages are represented by open circles, the mean lengths for each age by closed circles. The solid line is a von Bertalanffy curve fitted for ages 5–30, for which the model parameters are given.

($C_{\text{actual}} = 554$; Table 2). Catch-curve analysis of the adjusted catch yielded a Z equal to 0.22 ± 0.03 (SE; Figure 4A) and demonstrated a relatively high fit ($r^2 = 0.75$), although residuals exhibited a slight curvilinear pattern (Figure 4B).

Observed RSI was highest in 1988 (RSI = 1.0) and lowest in 1979 (RSI = 0.13) during the period 1979–1999 (Figure 5). Unadjusted age structure corroborated RSI results, 13-year-olds comprising the most numerous age-class ($n = 95$). No recruits were predicted from 1976, 1977, and 1980. Hindcast estimates of cohort abundances varied up to 10-fold, estimated yearling abundances ranging from 52,044 in 1989 (1988 year-class) to 5,961 yearlings in 1995 (1994 year-class; Figure 5). Mean yearling abundance for the 1988–1991 year-classes was 44,324, which was substantially higher than mean abundances for year-classes 1979–1987 (18,740) and 1992–1999 (11,899). Slight differences between year-class representation occurred

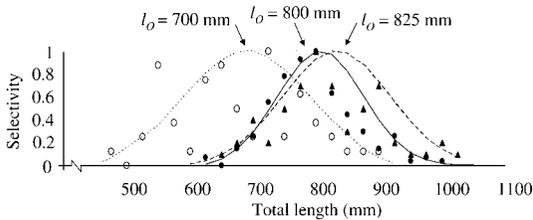


FIGURE 3.—Gear selectivity curves with the optimal capture length (l_o) for each mesh size (10.2-cm mesh: open circles, dotted curve; 15.2-cm mesh: filled circles, solid curve; and 17.8-cm mesh: triangles, dashed curve).

TABLE 2.—Catch of shortnose sturgeon by age-class, with mean TL, catch per mesh, and actual (C_{actual}) and adjusted (C_{adjusted}) catches over the course of field sampling. Instantaneous annual mortality, Z , is shown in the last row; the final value shown (0.22) was the one used in calculations.

Age-class and mortality	Mean TL (mm)	Mesh size (cm)			C_{actual}	C_{adjusted}
		10.2	15.2	17.8		
5	561	7	1	0	8	165
6	601	4	1	0	5	121
7	593	4	1	0	5	127
8	661	4	6	0	10	106
9	678	6	8	0	14	59
10	753	2	20	2	24	34
11	739	6	27	7	40	78
12	761	8	42	12	62	89
13	787	7	71	17	95	111
14	796	9	55	12	76	89
15	805	4	47	14	65	69
16	828	1	49	14	64	67
17	821	0	25	6	31	31
18	846	0	20	6	26	27
19	840	0	9	0	9	9
20	858	0	5	1	6	7
21	880	0	2	1	3	4
22	851	0	2	1	3	3
23	858	0	3	0	3	4
25	865	0	1	0	1	1
26	984	0	0	1	1	6
29	830	0	1	0	1	1
30	981	0	1	0	1	30
Z		0.3	0.22	0.2	0.42	0.22

between RSI and hindcast yearling cohort abundances due to the inclusion of several year-classes in apportioning yearling abundance (utilizing abundance $\approx 61,000$ for ages 1–30) that were excluded from the RSI calculation.

Based on our growth model and the mean size of shortnose sturgeon captured by the Hudson River Utilities Fall Juvenile Survey (TL = 670 mm; Bain et al. 1997), we estimated the average age of shortnose sturgeon captured by the trawl to be 6–10 years. Iterative lagging of the trawl catch-per-unit-effort (CPUE) data by yearly increments yielded significant, positive correlation values for the 6–8-year interval ($r_s > 0.5$; $P \leq 0.04$), though significant correlations existed for each of the 4–8-year lag periods ($r_s > 0.4$; $P \leq 0.05$). Lagging trawl data by 6 years satisfied the size-at-age estimate and resulted in the highest correlation ($r_s = 0.58$; $P = 0.01$) with reconstructed recruitment patterns (Figure 6).

Significant correlations were detected between RSI estimates and the three monthly–seasonal metrics (i.e., mean, CV, and slope) calculated from flow and temperature data. Several parameter metrics from the year preceding spawning events were significantly correlated with RSI estimates. Mean flow ($238.9 \text{ m}^3/\text{s}$) and daily $d\text{Flow}$ ($4.6 \text{ m}^3 \cdot \text{s}^{-1} \cdot \text{d}^{-1}$) during the fall

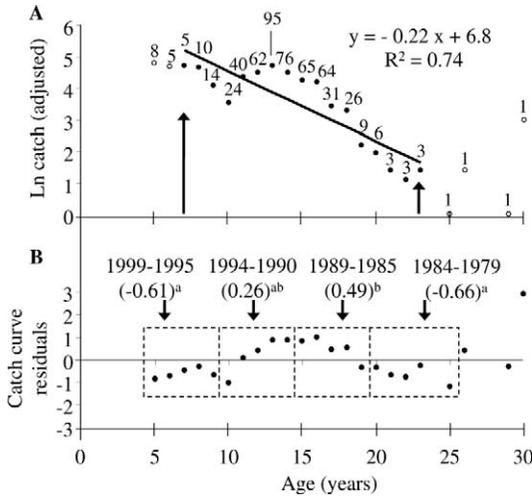


FIGURE 4.—In panel (A) the \ln_e transformed adjusted catch is plotted against age for Hudson River shortnose sturgeon. The solid line is a least-squares linear regression curve that was fitted to recruited ages only (filled circles). Above each symbol is the associated subsample size. In panel (B) catch-curve residuals are plotted against age, with four year-class stanzas denoted by the dashed boxes. The mean residual for each year-class stanza is given in parentheses; values with different superscripts are significantly different at $\alpha = 0.05$ (Tukey–Kramer test protected against experiment-wise error inflation).

(September and October combined) respectively showed positive correlations of r_s equal to 0.77 ($P = 0.005$) and r_s equal to 0.60 ($P = 0.05$) with RSI of yearlings spawned the following year. Variability of October water temperatures (CV) preceding spawning also yielded a highly significant correlation with RSI ($r_s = 0.83$; $P = 0.001$), and daily $dTemp$ ($-0.21^\circ C/d$) displayed a negative relationship ($r_s = -0.80$; $P = 0.002$). Correlations between spring hydrograph and temperature (spawning period: May, June) and RSI were not detected. Analysis of the late juvenile period similarly failed to detect correlations between RSI patterns and environmental parameters.

Discussion

The results of our study show that, within the Hudson River population, (1) annual recruitment of shortnose sturgeon can vary nearly 10-fold, (2) several strong year-classes coincided with the period of overall population growth, and (3) environmental conditioning of prespawn adults may play an important role in subsequent year-class strength. These findings have implications for management of the Hudson River population segment and may be broadly applicable to populations in other river systems. Also, this is an

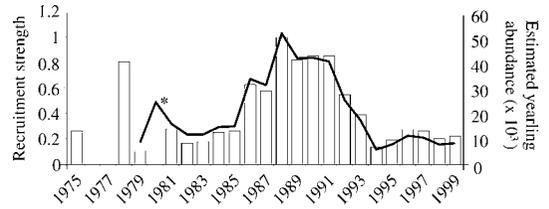


FIGURE 5.—Indexes of yearly recruitment success for Hudson River shortnose sturgeon based on actual catch adjusted for gear selectivity, effort, and cumulative mortality. The bars show relative annual recruitment strength and the solid line estimated cohort abundance at age 1, both with respect to hatch year (1975–1999). The abundance of the 1980 year-class (asterisk) was estimated from catch-curve analysis.

important, initial attempt to quantify recruitment processes in shortnose sturgeon, a central and as yet unaddressed aspect of the species’ ecology (NMFS 1998).

As a prerequisite to determining population demographics, annuli in pectoral spines were validated as an appropriate aging structure for Hudson River shortnose sturgeon. Though our precision (CV = 4.0%) compared favorably with studies of other acipenserids (e.g., white sturgeon: CV = 7.8%, Rien and Beamesderfer 1994; Atlantic sturgeon *A. oxyrinchus*: CV = 4.8%, Stevenson and Secor 1999) and marginal increment analysis supported the seasonal elaboration of annuli in the Hudson River population, age determination based on fin-spine cross sections and subsequent application to demographic analyses is subject to several assump-

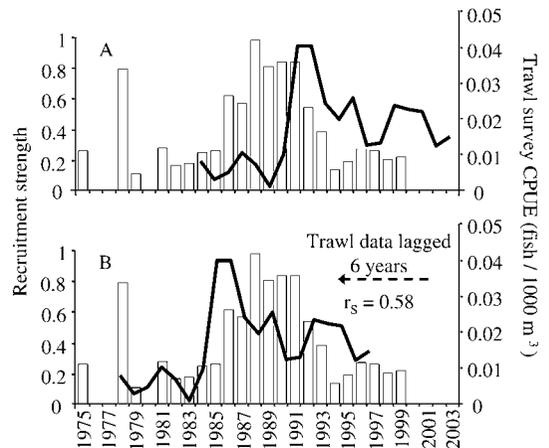


FIGURE 6.—Panel (A) shows hindcast values of annual shortnose sturgeon recruitment strength (bars) along with the CPUE values (solid line) obtained by the utilities-sponsored Fall Juvenile Trawl Survey. Panel (B) shows the same data with CPUE lagged by 6 years; the correlation between the latter two sets of values (r_s) is also given.

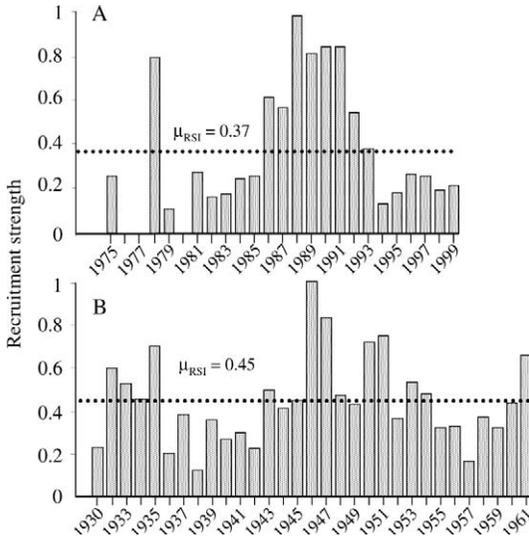


FIGURE 7.—Hindcast values of the recruitment strength index (RSI) for shortnose sturgeon from (A) the Hudson River (this study) and (B) the St. John River (data from Dadswell 1979). The year-classes included in each time series are given on the *x*-axes, and the mean RSI (μ_{RSI}) is shown for both systems.

tions. Inaccurate age determinations (assuming no bias) would tend to obscure actual year-class abundances, thereby dampening particularly strong year-classes (McAdam et al. 2005) and reducing estimates of interannual variability. Inaccuracy in aging coupled with bias (e.g., underestimation of estimated age with increasing actual age) would engender more complex deviations in hindcast patterns depending on the nature of the bias. Although we addressed these assumptions through a partial validation exercise, a certain level of uncertainty is inherent to structure-based aging, and further work using mark-recapture or similar techniques is critical to fully validate age determinations for this species.

Our data suggest shortnose sturgeon in the Hudson River have experienced a series of strong year-classes from 1988 to 1991 (Figure 5), supporting our central hypothesis that recruitment dynamics may have played a central role in recent increases in abundance. A pattern of basal annual recruitment interspersed with brief periods of highly successful year-classes would be expected of a species such as the shortnose sturgeon based on a periodic life history strategy (e.g., delayed maturation, high fecundity, and iteroparous spawning) (Winemiller and Rose 1992) and variability in interannual hydrological conditions. The population appears to have experienced substantial recruitment (>5,900 yearlings) annually for over two decades and

the resultant demographic structure is indicative of a robust population (i.e., no gaps in age structure). The period of enhanced recruitment 11–18 years ago (1993–1986) was corroborated through bycatch of adult shortnose sturgeon during the Hudson River Utilities Fall Juvenile Survey (Figure 6). Because survey gear and sampling design are standardized, interannual changes in the trawl survey shortnose sturgeon CPUE should accurately reflect changes in annual abundance of those fish vulnerable to the gear. A decline in recruitment from 1992 to 1994, followed by a period of relatively small year-classes, was observed in both in our age-based demographic analysis and the trawl survey CPUE. Interestingly, in more recent years lower recruitments are coincident with record high abundance levels. If recruitments become regulated as the population approaches carrying capacity, then dampened variability in year-class strength is expected in future years. Whereas physical disruption by conspecifics during spawning has not been observed among shortnose sturgeon (B. Kynard, Conte Anadromous Fish Research Center, personal communication), there may be other processes (e.g., size-dominant hierarchy; Kynard and Horgan 2002) linked to population density that affect variability of annual recruitment success.

Understanding the magnitude of variability in recruitment is a crucial component of fisheries management; our analysis indicates that year-class strength for the Hudson River shortnose sturgeon population varied nearly 10-fold over a 20-year period (1979–1999). The relative magnitude of recruitment variability is similar to that reported by Dadswell (1979) for the St. John River, Canada, population of shortnose sturgeon (Figure 7). The St. John population experienced moderately variable year-class strength (CV = 45%), RSI values ranging from 0.12 (1938) to 1.0 (1946). This is lower than the 66% CV we observed in the Hudson River population, although the longer time series for the St. Lawrence population would tend to statistically depress CV. A review of the available literature suggests other species of sturgeon demonstrate similar interannual variability in recruitment. A 1997 study by Nilo et al. observed the strongest year-class within the St. Lawrence River lake sturgeon population was seven times more numerous than the most depauperate one over a 12-year period. Published reconstructions of recruitment patterns suggest interannual variability on the order of 3.5-fold (Paragamian et al. 2005) to 6.5-fold (McAdam et al. 2005) for white sturgeon prior to systemic recruitment depression associated with damming and river channel modification (Coutant 2004). Directed sampling of juvenile sturgeon has yielded similar recruitment

variability with index values of age-0 white sturgeon (E_p : ratio of positive incidence tows to total tows, 6-year series) ranging from 0.04 to 0.82 (Counihan et al. 1999) and juvenile (late age 1, early age 2) Atlantic sturgeon (mean CPUE per 24 h net-day, 11-year series) from 0.1 to 2.25 (Armstrong and Hightower 2002). Studies such as these do not measure recruitment directly, but they suggest substantial interannual variability in year-class strength among anadromous sturgeon species.

Annual reproduction relies on an environmentally mediated endogenous mechanism in sturgeons and other fishes (de Vlaming 1972; Buckley and Kynard 1985). Although hydrographic conditions (e.g., temperature, flow, dissolved oxygen) during the spring have frequently been implicated in recruitment success of anadromous fishes (Crecco and Savoy 1984; Maurice et al. 1987; Stevens et al. 1987; Paragamian and Wakkinen 2002), there was no correlation between spring flow or temperature and year-class strength. In a synoptic compendium of shortnose sturgeon research, Dadswell et al. (1984) concluded that temperature "is probably the major factor governing spawning," spring freshet and substrate composition also being important. Spawning has been observed within a restricted range of water temperature (approximately 9–14°C) and current velocity (0.3–1.8 m/s; Dadswell et al. 1984; Kieffer and Kynard 1996; Kynard 1997), suggesting these and perhaps other environmental cues elicit a threshold-type response in regards to spawning activity. In a similar analysis, Nilo et al. (1997) found significant correlations between year-class strength in the St. Lawrence River lake sturgeon population and both spring flow volume in the Des Prairies River and the daily rate of increase in St. Lawrence River temperatures. The absence of a correlation between spring river conditions and annual recruitment may indicate that the scale of the analysis was overly coarse to detect a relationship or that other environmental parameter(s) may be controlling spawning success and egg-larval survival in the Hudson River.

The positive correlation between the rate of change of October water temperature and fall flow with recruitment success of the following year suggests that these factors may index a suite of environmental cues that initiate the final stages of gonadal development. While these metrics possess at least some degree of covariance, it is intriguing that those years in which river temperature drops rapidly while flow increases rapidly are positively associated with subsequent year-class success. Prespawn conditioning has been recognized as an important component of inducing gametogenesis in captive white sturgeon (Webb et al. 1999; Webb et al. 2001). Ambient water temperature during

the gametogenic and vitellogenic stages was shown to be a significant factor in determining the success of subsequent spawning of white sturgeon (Doroshov et al. 1997; Webb et al. 1999).

In conjunction with life history traits such as longevity and fecundity, knowledge of recruitment patterns among fish species are essential to assess current stock status and forecast demographic trends. This is especially pertinent for rare and endangered species such as shortnose sturgeon for which there still exists high uncertainty in the status and possible recovery of populations (NMFS 1998). Here, we have shown a period of about 20 years of sustained annual recruitments contributing to the recovery of Hudson River shortnose sturgeon. Our data suggest shortnose sturgeon in the Hudson River produced several particularly strong year-classes that translated into substantial population growth. Population growth through the formation of strong year-classes is well known to occur for anadromous species, an expectation formally demonstrated for sturgeon using an elasticity analysis (Gross et al. 2002). Consideration of abundance and recruitment variability of shortnose sturgeon in the Hudson River and elsewhere (e.g., Savannah and Delaware rivers) is hampered by the lack of robust historical data. Additionally, what data exist for shortnose sturgeon can be biased through misclassification and combination with its congeneric species, Atlantic sturgeon (Murawski and Pacheco 1977; Gilbert 1989). With few exceptions (most notably Dadswell 1979), information on abundance, recruitment variability, stock-recruitment relationships, and recruitment patterns is limited and will rely on current and future studies of extant age structure.

Acknowledgments

This work was supported by the Hudson River Foundation. Steven Nack provided valuable assistance in the field. We thank Mark Bain, Mark Mattson, and Randy J. Alstadt for provision of data; and Boyd Kynard and Michael J. Parsley for their insight and correspondence. Thanks to Richard Beamish, an associate journal editor, and three anonymous reviewers for constructive critical review of this manuscript; Christopher L. Rowe and Robert H. Hilderbrand provided comments on an earlier draft.

References

- Armstrong, J. L., and J. E. Hightower. 2002. Potential for restoration of the Roanoke River population of Atlantic sturgeon. *Journal of Applied Ichthyology* 18:475–480.
- Bain, M. B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. *Environmental Biology of Fishes* 48:347–358.

- Bain, M. B. 2001. Sturgeon of the Hudson River: ecology of juveniles. Report to the Hudson River Foundation, New York.
- Bain, M. B., S. Nack, and W. Dovel. 1997. Trends in the abundance of Hudson River sturgeons. Cornell University, Department of Natural Resources, Sturgeon Notes 4, Ithaca, New York.
- Boreman, J. 1997. Sensitivity of North American sturgeon and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.
- Buckley, J., and B. Kynard. 1985. Habitat use and behavior of pre-spawning and spawning shortnose sturgeon, *Acipenser brevirostrum*, in the Connecticut River. Pages 111–117 in F. P. Binkowski and S. I. Doroshov, editors. *North American sturgeons: biology and aquaculture potential*. Dr W. Junk, Dordrecht, The Netherlands.
- Campana, S. E. 2001. Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59:197–242.
- Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1208–1210.
- Collins, M. R., S. G. Rogers, T. I. J. Smith, and M. L. Moser. 2000. Primary factors affecting sturgeon populations in the southeastern United States: fishing mortality and degradation of essential habitats. *Bulletin of Marine Science* 66:917–928.
- Counihan, T. D., A. I. Miller, and M. J. Parsley. 1999. Indexing the relative abundance of age-0 white sturgeons in an impoundment of the lower Columbia River from highly skewed trawling data. *North American Journal of Fisheries Management* 19:520–529.
- Coutant, C. C. 2004. A riparian habitat hypothesis for successful reproduction of white sturgeon. *Reviews in Fisheries Science* 12:23–73.
- Crecco, V. A., and T. F. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1216–1223.
- Dadswell, M. J. 1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichthyes: Acipenseridae), in the Saint John River estuary, New Brunswick, Canada. *Canadian Journal of Zoology* 57:2186–2210.
- Dadswell, M. J., B. D. Taubert, T. S. Squiers, D. Marchette, and J. Buckley. 1984. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818. NOAA Technical Report NMFS 14 and FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 140.
- de Vlaming, V. L. 1972. Environmental control of teleost reproductive cycles: a brief review. *Journal of Fish Biology* 4:131–140.
- Doroshov, S. I., G. P. Moberg, and J. P. van Eenennaam. 1997. Observation on the reproductive cycle of cultured white sturgeon, *Acipenser transmontanus*. *Environmental Biology of Fishes* 48:265–278.
- Dovel, W. L. 1979. The biology and management of shortnose and Atlantic sturgeon of the Hudson River. New York State Department of Environmental Conservation, AFS9-R, Albany.
- Dovel, W. L., A. W. Pekovitch, and T. J. Berggren. 1992. Biology of the shortnose sturgeon (*Acipenser brevirostrum* LeSueur, 1818) in the Hudson River estuary, New York. Pages 187–216 in C. L. Smith, editor. *Estuarine research in the 1980s*. State University of New York Press, Albany.
- Geoghegan, P., M. T. Mattson, and R. G. Keppel. 1992. Distribution of the shortnose sturgeon in the Hudson River estuary, 1984–1988. Pages 217–227 in C. L. Smith, editor. *Estuarine research in the 1980s*. State University of New York Press, Albany.
- Gilbert, C. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight)—Atlantic and shortnose sturgeons. U.S. Fish and Wildlife Service Biological Report 82(11.122). U.S. Army Corps of Engineers Technical Report EL-82-4.
- Gross, M. R., J. Repka, C. T. Robertson, D. H. Secor, and W. van Winkle. 2002. Sturgeon conservation: insights from elasticity analysis. Pages 13–30 in W. van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. *Biology, management, and protection of North American sturgeon*. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Haas, R. E., and C. W. Recksiek. 1995. Age verification of winter flounder in Narragansett Bay. *Transactions of the American Fisheries Society* 124:103–111.
- Hamley, J. M. 1975. Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada* 32(11): 1943–1969.
- Hovgård, H., and H. Lassen. 2000. Manual on estimation of selectivity for gillnet and longline gears in abundance surveys. FAO Fisheries Technical Paper 397.
- Kieffer, M., and B. Kynard. 1996. Spawning of the shortnose sturgeon in the Merrimack River, Massachusetts. *Transactions of the American Fisheries Society* 125:179–186.
- Kynard, B. 1997. Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes* 48:319–334.
- Kynard, B., and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, and shortnose sturgeon, *A. brevirostrum*, with notes on social behavior. *Environmental Biology of Fishes* 63:137–150.
- Maurice, K. R., R. W. Blye, P. L. Harmon, and D. Lake. 1987. Increased spawning by American shad coincident with improved dissolved oxygen in the tidal Delaware River. Pages 79–88 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. *Common strategies of anadromous and catadromous fishes*. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- McAdam, S. O., C. J. Walters, and C. Nistor. 2005. Linkages between white sturgeon recruitment and altered bed substrates in the Nechako River, Canada. *Transactions of the American Fisheries Society* 134:1448–1456.
- Moser, M. L., M. Bain, M. R. Collins, N. Haley, B. Kynard, J. C. O'Herron, II, G. Rogers, and T. S. Squiers. 2000. A protocol for use of shortnose and Atlantic sturgeons. NOAA Technical Memorandum NMFS-OPR-18.

- Murawski, S. A., and A. L. Pacheco. 1977. Biological and fisheries data on Atlantic sturgeon, *Acipenser oxyrinchus* (Mitchill). National Marine Fisheries Service, Technical Series Report 10, Highlands, New Jersey.
- Nilo, P., P. Dumont, and R. Fortin. 1997. Climatic and hydrological determinants of year-class strength of St. Lawrence River lake sturgeon (*Acipenser brevirostrum*). Canadian Journal of Fisheries and Aquatic Sciences 54:774–780.
- NMFS (National Marine Fisheries Service). 1998. Recovery plan for the shortnose sturgeon (*Acipenser brevirostrum*). Prepared by the Shortnose Sturgeon Recovery Team, for the National Marine Fisheries Service, Silver Spring, Maryland.
- Paragamian, V. L., and V. D. Wakkinen. 2002. Temporal distribution of Kootenai River white sturgeon spawning events and the effect of flow and temperature. Journal of Applied Ichthyology 18:542–549.
- Paragamian, V. L., R. C. P. Beamesderfer, and S. C. Ireland. 2005. Status, population dynamics, and future prospects of the endangered Kootenai River white sturgeon population with and without hatchery intervention. Transactions of the American Fisheries Society 134:518–532.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Department of Environment Fisheries and Marine Service, Ottawa.
- Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of white sturgeon age estimates from pectoral fin rays. Transactions of the American Fisheries Society 123:255–265.
- Root, K. V. 2002. Evaluating risks for threatened aquatic species: the shortnose sturgeon in the Connecticut River. Pages 45–54 in W. van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Rothschild, B. J., and G. T. DiNardo. 1987. Comparison of recruitment variability and life history data among marine and anadromous fish. Pages 531–546 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Secor, D. H., and E. J. Niklitschek. 2001. Hypoxia and sturgeons. Chesapeake Biological Laboratory, TS-314001-CBL, Solomons, Maryland.
- Secor, D. H., P. J. Anders, W. van Winkle, and D. A. Dixon. 2002. Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. Pages 3–10 in W. van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Stevens, D. E., H. K. Chadwick, and R. E. Painter. 1987. American shad and striped bass in California's Sacramento-San Joaquin River system. Pages 66–78 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Stevenson, J. T., and D. H. Secor. 1999. Age determination and growth of Hudson River Atlantic sturgeon, *Acipenser oxyrinchus*. Fishery Bulletin 97:153–166.
- USGS (United States Geological Survey). 2005. Surface water data for USA: USGS surface-water monthly statistics: Hudson River at Green Island, New York, monitoring station 01358000. Available: <http://nwis.waterdata.usgs.gov>. (May 2005).
- von Bertalanffy, L. 1938. A quantitative theory on organic growth. Human Biology 10:181–213.
- Webb, M. A. H., J. P. van Eenennaam, S. I. Doroshov, and G. P. Moberg. 1999. Preliminary observations on the effects of holding temperature on reproductive performance of female white sturgeon, *Acipenser transmontanus* Richardson. Aquaculture 176:315–329.
- Webb, M. A. H., J. P. van Eenennaam, G. W. Feist, J. Linares-Casenave, M. S. Fitzpatrick, C. B. Schreck, and S. I. Doroshov. 2001. Effects of thermal regime on ovarian maturation and plasma sex steroids in farmed white sturgeon, *Acipenser transmontanus*. Aquaculture 201:137–151.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implication for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.
- Woodland, R. J. 2005. Age, growth, and recruitment of Hudson River shortnose sturgeon (*Acipenser brevirostrum*). Master's thesis. University of Maryland, College Park.
- Zar, J. H. 1999. Biostatistical analysis, 4th edition. Pearson Education, Inc., Delhi, India.