
#### Abstract

Title of Thesis:

\title{ AGE, GROWTH AND RECRUITMENT OF HUDSON RIVER SHORTNOSE STURGEON (ACIPENSER BREVIROSTRUM) }


Ryan J. Woodland, Master of Science, 2005
Thesis Directed By:
Professor David H. Secor, Department of Marine, Estuarine \& Environmental Science

Shortnose sturgeon (Acipenser brevirostrum), an Endangered Species, has experienced a several-fold increase in abundance in the Hudson River in recent decades. Age structure and growth were investigated to evaluate the hypothesis that improvements in water quality during the late 1970s stimulated population recovery. Specimens were captured using gill nets bi-monthly 2003 to 2004. Annuli in fin spine sections were determined to form at an annual rate and yielded age estimates of $5-30$ years for sizes $49-105 \mathrm{~cm}$ Total Length $(\mathrm{n}=554)$. Hindcast year-class strengths, corrected for gill net mesh selectivity and cumulative mortality indicated high recruitments (28,000-43,000 yearlings) during 1986-1992, which were preceded and succeeded by c. 5 year-periods of lower recruitment (5,000-15,000 yearlings). Results indicated that Hudson River shortnose sturgeon abundance increased due to the formation of several strong year-classes occurring about five years subsequent to improved water quality in important nursery and forage habitats in the upper Hudson River estuary.

# AGE, GROWTH AND RECRUITMENT OF HUDSON RIVER SHORTNOSE STURGEON (ACIPENSER BREVIROSTRUM) 

## By

Ryan J. Woodland

Thesis submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of

Master of Science
2005

Advisory Committee:
Professor David H. Secor, Chair
Assistant Professor Christopher L. Rowe
Assistant Professor Robert H. Hilderbrand
© Copyright by
Ryan J. Woodland
2005

## Dedication

I'd like to dedicate this work to my family for their encouragement, support and limitless patience.

## Acknowledgements

First, I'd like to thank my advisor, Dr. David H. Secor, for his direction and support during my Masters research. His mentorship helped to make my work a wonderful and exciting experience. I'd like to extend similar thanks to the other members of my committee, Drs. Christopher L Rowe and Robert H. Hilderbrand for their much appreciated advice and valuable feedback.

This work would not have been possible without the knowledge and assistance of Steven Nack on and about the Hudson River. I'd like to thank Scott McGuire and Bob Murphy for their help in the field and Jody Callihan for his help, advice and commiseration in the lab. Thanks to Vincent Mudrak, James Henne, Kent Ware, Roman Crumpton, Haile Macurdy, Carlos Eschevarria and Jaci Zelco for their assistance in acquiring samples from the USFWS National Fish Hatchery stock. I'd like to thank Drs. Frank Chapman, Doug Peterson, and Mark Bain for their interest, encouragement and their dedication to the shortnose sturgeon. Similarly, Steven Leathery and Jennifer Jefferies of the Office of Protected Resources; Sheila Eyler of the USFWS; Mark Collins of the South Carolina DNR; Mark Mattson of Normandeau Assoc.; Bill Andrews of the NYDEC; and also Vicky Kelly and Dave Fischer of the Institute for Ecological Studies for their assistance in locating and providing data used in some of the analyses included in this project.

A final, crucial thank you to the Hudson River Foundation, the University of Maryland Center for Environmental Science and Chesapeake Biological Laboratory for funding and supporting my research.

## Table of Contents

Dedication ..... ii
Acknowledgements ..... iii
Table of Contents ..... iv
List of Tables ..... vi
List of Figures ..... vii
Introduction ..... 1
Hypotheses and Goals ..... 10
Age Determination ..... 11
Growth and Mortality Rate ..... 11
Year-class Strength ..... 12
Methods ..... 13
Field Sampling ..... 13
Laboratory Methods ..... 16
Age Precision Tests and Age Validation ..... 17
Growth ..... 23
von Bertalanffy Growth Model ..... 23
Gompertz Growth Model ..... 24
General Growth Models ..... 25
Mark-recapture ..... 25
Gear Selectivity ..... 27
Baranov Model ..... 29
Holt Model ..... 30
Regression Model ..... 31
Recruitment ..... 32
Fall Juvenile Survey ..... 34
Environment: Flow ..... 35
Results ..... 37
Field Sampling ..... 37
Age Precision Tests and Age Validation ..... 41
Growth ..... 51
Gear Selectivity ..... 55
Recruitment ..... 60
Fall Juvenile Survey ..... 64
Environment: Flow ..... 69
Discussion ..... 72
Age Determination ..... 73
Growth ..... 77
Recruitment ..... 85
Gear Selectivity ..... 85
Mortality ..... 86
Age-structure ..... 87
Management Implications ..... 90
Appendix ..... 93
References ..... 107

## List of Tables

Table 1. Estimated status of shortnose sturgeon in eight river systems. Adapted from the National Marine Fisheries Service Recovery Plan for Shortnose Sturgeon (Acipenser brevirostrum), 1998 2
Table 2. Permitted capture and sampling schedule under NMFS Permit to Take Endangered Species \#1360. ..... 15

Table 3. Tag and meristic data of previously marked shortnose sturgeon recaptured during field sampling (from USFWS sturgeon tagging database). $\mathrm{FL}_{0}=$ Fork Length at tagging, $\mathrm{FL}_{\mathrm{R}}=$ Fork Length at recapture, $\mathrm{TL}_{0}=$ Total Length at tagging, $\mathrm{TL}_{\mathrm{R}}=$ Total Length at recapture, $\mathrm{Wt}_{0}=$ weight at tagging, $\mathrm{Wt}_{\mathrm{R}}=$ weight at recapture .26
Table 4. Statistical analyses used to diagnose accuracy of age determinations for hatchery raised sturgeon. ..... 45

Table 5. Mean Marginal Increment Ratio values (MIR) by sampling month and season $\pm$ $95 \%$ Confidence interval. Means with any identical letters are not significantly different at $\alpha=0.05$ (Tukey-Kramer protected against experimentwise error inflation).49

Table 6. Growth during time at large for recaptures of previously marked shortnose sturgeon during field sampling.

Table 7. Catch by age class with mean Total Length (TL), catch per mesh, actual ( $\mathrm{C}_{\text {actual }}$ ) and adjusted ( $\mathrm{C}_{\text {adjusted }}$ ) catches of shortnose sturgeon over the course of field sampling. In the bottom row is estimated mortality, Z , calculated for each mesh, actual, and adjusted values, Z used in calculations, 0.22 , given in boldface.62

Table 8. Mean catch curve residual values grouped by age-class stanzas. See Figure 21 for catch curve. Means with any identical letters are not significantly different at $\alpha=$ 0.05 (Tukey-Kramer protected against experimentwise error inflation).65

Table 9. Correlation of yearling recruitment strength index (RSI) values relative to shortnose sturgeon bycatch from the Hudson River utilities sponsored Juvenile Fall Survey, lagged over yearly increments

Table 10. Precision in ageing studies of Acipenser and other fish species of varying longevity, reported as average percent error (APE) and coefficient of variation (CV).74

Table 11. Growth parameters from the von Bertalanffy growth function estimated for shortnose sturgeon across their range. Boldface row indicates parameters derived during this study. 80

## List of Figures

Figure 1. Shortnose sturgeon bycatch catch-per-unit effort (CPUE) from the Hudson River utilities Fall Juvenile Survey 1985-1999.

Figure 2. Time series of spring-fall dissolved oxygen conditions in the Hudson River during the 1970s directly downstream of the Albany, NY area. The dotted line (c. 5 mg $\mathrm{L}^{-1}$ ) indicates an approximate threshold for hypoxia in sturgeons (Secor \& Niklitschek 2001). Data from Leslie et al. 1988

Figure 3. Lateral view of adult (upper image) and juvenile shortnose sturgeon (adult photo courtesy of J.Jensen, www.fishbase.org). Juvenile image has been expanded to show morphological detail (lower image).

Figure 4. Annual distribution of shortnose sturgeon within the Hudson River estuary. Seasonal habitat for life-stages is depicted with reference to the fresh/brackish interface (dashed lines) and the three primary sampling areas (alternating dashed and dotted line). Figure modified from Bain 1999.

Figure 5. Posterior lobe from a mounted shortnose sturgeon pectoral spine (transverse section) photographed under reflected light conditions at 450 X magnification. The opaque and translucent zones from a single annulus are indicated. Within the dashed box, a false or 'supernumary' annulus is differentiated from the 'true' annulus.

Figure 6. Posterior lobe of a shortnose sturgeon pectoral spine (36 X magnification) with annuli enumerated according to their position relative to the outermost annulus (marginal increment). Annuli are demarcated by the circles and increment width for each annulus is indicated by the brackets.

Figure 7. Catch per unit effort (CPUE) of Hudson River shortnose sturgeon over the course of the sampling period (2003-04). CPUE for each sampling period by gear type is shown in panel. ................................................................................................................ 38

Figure 8. Total catch $(\mathrm{n}=587)$ of shortnose sturgeon over the course of the sampling period (2003-04) by A) weight ( kg ) and B) Total Length (mm).

Figure 9. Distribution of estimated ages from interpretable spines ( $n=554$ )................. 40
Figure 10. Transverse sections of pectoral spines viewed under reflected light microscopy. Common sources of ageing error are indicated by arrows in each image. A) Spine showing initial stages of resorbtion of calcified material, canalization and proteinaceous deposits. B) Inclusion of secondary rays within the posterior lobes; inclusion can vary from two, one or none within the primary spine. C) Inconsistent annulus widths. D) "Crowding" of annuli near edge of spine.

Figure 11. Age-bias plot of subsampled spines $(\mathrm{n}=55)$ for Hudson River shortnose sturgeon. Mean second ages are plotted with $95 \%$ confidence intervals. The 1:1 ratio line is shown.

Figure 12. Analysis of age determinations of hatchery-raised shortnose sturgeon ( $\mathrm{n}=$ 46). A) Paired differences of estimated minus true ages (residuals) plotted against actual age (abscissa) with positive (young fish, 1-6 years) and negative (older fish, 7-20 years) bias clearly visible. B) Estimated ages (y-axis) plotted against actual ages (abscissa) with a linear regression (least squares) line (solid line) relative to the $1: 1$ line (dotted line)... 46

Figure 13. Transverse sections of pectoral spines from four different hatchery-raised shortnose sturgeon. A \& B) depict hatchery spines that appear to be laying down consistent increments without noticeable deformation or artificial structures. C \& D) depict spines that are deteriorated, possess multiple false structures and large calcareous deposits. ........................................................................................................................... 48

Figure 14. Mean seasonal Marginal Increment Ratios (MIRs) with 95 \% C.I. A) Overall Marginal Increment Analysis (MIA, ages 5-26). B) Reduced set MIA (ages 10-17). Seasonal MIR values that have different letters above them are significantly different at $\alpha$ $=0.05$ (Tukey-Kramer protected against experimentwise error inflation). 50

Figure 15. Growth curves calculated for mean Total Length (mm) and mean weight (kg) on age (years) with range of size values indicated by vertical bars and denoted by circles. Filled circles were used in the analysis, open circles were not. A \& B) $\log _{e}$ growth function; C \& D) Polynomial (quadratic) growth function; E \& F); von Bertalanffy growth function; $\mathrm{G} \& \mathrm{H}$ ) Gompertz growth function.

Figure 16. Size-at-age data for Hudson River shortnose sturgeon (combined sex data). Length-age data given by open circles (A) with mean length-at-age given by closed circles with fitted von Bertalanffy curve for ages 5-30 (B). Weight-age data given by open circles (C) with mean weight-at-age given by closed circles with fitted von Bertalanffy curve for ages 5-30 (D).

Figure 17. Growth trajectories of tagged shortnose sturgeon recaptured during sampling. Mean growth rate during time at large was $11 \pm 5 \mathrm{~mm}$ year $^{-1}$, with trajectories of growth exceeding the mean falling above the shaded area and those below falling within the shaded area. Maximum and minimum observed growth rates are indicated by the arrows.

Figure 18. Mean annual growth ( $\mathrm{mm} \mathrm{yr}^{-1}$ ) plotted against length at recapture (mm) for shortnose sturgeon tagged and recaptured from the Hudson River.

Figure 19. Selectivity curves for each mesh ( 10.2 cm mesh: open circles, 15.2 cm mesh: filled circles, 17.8 cm mesh: filled triangles) overlaid on catch values standardized to 1 . Plots A-C are curves generated from the Holt model, plots D-F are curves generated from the Regression model, and plots G-I are generated from the Baranov model. 59

Figure 20. Baranov selectivity curves generated for each of the mesh sizes. Optimal capture length $l_{O}$ is denoted by arrows for each mesh size.

Figure 21. A) Natural log transformed adjusted catch (y-axis) plotted against age for Hudson River shortnose sturgeon. Least-squares linear regression was fitted to filled data given by filled circles only. Above each symbol is the associated subsample size. B) Catch curve residuals plotted against age (abscissa) with four year-class stanzas denoted by the dashed boxes.

Figure 22. Index of yearly recruitment success based upon actual catch adjusted for gear selectivity, effort and cumulative mortality. Relative cohort strengths (y-axis) are plotted against hatch year (abscissa). 66

Figure 23. Estimated age 1 cohort abundance for Hudson River shortnose sturgeon, ages 5-30 years. 67

Figure 24. A) Hindcast annual recruitment strengths (open bars) versus shortnose sturgeon CPUE from the Hudson River utilities sponsored Fall Juvenile Trawl Survey. B) Trawl bycatch CPUE lagged by 6 years and overlaid on hindcast recruitment strengths.

Figure 25. Time series of mean monthly flow volume ( $\mathrm{ft}^{3}$ minute $^{-1}$, primary y-axis) collected from Green Island, New York (1946-2002, USGS) with hindcasted recruitment strength (secondary y-axis) overlaid on flow for corresponding years (Blow-up window) of 1974-1997.

Figure 26. Von Bertalanffy growth parameters $\mathrm{FL}_{\infty}$ (primary y-axis) and k (secondary yaxis) plotted against latitude.81

Figure 27. Predictions of Fork Length-at-age from von Bertalanffy growth models (combined sex models) for three different estuaries across the latitudinal range of shortnose sturgeon. Sources for each curve: 1) Dadswell et al. 1984, 2) current study, 3) Dadswell et al. 1984, 4) Dadswell 1979.

## Introduction

## Throughout their range, shortnose sturgeon (Acipenser brevirostrum)

 populations have been negatively affected by anthropogenic changes to their habitats. Decreased water quality, habitat destruction, blockage of spawning runs and incidental/intentional harvest (Kynard 1997, NMFS 1998, Collins et al. 2000, Secor \& Niklitschek 2001, Root 2002) have effected reduced abundance or localized extirpations (e.g. Chesapeake Bay) in some instances (Secor et al. 2002). As a result, shortnose sturgeon were federally protected range-wide in 1973 pursuant to the Endangered Species Act (ESA) in the United States and are considered a species of special concern under the Canadian Species at Risk Act (SARA).Yet, while many shortnose sturgeon populations number in the hundreds (Table 1), the Hudson River population may be as high as 55,000 fish (Bain et al. 2000). Due to their life history traits (i.e., periodic strategist sensu Winemiller \& Rose 1992), low rates of overall population growth and recovery are expected for shortnose sturgeon (Boreman 1997; Gross et al. 2002). In contrast, results from mark-recapture studies on the Hudson River indicate population growth from c . 10,000 individuals in 1980 to c. 55,000 by 1995 (Bain et al. 2000), a $450 \%$ increase over this 15-year period. Shortnose sturgeon bycatch data from the Fall Juvenile Survey sponsored by a consortium of Hudson River utilities corroborated a population increase during this period (Figure 1). An elasticity analysis conducted by Gross et al. (2002) indicates that such rapid population growth is unlikely to be the result of enhanced survival rates among sub-adult and adult life stages (i.e., due to protection from harvest). Rather, rapid population growth in sturgeons can only

Table 1. Estimated status of shortnose sturgeon in eight river systems. Adapted from the National Marine Fisheries Service Recovery Plan for Shortnose Sturgeon (Acipenser brevirostrum), 1998.

| River | Study period | Population Estimate | $95 \%$ Confidence Interval |
| :---: | :---: | :---: | :---: |
| Saint John | $1973-1977$ | 18,000 | $12,600-23,400$ |
| Kennebec | $1977-1981$ | 7,222 | $5,046-10,765$ |
| Merrimack | $1989-1990$ | 33 | $18-89$ |
| Connecticut | $1976-1978$ | 714 | $280-2,856$ |
| Hudson | 1995 | 38,024 | $26,427-55,072$ |
| Delaware | $1981-1984$ | 14,080 | $10,079-20,378$ |
| Ogeechee | 1993 | 361 | $326-400$ |
| Altamaha* | 2004 | 2,862 | $1,069-4,226$ |



Figure 1. Shortnose sturgeon bycatch catch-per-unit effort (CPUE) from the Hudson River utilities Fall Juvenile Survey 1985-1999.
occur due to changes in first year survival and the formation of strong annual cohorts (year-classes). These results lead to two questions: 1) 'Why did the abundance of shortnose sturgeon increase dramatically in the Hudson River?' and 2) 'Why did this occur during the period 1980-1995?'

The increase in shortnose sturgeon abundance in the Hudson River was preceded by improved water quality during the previous decade, as mandated by the Clean Water Act (CWA) of 1970. Prior to the 1970's, dissolved oxygen (DO) concentrations in the 60 km stretch of the Hudson River below Albany (c. km from river mouth $[\mathrm{rkm}]=235)$ dropped precipitously with the onset of summer $\left(\mathrm{c} .2 \mathrm{mg} \mathrm{L}^{-}\right.$ ${ }^{1}$ ), reaching a nadir in the early fall ( $<1 \mathrm{mg} \mathrm{L}^{-1}$; Figure 2 ; Leslie et al. 1988). This stretch of the river, known as the "Albany Pool" (Boyle 1969), coincides with approximately $40 \%$ of the shortnose sturgeon's estimated nursery habitat (Dovel et al. 1992, Haley 1999). Thus, the hypoxic Albany Pool may have functioned as a recruitment bottleneck, rendering much of the summertime nursery habitat unsuitable for juvenile shortnose sturgeon (Secor and Niklitschek 2001). As a result of the CWA, stringent standards on industrial and municipal effluent precipitated the return of normoxia to the Albany region by 1978 (Figure 2).

The Hudson River shortnose sturgeon population is centered within the species' historical range, which stretches from the St. John River in New Brunswick southward to Florida’s St. Johns River (Vladykov \& Greeley 1963, Dadswell et al. 1984). Present day distribution mirrors historical patterns in the northern region while extirpations and unknown population status characterizes many populations in


Figure 2. Time series of spring-fall dissolved oxygen conditions in the Hudson River during the 1970s directly downstream of the Albany, NY area. The dotted line (c. 5 $\mathrm{mg} \mathrm{L}^{-1}$ ) indicates an approximate threshold for hypoxia in sturgeons (Secor \& Niklitschek 2001). Data from Leslie et al. 1988.
the Mid-Atlantic and southern portion of the species' range (Dadswell et al. 1984, NMFS 1998, Collins et al. 2000).

The anadromous shortnose sturgeon (Figure 3) is the smallest of North America's coastal sturgeons, and inhabits large, estuarine systems ranging from full salinity (> 30 psu ) to damlocked non-tidal fresh water (e.g., upper Connecticut River) (Greeley 1937, Dadswell 1979, Taubert 1980, Dovel et al. 1992, Collins \& Smith 1997, Kynard 1997). The largest individual on record is also the oldest: a 143 cm Total Length (TL) female weighing 23.6 kg was captured from the St. John River in New Brunswick, Canada having an estimated age of 67 years (Dadswell 1979). Depending upon latitude (in which maturation occurs later in northern latitudes), males become sexually mature at 2-11 years, and females at 4-18 years (Dadswell et al. 1984).

Shortnose sturgeon display a punctuated iteroparous spawning strategy in which adults of both sexes spawn intermittently (c. every 2-11 years), substantially curtailing reproductive rates in comparison to annual spawners (Dadswell et al. 1984, Boreman 1997). The spring spawning event follows an upstream migration and typically occurs over hard substrate in moderate to swift flow velocities ( $37-180 \mathrm{~cm}$ $\sec ^{-1}$ ) with water temperatures ranging from 9 to $15{ }^{\circ} \mathrm{C}$ (Taubert 1980, Dadswell et al. 1984, Kynard 1997). Initially, embryos (1-8 days post-hatch) orient to benthic structure followed by a shift in orientation towards the water column that initiates a diurnal downstream dispersal to juvenile nursery habitats (Richmond \& Kynard 1995, Kynard \& Horgan 2002).


Figure 3. Lateral view of adult (upper image) and juvenile shortnose sturgeon (adult photo courtesy of J.Jensen, www.fishbase.org). Juvenile image has been expanded to show morphological detail (lower image).

In the Hudson River and most other estuaries, young-of-the-year (YOY) shortnose sturgeon make exclusive use of freshwater habitats before becoming euryhaline (Niklitschek (2001). Larval and YOY nursery habitat in the Hudson River extends downstream from the spawning grounds near the Federal Dam in Troy, NY (rkm 246), and encompasses much of the tidal freshwater portion of the estuary (Bain 1997). Sub-adults and adults form dense seasonal aggregations in well-defined areas (Dadswell 1979, Dovel 1992, Buckley \& Kynard 1985, Kynard 1997). In the Hudson River, non-spawning adults and juvenile shortnose tend to over-winter near the fresh/brackish water interface in the Haverstraw Bay region (rkm 54-61; Figure 4; Bain 1997). A second overwintering aggregation occurs near Kingston (rkm 140), serving as a staging area for ovigerous adults participating in the following spring's spawning migration (Bain 1997).

Shortnose sturgeon, like many congenerics., are sensitive to hypoxia and display negative metabolic and behavioral responses in the presence of low ambient DO levels (Secor \& Gunderson 1998, Secor \& Niklitschek 2001, Campbell \& Goodman 2004). A recent study by Campbell and Goodman (2004) found juvenile ( $\leq$ 134 day-old) shortnose sturgeon to be unusually sensitive to low DO in acute tests (24 h), with $50 \%$ mortality occurring at $2.2 \mathrm{mg} \mathrm{L}^{-1}$ and $26^{\circ} \mathrm{C}$ for 134 day-old fish. In the same study, lethal concentrations for younger fish occurred at similar or higher concentrations, ranging from $2.2 \mathrm{mg} \mathrm{L}^{-1}$ (104 day-old) to $2.7 \mathrm{mg} \mathrm{L}^{-1}$ ( 77 day- old). These results agreed with prior work by Jenkins et al. (1993) who reported a similar pattern of sensitivity to hypoxia in juvenile shortnose sturgeon.


Figure 4. Annual distribution of shortnose sturgeon within the Hudson River estuary. Seasonal habitat for life-stages is depicted with reference to the fresh/brackish interface (dashed lines) and the three primary sampling areas (alternating dashed and dotted line). Figure modified from Bain 1999.

## Hypotheses and Goals

My thesis is that the rapid population growth by Hudson River shortnose sturgeon observed during the 1980-1995 period was due to improved water quality in nursery habitats. To evaluate the link between recovering water quality and increasing shortnose sturgeon abundance, I retrospectively estimated past year-class strengths from the age structure of the extant population. I predicted that year-class strengths adjusted for gear efficiency and cumulative mortality effects would be higher after 1980 than before 1980. The pattern of incidental captures of shortnose during the Hudson River Utilities Juvenile Fall Survey (1985-2003) provides evidence that the 1980s were a pivotal decade in which a large pulse of sturgeon recruited to the adult population (individuals tend to be susceptible to survey gear at lengths $>500 \mathrm{~mm}$ ). These anecdotal data support the hypothesis that one or more very strong year-classes recruited to the population during the 1980s.

High spring freshet volume associated with seasonal precipitation and climatic conditions (e.g. rate of snow-melt, water temperature, etc.) has been implicated in favoring spawning success among anadromous species (Stevens et al. 1987, Secor 2000, Jung \& Houde 2003). Therefore, I predicted that spring freshet volume in the Hudson River would be positively correlated with YOY survival and subsequent recruitment. This secondary analysis was incorporated to examine the possibility that strong recruitment events during the 1980s stemmed from favorable flow conditions rather than improved DO levels.

Direct sampling and ageing of Hudson River shortnose sturgeon supplied estimates of current growth and mortality, age structure of the standing stock, and the
relative abundances of previous year classes. In particular, I used shortnose sturgeon longevity to provide a retrospective analysis of annual recruitments as far back as the late 1970s. In order to investigate the current demographics of this population and accurately hindcast recruitment events, I focused my research on three specific objectives:

## Age Determination

The development of an accurate and precise ageing methodology was a critical goal of my thesis. Although an age determination technique has not yet been validated for shortnose sturgeon, ageing of Acipenser sp. is typically carried out by enumerating concentric growth structures on thin cross-sections of the ossified anterior spine of a pectoral fin (Cuerrier 1951, Rossiter et al. 1995, Stevenson and Secor 1999). A comprehensive study conducted by Brennan and Cailliet (1989) analyzed a suite of calcified structures (i.e., pectoral fin spines, opercles, clavicles, cleithra, scutes and medial nuchals) collected from white sturgeon (A. transmontanus) and reported that pectoral spines provided the highest level of inter- and intra-reader precision among all structures evaluated. The use of pectoral spines is also preferable to other structures because it has been shown to be non-deleterious to shortnose sturgeon (Collins and Smith 1996).

## Growth and Mortality Rate

I estimated present vital rates of the Hudson River population and contrasted with mark-recapture estimates and literature values from the Hudson River and other systems. Intra- and inter-system comparisons of vital rates allowed corroboration of
age estimates with previous studies. I was also interested in detecting differences in observed versus expected mortality patterns as a means of evaluating past year-class strengths (see below).

## Year-class Strength

To accurately hindcast annual recruitment strengths, gear selectivity and population mortality rate were modeled to adjust the current age structure. Annual year-class strengths were compared and tested for dominant cohorts, temporal trends, and correlation with other records of abundance and environmental variables.

## Methods

## Field Sampling

Prior to sampling, protocols for capture and handling shortnose sturgeon were reviewed and approved by the National Marine Fisheries Service Protected Species Division (Permit No. 1360-01), NY State Department of Environmental Conservation, and the Institutional Animal Care and Use Committee of University of Maryland Center for Environmental Science. Our methods adhered to the proscribed capture, care and handling protocols for shortnose sturgeon published by NMFS (NMFS 2000).

I conducted field sampling on the Hudson River 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 4) (Dovel 1992, Dadswell 1984, Bain 1997). Fall and late winter sampling (November-2004, March/November-2005) was conducted at Esopus Meadows Point (rkm 134), targeting an over-wintering aggregation assumed to consist of primarily pre-spawn adults and juveniles. Spring sampling (April-2005) was carried out at the spawning grounds near Albany, several kilometers south of the Federal dam at Troy (rkm 245). Summer sampling (June-August-2005) locations varied but were concentrated in the Catskill area (rkm 172) because the species tends to disperse during summer (Bain 1997). Based on a statistical analysis using a test dataset derived from research conducted on shortnose in the St. John River estuary, New Brunswick (Dadswell 1979), target sampling goals were set in terms of overall sample size and monthly sample size (D. Secor, pers.
comm.). These sampling goals were established to provide reasonable power in subsequent analyses (e.g., growth rate, mortality, marginal increment analysis) while minimizing capture and/or handling stress in accordance with our Endangered Species Permit (Table 2).

Gill nets used for sampling were constructed of \#6 single strand, clear monofilament rigged with a foam-core float line and lead-core line, measuring 0.91 m high by 30.5 m in length. We attached concrete anchors and floats to the distal ends of the lead line and float line respectively as a means of anchorage and retrieval. Mesh sizes of 10.1, 15.2 and 17.8 cm (stretch) were selected based on previous research, which showed these meshes captured all sizes shortnose sturgeon beyond 48 cm Fork Length (FL) (Dadswell 1979). Nets were set perpendicular to the river channel during slack tide and allowed to soak from 3 to 60 minutes, depending on the rate of capture for a given location and day. We employed a YSI® meter to measure water temperature, salinity and dissolved oxygen at most sampling sites (the meter was unavailable during summer sampling). Latitude and longitude were also recorded at each sampling location using GPS.

Captured sturgeon were carefully extricated from the net and immediately transferred to floating recovery pens. Sturgeon were weighed to the nearest 10 grams with a spring scale then measured for FL and Total Length (TL) to the nearest millimeter. During the spring sampling period, an attempt was made to sex fish based on external features associated with spawning (Dadswell 1979). Sturgeon were scanned on their dorsal surface with a Passively Induced Transponder tag reader (Pocket Reader EX®, Biomark, Inc.) to identify internal tags, and were visually

Table 2. Permitted capture and sampling schedule under NMFS Permit to Take Endangered Species \#1360.

| Allowable capture | Actual capture | Life stage | Purpose | Region | Sampling schedule |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 190 | 191 | Juvenile/Adult | Population age structure, growth rate | ${ }^{\dagger}$ Haverstraw area (rkm 50-60) | November 1 December 20, 2003 |
| 190 | 141 | Juvenile/Adult | Population age structure, growth rate | Kingston area (rkm 140) | March 1 April 30, 2004 |
| 190 | 176 | Juvenile/Adult | Population age structure, marginal increment analysis | Albany-Troy area (rkm 230-245) | $\begin{gathered} \text { May } 10- \\ \text { June 30, } 2004 \end{gathered}$ |
| 100 | 36 | Juvenile/Adult | Population age structure, marginal increment analysis | Newburg-Kingston (rkm 90-140) | June 15 - <br> November 30, 2004 |
| 70 | 56 | Juvenile/Adult | Age validation | Warm Springs (GA), Bears Bluff (SC), UF Gainesville (FL) | November 1, 2003 - <br> November 30, 2004 |
| 34* | - | Juvenile/Adult | Accidental morality | - | November 1, 2003 - <br> November 30, 2004 |
| 740 | 600 |  |  |  |  |

[^0]examined for external tags. Past and ongoing studies of shortnose sturgeon by other scientists have applied both external and internal tags to track migration and habitat use patterns, and measure abundance (Dovel 1992, Bain 1997, NMFS 1998).

A one-centimeter section of pectoral spine was removed from one of the pectoral fins approximately 1 cm distal from the point of articulation with the pectoral girdle. This minimized the risk of losing proximal annuli associated with growth during the early life period while preventing damage to the artery occurring at the articulation of the spine (Rien \& Beamesderfer 1994). Pruning shears were used to cut through the pectoral spine and a knife employed to separate the most anterior spine from adjacent secondary spines and the supporting membrane of the fin. Collins and Smith (1996) demonstrated that full removal of the primary ray (spine) of the pectoral fin had no deleterious effect on either the growth or survival of shortnose sturgeon. Spines were stored and numbered to allow cross-reference with collection data. Following removal of the spine section, the remaining spine was disinfected with iodine prior to releasing the fish. Effort was made to minimize handling times (i.e., time outside of staging or recovery pens); fish were allowed to recover from the capture process before examination and spine removal. All individuals were released alive and in apparently good condition.

## Laboratory Methods

Spine samples were dried under a fume hood for a period of at least three weeks. Excess flesh was either mechanically removed with a knife or allowed to decay via microbial activity. Spine samples were then glued to an epoxy foundation and sectioned along the transverse plane to 1-2 mm thickness using a Buehler Isomet
${ }^{\circledR}$ low-speed saw. Sections were then fastened to petrographic glass microscopy slides with thermoplastic glue. If required to improve visual contrast of annular zones, sections were ground using wetted 800-1200 grit sand paper and polished by hand using a $0.3 \mu \mathrm{~m}$ alumina slurry on mounted polishing felt.

Annuli were identified and enumerated under 105-1350 X magnification using a stereo-microscope. For the purpose of our study, we defined an annulus as a bipartite structure of alternating opaque and translucent bands when viewed under reflected light (Stevenson \& Secor 1999). Narrow translucent zones were assumed to form during the winter/spring month, whereas wide opaque zones were assumed to represent growth during the summer/fall feeding periods (Brennan \& Cailliet, 1991, Rien \& Beamesderfer 1994). To distinguish "true" from supernumary annuli, only those annuli were tallied in which the translucent zone formed a distinct continuous band throughout the posterior lobes of the section (Figure 5). Live-feed video was used for training purposes, providing a real-time image of spine sections that allowed for simultaneous interpretations of annuli by multiple readers. A digital camera in conjunction with imaging software was used to aid in ageing, cataloging and referencing spine samples.

## Age Precision Tests and Age Validation

All samples were aged twice without knowledge of sturgeon size, date of capture, sampling location, or prior age estimates. Between each age estimation round, samples were randomized to decrease the likelihood of individual spines being recognized. Age validation techniques included tests of precision and accuracy. Within-reader tests of precision were conducted on a test-sample of 55 spines,


Figure 5. Posterior lobe from a mounted shortnose sturgeon pectoral spine (transverse section) photographed under reflected light conditions at 450 X magnification. The opaque and translucent zones from a single annulus are indicated. Within the dashed box, a false or 'supernumary' annulus is differentiated from the 'true' annulus.
randomly chosen from a total of 579 specimens. This same test-sample was used to assess whether precision and bias remained constant during the course of assigning ages for field-collected sturgeons. Precision was evaluated with a paired t-test, testing the hypothesis that differences between paired interpretations of the same fin spine $=0$. Age estimates derived during the primary ageing exercise $(\mathrm{n}=579)$ were compared with those from the precision test for temporal drift in my ageing technique. An age bias plot and an age frequency table were constructed to visualize within-reader precision (Campana et al. 1995).

Precision was assessed using two indices of bias, Average Percent Error (APE) (Beamish \& Fournier 1981) and the Coefficient of Variation (CV) (Chang 1982). The APE was calculated as:

$$
A P E=100 \times\left(\frac{1}{R}\right) \sum_{i=1}^{R} \frac{|X i j-X j|}{X j}
$$

and CV was calculated as:

$$
C V=100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X i j-X j)^{2}}{R-1}}}{X j}
$$

where $R$ is the number of reads per sample, $X i j$ is the $i$ th age determination of the $j$ th fish, and $X j$ is the mean estimated age of the $j$ th fish. Both methods yield a single index value for each spine, which then was averaged across all spines to generate a mean index of precision (Campana et al. 1995). Index values were used to evaluate whether (1) 'drift' or gradually shifting age determinations occurred over the period of analysis, (2) studies from the literature reported similar error rates in age interpretations, and (3) systematic biases, such as increased error with larger and
older fish, occurred (Campana et al. 1995). Drift was evaluated by grouping individual CV values into four (each numbering 138 or 139) bins, which were arrayed in time across the period of age determinations. A Kruskal-Wallace non-parametric test of means was used to test for a temporal shift in CV across the bins. Age-based systematic bias was also investigated using a Kruskal-Wallace non-parametric test of means. Spines were binned into four successive categorical age classes for the latter analysis.

Ageing accuracy is a measure of "correctness", the error present between an estimate and the actual value. Accuracy is a problem common to ageing studies of wild fish; samples of hard structures (spine, otolith, scale) from known-age individuals are rare. First, I tested the hypothesis that annuli are deposited at a yearly rate by conducting a marginal increment analysis (MIA) (Haas \& Resnick 1995, Campana 2001). This technique evaluates the seasonal progression of annulus formation by measuring the opaque zone deposited after the last identifiable translucent zone at the margin of the fin spine section (Stevenson \& Secor 1999). MIA utilizes the marginal increment ratio (MIR):

$$
M I R=M I \times \frac{1}{A}
$$

where $M I$ is the width of the outermost opaque zone, measured from the most distal translucent zone to the edge of the section, and $A$ is the mean width of the three annuli deposited prior to the marginal increment (Figure 6).

Width of marginal increments were measured using digital analysis software (ImageJ ©). For the mean monthly MIRs, I chose 25 samples at random for


Figure 6. Posterior lobe of a shortnose sturgeon pectoral spine (36 X magnification) with annuli enumerated according to their position relative to the outermost annulus (marginal increment). Annuli are demarcated by the circles and increment width for each annulus is indicated by the brackets.
increment analysis with the exception of the August sample, in which the 25 spines represented the entire sample for that month. Mean MIR values for each sampling period (c. 2 month intervals) were calculated and analyzed for trends in annulus formation. The monthly progression of mean MIR values were evaluated with a series of pair-wise means comparisons (Tukey-adjusted). Following procedures to diagnose the assumptions of ANOVA, mean monthly MIR values were grouped by season (Spring, Summer and Fall) to correct for heterogeneity of residual variance between months. March and April samples were classified as Spring, June and August samples as Summer, and both November samples (2003 \& 2004) were combined into a Fall sample.

To evaluate the accuracy of individual ages, 59 pectoral spines were collected from known-age, hatchery-raised shortnose sturgeon from three facilities. Twentysix spines (4-9 years old) were obtained from the USFWS Warm Springs National Fish Hatchery in Warm Springs, GA; 25 spines (3-20 years old) were collected from the USFWS Bears Bluff National Fish Hatchery on Wadmalaw Island, SC; and 8 spines (8-20 years old) were collected from the Fisheries and Aquatic Sciences facility of the University of Florida, Gainesville, FL. As age data were not available for 13 of the 59 spines, only 46 spines were used in this analysis. Spines were removed from the hatchery fish, then sectioned and annuli enumerated as described above for field-caught specimens. Comparisons of known and estimated ages were made using a paired t -test and linear regression analysis. The effects of known age and hatchery source on accuracy were investigated using a Kruskal-Wallace nonparametric test of means. To evaluate known-age effect, samples were classified into
young (1-6 years) or old (7-20 years) age groups to satisfy the requirement of homogeneity of variance between groups.

## Growth

I derived age estimates from pectoral spines to construct mixed-sex growth models using the von Bertalanffy (1938) and Gompertz (Weatherley \& Gill 1987) growth equations. Least-squares regression was used to fit linear, exponential and curvilinear functions to the size-at-age data to verify the most parsimonious model. Only sturgeon of estimated age 5-23 years were included in the growth models. By limiting the ages of sturgeon included in the analysis I was able to model growth based upon age-classes for which multiple observations were available. Growth models were fit to mean size-at-age for TL ( mm ) and weight $(\mathrm{kg})$. Using mean size-at-age values prevented more abundant age-classes in the catch data from disproportionately influencing parameter estimates. I assessed fit based on the relationship of predicted growth curves to actual data through visual examination of residuals and the coefficient of determination.

## von Bertalanffy Growth Model

Parameters for the growth model were derived through an iterative procedure (Excel, Solver ©) that minimized the least squares of predicted minus the observed length-at-age. The TL-based von Bertalanffy growth model is described by the equation:

$$
T L_{t}=T L_{\infty}\left[1-\exp ^{-K\left(t-t_{0}\right)}\right]
$$

where $\mathrm{TL}_{\mathrm{t}}$ is the mean predicted length $(\mathrm{mm})$ at age t (years), $\mathrm{TL}_{\infty}$ is the average asymptotic length of the species, t 0 is the x -intercept corresponding to the predicted age at which size is 0 mm , and K is the Brody growth coefficient (Ricker 1975).

Predicted weight-at-age from the von Bertalanffy growth model required a preliminary calculation of the allometric growth parameter b (Hillborn \& Walters 1992), according to the following equation:

$$
w_{t}=a(T L)^{b}
$$

which was fitted by regression. The von Bertalanffy growth equation for weight at age is:

$$
W_{t}=W_{\infty}\left[1-\exp ^{-K\left(t-t_{0}\right)^{b}}\right]
$$

where $\mathrm{W}_{\mathrm{t}}$ is the mean predicted weight $(\mathrm{kg})$ at age t (years), $\mathrm{W}_{\infty}$ is the average asymptotic weight $(\mathrm{kg})$ of the species, and t 0 and k are defined as per the length-atage model above (Ricker 1975).

Initial estimates of growth parameters were calculated using Ford-Walford plots (Ricker 1975). Subsequent iterative solving of parameters used mean size-atage to predict model parameters.

## Gompertz Growth Model

The Gompertz growth model is typically successful at representing growth in weight and represents a more sigmoidal shape than the von Bertalannfy growth model, though it can also be applied to length-at-age data (Ricker 1975). The Gompertz model used to describe growth in weight:

$$
w_{t}=w_{0} \exp ^{G\left(1-\exp ^{-g t}\right)}
$$

where $w_{t}$ is weight at age $t, w_{0}$ is the predicted weight at age $t_{0}, G$ is the instantaneous growth rate at age $\mathrm{t}_{0}$, and g describes the rate at which G decreases over time. The model was the same for length-at-age:

$$
T L=l_{0} \exp ^{G\left(1-\exp ^{-g t}\right)}
$$

with operational definitions of the parameters identical to those for weight.

## General Growth Models

Three other models were fit to the size-at-age data for both weight and TL to describe shortnose sturgeon growth stanzas. The generalized growth models were linear, exponential, and curvilinear (quadratic):

$$
\begin{aligned}
& y=\beta(x)+\alpha \\
& y=\alpha \exp ^{\beta x} \\
& y=\beta_{2} x^{2}+\beta_{1} x+\alpha
\end{aligned}
$$

As in the case of the von Bertalanffy and Gompertz models, these generalized growth models were fit to the mean size-at-age data through least-squares regression. The generalized growth models were applied across the same interval of age-classes (5-23 years) as the von Bertalanffy and Gompertz models.

## Mark-recapture

Original capture data were obtained from the USFWS (Maryland Fishery Resources Office, Annapolis, MD) for sturgeon with identification tags (e.g., PIT, Floy, Carlin) from previous studies. It was sometimes necessary to predict TL (mm) and weight ( kg ) data points from the available Fork Length (FL) data (Table 3).

Table 3. Tag and meristic data of previously marked shortnose sturgeon recaptured during field sampling (from USFWS sturgeon tagging database). $\mathrm{FL}_{0}=$ Fork Length at tagging, $\mathrm{FL}_{\mathrm{R}}=$ Fork Length at recapture, $\mathrm{TL}_{0}=$ Total Length at tagging, $\mathrm{TL}_{\mathrm{R}}=$ Total Length at recapture, $\mathrm{Wt}_{0}=$ weight at tagging, $\mathrm{Wt}_{\mathrm{R}}=$ weight at recapture.

| Tagging date | PIT Tag \# | Floy <br> Tag \#(s) | $\mathrm{FL}_{0}$ <br> $(\mathrm{~mm})$ | $\mathrm{FL}_{\mathrm{R}}$ <br> $(\mathrm{mm})$ | $\mathrm{TL}_{0}$ <br> $(\mathrm{~mm})$ | $\mathrm{TL}_{\mathrm{R}}$ <br> $(\mathrm{mm})$ | $\mathrm{Wt}_{0}$ <br> $(\mathrm{~kg})$ | $\mathrm{Wt}_{\mathrm{R}}$ <br> $(\mathrm{kg})$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 3/18/1996 | 2224160E70 |  | 645 | 683 | 760 | 800 | 2.58 | 3 |
| 7/2/1997 | 41132D5C1E |  | 674 | 721 | $* 784$ | 839 | 2.36 | 3.2 |
| 5/5/1995 | 221E2C707F |  | 570 | 635 | $* 659$ | 715 | 1.6 | 2.1 |
| 4/12/1994 | 1F3D6B0732 | \#3161 | 568 | 555 | $* 656$ | 655 | $* 1.64$ | 1.8 |
| 3/17/1995 | 22021C7240 | \#7162 \& \#7161 | 665 | 705 | $* 773$ | 811 | 2.12 | 2.8 |
| 4/15/1994 |  | \#4814 \& \#4813 | 630 | 629 | $* 731$ | 735 | $* 2.16$ | 2.2 |
| 11/14/1996 | 410A5D414D |  | 645 | 710 | 752 | 820 | 2.18 | 2.7 |
| 12/7/1994 | 1F485E0338 | \#5748 \& \#5747 | 705 | 758 | $* 821$ | 900 | 3.4 | 3.3 |
| 4/9/1996 | 413931453C |  | 620 | 650 | 705 | 745 | 2.07 | 3 |
| 4/22/1995 | 223342765A |  | 605 | 640 | $* 701$ | 746 | $* 1.8$ | 2.2 |
| 5/9/1997 | 41455C147B |  | 652 | 686 | $* 757$ | 799 | 1.36 | 2.3 |
| 11/27/1995 | 227D614015 |  | 615 | 670 | $* 713$ | 780 | 2.02 | 2.4 |
| 3/20/1996 | 2223761752 |  | 730 | 852 | 855 | 985 | 3.55 | 4.5 |
| $11 / 21 / 1995$ | 227D170F56 |  | 660 | 727 | $* 767$ | 856 | $* 2.47$ | 4 |
| 12/6/1994 | 1F4875574D | \#5266 \& \#5364 | 735 | 809 | $* 857$ | 947 | 3.5 | 4.7 |
| 5/22/1996 | 4138575F49 |  | 685 | 733 | 815 | 865 | 2.76 | 3.7 |
| 3/15/1995 | 22022F7652 | \#6712 \& \#67111 | 660 | 695 | $* 767$ | 795 | 2.32 | 2.4 |
| $11 / 21 / 1995$ | 2270450803 |  | 695 | 715 | $* 809$ | 832 | $* 2.9$ | 3.05 |
| $11 / 14 / 1996$ | 410A540054 |  | 675 | 790 | 815 | 940 | 2.5 | 4.4 |
| 6/3/1996 | 4139357F3F |  | 545 | 630 | 625 | 630 | 2.48 | 1.35 |

*TL or weight extrapolated from FL, transformations based on relationships calculated from the
current study.

Transformation of supplied FL to TL $(\mathrm{n}=13)$ was carried out using a TL-FL relationship generated from our dataset:

$$
T L=1.16^{*} F L
$$

$\left(n=580 ; R^{2}=0.94\right)$ for this purpose. It was also necessary to estimate sturgeon weight at the time of original tagging from FL data $(\mathrm{n}=6)$. Weight was predicted from FL by the equation:

$$
W t=0.127 \exp ^{\left(0.0045^{*} F L\right)}
$$

$\left(\mathrm{n}=580 ; \mathrm{R}^{2}=0.80\right)$. Growth increment over the interval between tagging and recapture was adjusted to yearly growth increments for both TL and weight responses. Back-calculated ages at tagging were derived from age determinations (hard part analysis) and independently predicted using the von Bertalanffy growth model for TL applied to the size at initial tagging. The two sets of age-at-tagging values were tested for significant differences (Paired t-test). Magnitude of incremental growth was tested for size-based trends in growth trajectories. Sturgeon were sorted by TL at recapture, larger fish were defined $\geq 800 \mathrm{~mm} \mathrm{TL}(\mathrm{n}=11)$ and smaller fish $<800 \mathrm{~mm} \mathrm{TL}(\mathrm{n}=10)$. Paired and unpaired t -tests were conducted to investigate the relationship between sturgeon size and back-calculated mean annual growth rate.

## Gear Selectivity

Gill nets are highly size-selective and introduce bias into demographic estimates that assume random sampling of a population (Hamley 1975). Therefore, it was necessary to adjust catch data based on the individual selectivity of each mesh
size (10.2, 15.2 and 17.8 cm ) used during field captures. Mesh selectivity values were estimated through manipulation of the selection equation:

$$
C_{l, m}=q_{l, m} N_{l} P_{m} s_{l, m} E_{m}
$$

where $\mathrm{C}_{l, m}$ is the catch of a given length class $l$ by mesh size $m, \mathrm{q}_{l, m}$ is the proportion of the population of length class $l$ that is vulnerable to the mesh (catchability), $\mathrm{N}_{l}$ is the population of a length class $l$ available to the mesh, $\mathrm{P}_{m}$ is the fishing power or efficiency of the mesh at retaining fish of size $l, \mathrm{~s}_{l, m}$ is the selectivity of $m$ and assumed to be size-dependent only, and $\mathrm{E}_{m}$ is the effort under which $m$ is deployed (Hovgård \& Lassen 2000).

Direct selectivity estimates are generated through mark-recapture studies or sampling populations of a known size distribution (Hamley 1975, Gulland 1983). While conducting field sampling, I attempted alternating fin clips of sampled sturgeon (right versus left) based on mesh size in which fish were captured to yield a direct estimate of the selectivity for each mesh size. However, only a single individual of the 587 total sturgeon captured was identified as a recapture. This was likely due to the high abundance of shortnose sturgeon present. I therefore employed indirect methods for estimating mesh selectivities.

Estimates of indirect gillnet selectivity were generated using the Baranov, Holt and Regression models (Hamley 1975, Hovgård \& Lassen 2000). Models were evaluated based on the agreement between predicted size-selectivity curves of catch versus the observed catch data. To minimize bias in estimates of gear selectivity, only catch data from sampling periods in which all nets were fished at the same location and day were used. Catch included in the analysis was therefore limited to

40-45 net minute deployments at the Esopus Meadows (March) and Albany (April) sampling locations. By limiting the data to these sampling periods, $\mathrm{E}_{m}$ was standardized among meshes as was the population $\mathrm{N}_{l}$ available to the gear. This also ensured physical river conditions (e.g., turbidity) were similarly affecting $\mathrm{C}_{l, m}$. Predicted selection curves were visually examined for a representative fit to the Esopus Meadows data, then plotted against the entire catch and again inspected for fit. The coefficient of determination (Ott \& Longnecker 2001) between observed and predicted values was calculated for each model as an indicator of fit.

## Baranov Model

The central assumption of the Baranov model (Baranov 1914) is the 'principle of geometric similarity' and states that selectivity between meshes sizes is proportional due to the geometric similarity of mesh construction and the morphological similarity of different sized fish of the same species (Hamley 1975). This implies that selectivity, s , is constant across all combinations of meshes and fish size for which the ratio of fish length to mesh size is the same:

$$
s(l, m)=s(k * l, k * m)
$$

where k is a constant (Hamley 1975). Given this assumption, it follows that each net (i.e., mesh size) is equally efficient at capturing some optimal length of fish, $l_{\mathrm{o}}$, dictated by the size of the mesh (Hovgård \& Lassen 2000). The catch equation can then be rearranged to the form:

$$
\frac{C_{l, m}}{E_{m}}=q_{l} * N l * s *\left[\frac{l}{m}\right]
$$

where the ratio of catch per unit effort $\left(\mathrm{C}_{l, m} \mathrm{E}_{m}{ }^{-1}\right)$ is proportional to the selectivity, $\mathrm{s}(l$ $m^{-1}$.

The NORMSEP procedure of FiSAT II © (FAO-ICLARM Fish Stock Assessment Tools 2000) was used to generate selectivity curves based on the assumptions of the Baranov model (Hovgård \& Lassen 2000). This procedure used maximum likelihood estimates to separate length-frequency bins for each mesh into normally distributed selectivity curves. Selection curves were scaled to a common maximum value of 1 (Hamley 1975).

## Holt Model

The Holt model (Holt 1963) does not rely on the principle of geometric similarity; rather it applies a standard linear regression to the catch data and assumes selectivity curves for each mesh follow a Gaussian distribution and have the same variance $\sigma^{2}$ (Hovgård \& Lassen 2000). The selection model is:

$$
s_{l, m}=\exp \left[-\frac{\left(C_{l, m}-k m^{2}\right)}{2 \sigma^{2}}\right]
$$

where k is a selection factor equal to $1 / \mathrm{K}$ with $\mathrm{K}=l_{o} / m$, and $\sigma^{2}$ is the variance associated with the curve (Hamley 1975, Hovgård \& Lassen 2000). Holt proposes that the logarithmically transformed catch ratio of a given length class between mesh sizes is proportional to the similarly transformed selectivity values for that length class:

$$
\ln \left(\frac{C_{l, m 1}}{C_{l, m 2}}\right)=\ln \left(\frac{s_{l, m 1}}{s_{l, m 2}}\right)
$$

This method used a least squares linear regression of the $\ln \left(\mathrm{C}_{l, m 1} \mathrm{C}_{l, m 2}{ }^{-1}\right)$ values plotted against the mode of each length class. The following equations provided the $y$-intercept $(\beta)$ and slope $(\alpha)$ :

$$
\begin{gathered}
\beta=\frac{k^{2}\left(m_{2}^{2}-m_{1}^{2}\right)}{2 \sigma^{2}} \\
\alpha=\frac{k\left(m_{1}-m_{2}\right)}{\sigma^{2}}
\end{gathered}
$$

Substituting and solving for the selection factor and variance (parameters k and $\sigma^{2}$ ) yielded:

$$
\begin{gathered}
k=\frac{2 \beta}{\alpha\left(m_{1}-m_{2}\right)} \\
\sigma^{2}=\frac{2 \beta\left[m_{1}-m_{2}\right]}{\alpha^{2}\left[m_{1}+m_{2}\right]}
\end{gathered}
$$

from which parameter values selectivity curves were generated.

Regression Model

The regression method used a matrix-based framework that employed a power transformation of the catch data followed by least-squares regression to account for the error structure (Hovgård 1996). A derivation of the selection equation yields an estimate of the population per size class:

$$
q N_{1}=\left[\frac{\sum_{m}\left(C_{l, m} E_{m} P_{m} s_{l, m}\right)^{\beta}}{\sum_{m}\left(P_{m} E_{m} s_{l, m}\right)^{2 \beta}}\right]^{\frac{1}{\beta}}
$$

This equation provided the least-squares estimate for $\mathrm{qN}_{l}$ values, which were then minimized through an iterative procedure that adjusted the $\mathrm{qN}_{l}$ 's to yield the leastsquares sum (Hovgård \& Lassen 2000):

$$
L s q=\sum_{m} \sum_{l}\left[C_{m, l}^{\beta}-\left(E_{m} P_{m} s_{l, m} q N_{l}\right)^{\beta}\right]^{2}
$$

The flexibility of the regression framework lies in the mutability of the model, providing a uniform method of describing a range of error structures (e.g., high to low contagion) (Hovgård \& Lassen 2000). Selection equation parameters $\mathrm{P}_{m}$ and $\mathrm{E}_{m}$ can be ignored if catch is limited to periods of equal effort per mesh and fishing power is the same among gears $\left(\mathrm{P}_{m 1}=\mathrm{P}_{m 2}=\ldots=\mathrm{P}_{m \mathrm{n}}=1\right)$.

A log-normal selection curve was assumed, with error terms following a Poisson distribution $(\beta=0.5)$ :

$$
s_{l, m}=\exp \left(\frac{\left(-0.5 *\left(\ln \left(\frac{l}{m}\right)-\ln k\right)^{2}\right)}{\sigma^{2}}\right)
$$

Non-linear least squares regression of the residuals (predicted - observed catch) was then used to solve for the selection factor k and the variance structure $\sigma^{2}$.

## Recruitment

Following correction of actual catch for gear selectivity, catch values for all age-classes across meshes were subjected to an effort modifier:

$$
C_{a d j}=\frac{C_{\text {sel }}}{\left(\frac{E_{\text {total }}}{E_{m}}\right)}
$$

where $\mathrm{C}_{\text {adj }}$ is the catch adjusted for gear selectivity and effort, $\mathrm{C}_{\text {sel }}$ is the partially adjusted catch (gear selectivity only), $\mathrm{E}_{\text {total }}$ is the total fishing effort (net minutes) and $\mathrm{E}_{\mathrm{m}}$ is the mesh specific fishing effort (net minutes).

Adjusted catch estimates, $\mathrm{C}_{\mathrm{adj}}$, for each estimated age-class were summed across meshes and the resultant age structure was subjected to a catch curve analysis (Ricker 1975). Adjusted catch values were logarithmically transformed (y-axis) and plotted against their corresponding age-classes along the abscissa. An estimate of the annual instantaneous mortality rate, Z , was generated by conducting a least-squares linear regression through the descending portion of the plot where slope $=\mathrm{Z}$. Analysis was limited to ages that had fully recruited to the gear. The presence of anomalous year-class strength, indicated by the deviation of adjusted catch-at-age from the predicted catch, was analyzed by applying ANOVA to the least-squares catch-curve residuals. Residuals were grouped into four successive stanzas composed of five year-classes each (e.g., Group ${ }_{1}=1999-1995$, etc).

The exponential decay model was then used to predict the relative strength of each year-class at age $=1$ year (yearlings) from the adjusted catch data:

$$
N_{t}=N_{1} \exp ^{-Z t}
$$

where $N_{t}$ is the cohort population at time $t, N_{1}$ is the cohort population at $t=1$ year of age, and Z is the estimate of the total annual mortality rate. Estimated age at capture was standardized to reflect a sampling date of November 2004 for all catch data (i.e., estimated ages for sturgeon captured during November 2003 were augmented by one year). Low catch numbers occurred for the oldest age-classes, so analysis was limited to age 5-26 years (1999-1979 year-classes). A recruitment strength index
(RSI) was calculated by assuming a constant $\mathrm{Z}=-0.22$ and standardizing the resultant year-class strengths to a relative scale of 1 . Year-class abundances at the transition to age 1 (yearlings) were estimated for the years 1979-1999, by apportioning 50,000 (approximate Hudson River population estimate, Bain et al. 2000) across the observed age class frequencies (corrected for gear selectivity and cumulative natural mortality). To account for the population fraction attributable to age-classes that were not sampled (i.e., $1-4,24,27 \& 28$ years), predicted abundances were generated assuming a constant annual mortality of $\mathrm{Z}=0.22$. Year-class assignments to abundance estimates were made by subtracting age from year of capture and were assumed to represent annual cohort strength of yearlings.

## Fall Juvenile Survey

Bycatch data (1985-2003) from the ongoing Hudson River Utilities Fall Juvenile Survey were obtained with permission from Dr. Mark Mattson, Normandeau Associates. Gear used in the survey 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). As a method of corroborating my hindcast year-class strength estimates, I compared trends in RSI estimates with shortnose sturgeon bycatch CPUE (catch 1000 $\mathrm{m}^{3-1}$ ) from the trawl survey. Trawl survey data was iteratively lagged in a succession of single-year time steps. The lagged time step with the highest regression correlation coefficient was considered the most representative fit.

## Environment: Flow

Historical annual flow data (years: 1973-1997, 2000) from the US Geological Survey's Green Island, NY monitoring station (\# 01358000) located at the Federal Dam in Troy was downloaded from the US Geological Survey website (USGS 2005). The dataset contained one mean flow volume datum $\left(\mathrm{ft}^{3} \mathrm{sec}^{-1}\right)$ per month of each calendar year downloaded, except for 1997 which only included flow volumes for January though September. Ambient water temperature was also included in the dataset; unfortunately the gaps in temperature data were quite pervasive and precluded the inclusion of water temperature as a variable in this analysis. The correlation of hydrographic conditions on RSI values of age 1 shortnose was evaluated using non-parametric correlation analysis (Spearman's rank-correlation coefficient) due to persistent non-normality of the data (Zar 2004). Analyses were constructed to identify correlations between flow volumes and both adult pre-spawn conditioning and early life history stages that may influence the success of annual recruitment.

Specifically, I tested for correlations between flow and the conditioning of pre-spawn adults as defined by the predicted strength of the following year's age 1 year-class. This was conducted by comparing monthly flow volumes from October to December to the following year's relative recruitment strength. This analysis was extended through January to April of the same year for which the recruitment estimates were developed. Secondly, variability in flow volume was investigated in terms of larval survival and subsequent influence on final yearling recruitment values. Flow from the months of May and June were compared to same-year recruitment
index values. Third, I tested for correlations between a given year's final recruitment strength and the concurrent summer, fall and winter (July-December) flow conditions. This provided a means of looking at flow as it related to the YOY juvenile period and the final recruitment strength index. Monthly flow volumes were compared singly, grouped by 2-3 month intervals and grouped by the entire range of values (pre-spawn adult only).

## Results

## Field Sampling

A total of 587 shortnose sturgeon were captured from three different sampling locations on the Hudson River. We captured 341 fish at Esopus Meadows during November 2003 and March 2004, targeting over-wintering and pre-spawn congregations. A total of 129 shortnose sturgeon was sampled during the spring spawning event near Albany in April 2004. Summer sampling yielded 83 individuals in the Catskill area during the months of June and August 2004. The final 43 fish were taken in November 2004, again from the over-wintering location near Esopus Meadows. Catch per unit effort (CPUE) was greatest during spring and fall sampling periods with a mean CPUE $\pm$ s.e. across months of $1.9 \pm 0.9$ fish minute ${ }^{-1}$ (Figure 7 A). Different meshes showed variable CPUE, with the 15.2 cm mesh yielding the highest mean CPUE across sampling months ( 0.33 fish minute ${ }^{-1}$ ). The CPUE for the
 respectively (Figure 7 B).

Size data for the total catch followed Gaussian distributions. The distribution of weights was slightly skewed with a mean of $2.78 \pm 0.04 \mathrm{~kg}$ (s.e.). The length distribution was left skewed with mean $\mathrm{TL}=783 \pm 4 \mathrm{~mm}$ (Figure 8). The modal age of the sample was 13 years with a maximum estimated age of 30 years (Figure 9). The largest individual captured was 1045 mm TL and weighed 9.0 kg . The smallest sturgeon measured 490 mm TL $(0.5 \mathrm{~kg})$ and was one of several estimated at 5 years of age.


Figure 7. Catch per unit effort (CPUE) of Hudson River shortnose sturgeon over the course of the sampling period (2003-04). CPUE for each sampling period by gear type is shown in panel.


Figure 8. Total catch $(\mathrm{n}=587)$ of shortnose sturgeon over the course of the sampling period (2003-04) by A) weight $(\mathrm{kg})$ and B) Total Length (mm).


Figure 9. Distribution of estimated ages from interpretable spines $(\mathrm{n}=554)$.

## Age Precision Tests and Age Validation

After eliminating damaged or unreadable spines $(\mathrm{n}=25)$, age estimates were produced for 554 pectoral spines. Spines were determined to be unreadable due to a suite of optical features that impeded age estimation (Figure 10). Supernumary annuli were present in most sections, caused by division of a single annulus into two or multiple lamellar structures. Spans of very narrowly spaced annuli, also termed 'banding' were observed; investigators have speculated that banding is associated with energy deferred from somatic growth to gonadal development in the years prior to a spawning event (Cuerrier 1951, Roussow 1957). Annular width was variable in most sections with a typical pattern of narrow multiple annuli near spine edges. The inclusion of secondary rays embedded within the primary spine was common though inclusions were typically easy to identify. Resorption or deposition of calcareous material and physical deterioration of spines were two primary reasons for rejecting sections and can pose a significant impediment to accurate interpretation of annuli.

Repeated age estimates were relatively precise with $40 \%$ of the spines assigned the same age in each round, $43 \%$ of the estimates $\pm 1$ year, $14 \% \pm 2$ years, and $3 \%$ of the estimate $\pm 3$ years or more. The greatest discrepancy encountered was 8 years, which occurred in a single specimen. Precision was high with an APE of $3.0 \%$ and a CV of $4.0 \%$ for the entire sample, and an APE of $6.0 \%$ and CV of $8.0 \%$ for the test subsample of 55 spines. Non-parametric tests of means for CV values binned by age-group indicated the absence of age related bias in precision (KruskalWallace $\chi^{2}=5.8, \mathrm{p}=0.12$ ). Similarly, there was no significant difference in mean


Figure 10. Transverse sections of pectoral spines viewed under reflected light microscopy. Common sources of ageing error are indicated by arrows in each image. A) Spine showing initial stages of resorbtion of calcified material, canalization and proteinaceous deposits. B) Inclusion of secondary rays within the posterior lobes; inclusion can vary from two, one or none within the primary spine. C) Inconsistent annulus widths. D) "Crowding" of annuli near edge of spine.

CV among groups binned by the order of interpretation (i.e., temporal bias or drift) (Kruskal-Wallace $\chi^{2}=2.8, p=0.43$ ).

Analysis of the test subsample $(\mathrm{n}=55)$ indicated that interpretation of annuli was variable though no temporal bias was apparent over the course of the ageing study. A paired t-test indicated that age estimates from the test sample were not significantly different from initial to final estimates $(t=1.67, p=0.28)$. A visual assessment of the age-bias plot indicated that my age interpretations were unbiased for shortnose sturgeon with estimated ages 5 to 30 years (Figure 11). Age estimation was very precise for sturgeon estimated at 5 to 16 years of age, with the $95 \%$ confidence intervals associated with these age-classes estimates overlapping the 1:1 ratio line. Precision was substantially less for sturgeon aged 17 and older with the $95 \%$ confidence intervals for five of the nine highest age-classes falling outside the 1:1 ratio line.

Age estimates for hatchery-reared shortnose sturgeon did not accurately correspond to known ages (Table 4). Although a nonparametric means comparison failed to find a significant difference between the estimated and actual ages $(Z=-$ $1.56, \mathrm{p}=0.12$ ), a visual examination of the residuals indicated a systematic bias (Figure 12 A ). Regression analysis of estimated ages on actual ages indicated a significant deviation from the 1:1 relationship, signifying a bias in age interpretations $(F=32.11, p<0.0001)$ (Figure 12, B). Similarly, contingency table analysis showed a significant age effect on accuracy $\left(\chi^{2}=9.94, p=0.002\right)$, with the difference between estimated and actual ages varying significantly between young (1-6 years) and older (7-20 years) fish. Estimated ages of younger fish typically fell above the


Figure 11. Age-bias plot of subsampled spines $(\mathrm{n}=55)$ for Hudson River shortnose sturgeon. Mean second ages are plotted with $95 \%$ confidence intervals. The 1:1 ratio line is shown.

Table 4. Statistical analyses used to diagnose accuracy of age determinations for hatchery raised sturgeon.

|  | Statistical test | Null hypothesis | Test statistic | $\begin{gathered} p \text { value } \\ (\alpha>0.5) \end{gathered}$ | Conclusions |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Parametric |  |  |  |  |  |
|  | Paired t-test | $\mathrm{H}_{0}$ : no difference between estimated and true ages | $\mathrm{t}=0.02$ | 0.99 | Reject alternative hypothesis: <br> No significant difference between estimated and true ages |
|  | Linear regression | $\mathrm{H}_{0}$ : accuracy of age estimates are unaffected by age of sturgeon | $\mathrm{F}=31.29$ | 0.0001 | Reject null hypothesis: <br> Slope of residuals is significantly different than zero |
| Nonparametric |  |  |  |  |  |
|  | Wilcoxon Nonparametric rank sum test | $\mathrm{H}_{0}$ : no difference between estimated and true ages | $\mathrm{Z}=1.56$ | 0.12 | Reject alternative hypothesis: <br> No significant difference between estimated and true ages |
|  | Kruskal-Wallis | $\mathrm{H}_{0}$ : accuracy of age estimates are unaffected by hatchery of origin | $\chi^{2}=3.03$ | 0.22 | Reject alternative hypothesis: No significant difference in accuracy among hatcheries |
|  | Wilcoxon Nonparametric rank sum test | $\mathrm{H}_{0}$ : accuracy of age estimates are unaffected by age of sturgeon | $\mathrm{Z}=-3.8$ | 0.0001 | Reject null hypothesis: <br> Significant difference between young (3-8 years) and older fish (14-20 years) |



Figure 12. Analysis of age determinations of hatchery-raised shortnose sturgeon ( $\mathrm{n}=$ 46). A) Paired differences of estimated minus true ages (residuals) plotted against actual age (abscissa) with positive (young fish, 1-6 years) and negative (older fish, 7-20 years) bias clearly visible. B) Estimated ages (y-axis) plotted against actual ages (abscissa) with a linear regression (least squares) line (solid line) relative to the $1: 1$ line (dotted line).

1:1 ratio line indicating a positive bias, while the estimated ages of older fish were less than the actual values, indicative of a negative bias. The microstructure of hatchery spines showed wide variation in the optical characteristics of annuli and related structures in comparison with spines from wild-captured individuals (Figure 13, A-D). Hatchery spines often showed irregular deposition of calcareous material and blurred or faint annuli. Physical deterioration and compaction was pronounced in several hatchery spines. Despite widely varying microstructures among individuals from hatcheries, the hatchery source itself did not affect the accuracy of age estimates $\left(\chi^{2}=3.03, \mathrm{p}=0.22\right)$.

Mean monthly marginal increment ratios increased steadily from a nadir in March to a maximum in November (Table 5). When monthly ratio values were grouped by season, the Spring ratio was significantly less than both the Summer $(\mathrm{t}=-2.54, \mathrm{p}=0.03)$ and Fall ratios $(t=3.8, p<0.001)$. Summer and Fall ratios were not significantly different $(t=1.34, \mathrm{p}=0.38)$ although the mean ratio value increased from Summer to Fall (Figure 14, A). Assumptions of the ANOVA model were met under the seasonal grouping, but not for the monthly comparisons. Due to low numbers within age-classes during some of the sampling periods and very small sample size for the individuals with the oldest estimated ages (i.e., ages $\geq 25, \mathrm{n}=1$ ), it was necessary to pool age-classes to produce composite monthly and seasonal MIR values. The youngest (5-7 years) and oldest (19-26 years) sturgeon included in the MIA were not present in all months or seasons. Sturgeon with estimated ages ranging from 12-15 years were included in all monthly and seasonal means, while each of the three seasonal means contained sturgeon aged 8 to 18 years. There was no indication


Figure 13. Transverse sections of pectoral spines from four different hatchery-raised shortnose sturgeon. A \& B) depict hatchery spines that appear to be laying down consistent increments without noticeable deformation or artificial structures. C \& D) depict spines that are deteriorated, possess multiple false structures and large calcareous deposits.

Table 5. Mean Marginal Increment Ratio values (MIR) by sampling month and season $\pm$ $95 \%$ Confidence interval. Means with any identical letters are not significantly different at.$=0.05$ (Tukey-Kramer protected against experimentwise error inflation).

| Sampling <br> month | Mean monthly MIR <br> with 95 \% C.I. | Sampling <br> season | Mean seasonal <br> MIR with 95\% C.I. |
| :--- | :---: | :---: | :---: |
| March | $0.55 \pm 0.07$ | Spring | $0.58^{\mathrm{a}} \pm 0.08$ |
| April | $0.65 \pm 0.12$ |  |  |
| June | $0.66 \pm 0.12$ | Summer | $0.73^{\mathrm{b}} \pm 0.09$ |
| August | $0.78 \pm 0.13$ |  |  |
| November (‘03) | $0.85 \pm 0.12$ | Fall | $0.80^{\mathrm{b}} \pm 0.09$ |
| November ('04) | $0.75 \pm 0.12$ |  |  |



Figure 14. Mean seasonal Marginal Increment Ratios (MIRs) with 95 \% C.I. A) Overall Marginal Increment Analysis (MIA, ages 5-26). B) Reduced set MIA (ages 10-17).
Seasonal MIR values that have different letters above them are significantly different at $\alpha$ $=0.05$ (Tukey-Kramer protected against experimentwise error inflation).
of bias when the seasonal MIA was repeated using a common age distribution subsample (10-17 years). Mean MIR values indicated a steadily increasing increment width from Spring (0.58) to Summer (0.73) to Fall (0.82) (Figure 14, B). Summer (Two sample t -test, $\mathrm{t}=-1.65, \mathrm{p}=0.05$ ) and Fall (Two sample t -test, $\mathrm{t}=-3.26, \mathrm{p}<0.001$ ) MIRs remained significantly greater than the Spring MIR, corroborating the results from the full sample MIA.

## Growth

Growth curves were calculated based on the sizes selectively captured during the study and therefore reflect growth rates of sub-adults and adults (ages 5-23 years). Sex determination in the field was unsuccessful for all but three very ripe males, which expressed milt upon application of pressure to the abdomen. This precluded determining sex-specific age-structure and growth models. Following application of all growth models (Figure 15) to size-at-age data, the von Bertalanffy growth function for weight and length was chosen as the most representative model. The von Bertalanffy growth curves derived from TL (mm) measurements was

$$
T L=1045 *\left(1-\exp ^{-0.07 *(t+7.42)}\right)
$$

with $R^{2}=0.93$, and $T L_{\infty}$ constrained to the maximum observed TL value of 1045 mm . The von Bertalanffy growth function was also determined using FL (mm) to ease parameter comparisons among literature values. The resultant growth function for FL was

$$
F L=925 *\left(1-\exp ^{-0.06 *(t+7.05)}\right)
$$



Figure 15. Growth curves calculated for mean Total Length (mm) and mean weight (kg) on age (years) with range of size values indicated by vertical bars and denoted by circles. Filled circles were used in the analysis, open circles were not. A \& B) $\log _{e}$ growth function; C \& D) Polynomial (quadratic) growth function; E \& F); von Bertalanffy growth function; $\mathrm{G} \& \mathrm{H}$ ) Gompertz growth function.
with $\mathrm{R}^{2}=0.92$, and $\mathrm{FL}_{\infty}$ constrained to the maximum observed FL value of 925 mm . The allometric growth exponent $b$ was calculated as $3.2\left(\mathrm{R}^{2}=0.85\right)$ from the catch data. The von Bertalanffy growth function for weight was

$$
W t=5.0 *\left(1-\exp ^{-0.1^{*}(t-4.31)^{3.2}}\right)
$$

with $\mathrm{Wt}_{\infty}$ constrained to $\geq 4.7 \mathrm{~kg}\left(95^{\text {th }}\right.$ percentile by weight observed) $\left(\mathrm{R}^{2}=0.97\right)$.
The Gompertz function described growth in length $\left(\mathrm{R}^{2}=0.87\right)$ as

$$
T L=10 * \exp ^{4.42\left(1-\exp ^{-0.43 t}\right)}
$$

with $1_{0}$ constrained at 10 mm to provide a biologically realistic representation of growth. Constraining $\mathrm{w}_{0}$ to 0.05 kg , the Gompertz growth function for weight $\left(\mathrm{R}^{2}=0.87\right)$ was

$$
W t=0.05 * \exp ^{4.59\left(1-\exp ^{-0.16 t}\right)}
$$

Though the Gompertz and tertiary growth models showed high correlations $\left(0.86 \leq R^{2} \geq\right.$ 0.97 ) and appeared to describe size-at-age relationships in an adequate fashion, the von Bertalanffy model was chosen based on precedent, ease of inter-study comparisons and the intrinsic biological meaning of the function's parameters (Figure 16).

During field sampling, twenty-one previously tagged shortnose sturgeon were captured (one of which was captured a second time). The majority of these fish possessed passive integrated transponder (PIT) tags $(\mathrm{n}=19)$, though five also carried external Floy ${ }^{\circledR}$ or Carlin ${ }^{\circledR}$ tags. Age estimates derived from hard part analysis for recaptures ranged from 9-24 years, yielding original age-at-tagging estimates from 4-


Figure 16. Size-at-age data for Hudson River shortnose sturgeon (combined sex data). Length-age data given by open circles (A) with mean length-at-age given by closed circles with fitted von Bertalanffy curve for ages 5-30 (B). Weight-age data given by open circles (C) with mean weight-at-age given by closed circles with fitted von Bertalanffy curve for ages 5-30 (D).

16 years (Table 6). Predicted age at tagging calculated from the von Bertalanffy growth function applied to length data from tagging events agreed with estimated ages $(t=-1.44, p=0.16)$. Elapsed time between tagging and recapture varied from 6 to 10 years with a mean $8.4 \pm 0.2$ years. Mean growth was $11 \pm 5 \mathrm{~mm} \mathrm{year}^{-1} \mathrm{TL}$, with an observed maximum and minimum growth rate of $19.3 \mathrm{~mm}^{\mathrm{mear}}{ }^{-1}$ and $4.6 \mathrm{~mm}^{\text {year }}{ }^{-}$ ${ }^{1}$, respectively (Figure 17). Annual growth rate was higher for larger fish (TL $>800$ $\mathrm{mm}, \mathrm{n}=10)$ than for smaller fish ( $\mathrm{TL}<800 \mathrm{~mm}, \mathrm{n}=10$ ), grouped by TL at time of recapture $(t=2.1, p=0.01)($ Figure 18$)$. Mean time at large was not significantly different between size bins $(\mathrm{t}=2.1, \mathrm{p}=0.4)$. Due to the absence of sufficient linear correlation, ANCOVA was inappropriate (covariate $=$ time at large $)$ to analyze differences in growth rate between size classes. Weight-based divisions of size at tagging did not show growth rate differences.

## Gear Selectivity

A visual inspection of the fitted Holt, Baranov and Regression models (Figure 19) was sufficient to recognize the Baranov model was the most representative for the sample dataset. When $\mathrm{R}^{2}$ coefficients were calculated across mesh sizes (i.e., 10.2, $15.2,17.8 \mathrm{~cm})$, the Baranov model demonstrated the best fit $\left(\mathrm{R}^{2}=0.53\right)$ to the dataset, while the Regression $\left(\mathrm{R}^{2}=0.3\right)$ and Holt $\left(\mathrm{R}^{2}=0.28\right)$ model coefficients were substantially lower. Standardizing selectivity curves to a common maxima of 1 was necessary given the unknown size-structure of the population (Hamley 1975), though it has been demonstrated through direct estimates of gear selectivity that gradations in mesh size yield different capture efficiencies (Hamley \& Reiger 1973).

Table 6. Growth during time at large for recaptures of previously marked shortnose sturgeon during field sampling.

| PIT tag \# | Floy tag \# | Growth (mm) |  |  | Time at large (years) | Estimated age (capture) | Predicted age (tagging) | Estimated age (tagging) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | FL | TL | Wt |  |  |  |  |
| 2224160 E 70 |  | 38 | 40 | 0.42 | 7.67 | 18 | 12 | 10 |
| 41132D5C1E |  | 47 | 116 | 0.84 | 6.33 | 22 | 10 | 16 |
| 221E2C707F |  | 65 | 104 | 0.5 | 8.5 | 12 | 6 | 4 |
| 1F3D6B0732 | 0316 | -13* | 46 | 0.16 | 9.58 | 17 | 6 | 7 |
| No Scan | 07161 / 07162 | 40 | 98 | 0.68 | 8.67 | 15 | 10 | 6 |
| No Tag | 04813 | -1* | 60 | 0.04 | 9.92 | 14 | 8 | 4 |
| 410A5D414D |  | 65 | 68 | 0.52 | 7.42 | 15 | 12 | 8 |
| 1F485E0338 | 05748 | 53 | 144 | -0.1 | 9.33 | 20 | 12 | 11 |
| 413931453C |  | 30 | 40 | 0.93 | 8 | 21 | 9 | 13 |
| 223342765 A |  | 35 | 97 | 0.4 | 9 | 18 | 7 | 9 |
| 41455C147B |  | 34 | 100 | 0.94 | 6.92 | 18 | 9 | 11 |
| 227D614015 |  | 55 | 121 | 0.38 | 8.42 | 17 | 7 | 9 |
| 2223761752 |  | 122 | 130 | 0.95 | 8.08 | 24 | 18 | 16 |
| 227D170F56 |  | 67 | 148 | 1.53 | 8.42 | 15 | 9 | 7 |
| 1F4875574D |  | 74 | 159 | 1.2 | 9.33 | 15 | 14 | 6 |
| 4138575F49 |  | 48 | 50 | 0.94 | 7.92 | 16 | 15 | 8 |
| No Scan | 06712 | 35 | 87 | 0.08 | 9.25 | 19 | 9 | 10 |
| 2270450803 |  | 20 | 87 | 0.15 | 9 | 20 | 11 | 11 |
| 410A540054 |  | 115 | 125 | 1.9 | 8 | 18 | 15 | 10 |

* Sturgeon showing negative growth (FL) during time at large.


Figure 17. Growth trajectories of tagged shortnose sturgeon recaptured during sampling. Mean growth rate during time at large was $11 \pm 5 \mathrm{~mm}$ year $^{-1}$, with trajectories of growth exceeding the mean falling above the shaded area and those below falling within the shaded area. Maximum and minimum observed growth rates are indicated by the arrows.


Figure 18. Mean annual growth ( $\mathrm{mm} \mathrm{yr}^{-1}$ ) plotted against length at recapture ( mm ) for shortnose sturgeon tagged and recaptured from the Hudson River.


Figure 19. Selectivity curves for each mesh ( 10.2 cm mesh: open circles, 15.2 cm mesh: filled circles, 17.8 cm mesh: filled triangles) overlaid on catch values standardized to 1. Plots A-C are curves generated from the Holt model, plots D-F are curves generated from the Regression model, and plots G-I are generated from the Baranov model.

Each mesh size had a unique $l_{O}$, that followed an intuitive pattern of increasing $l_{O}$ with increasing mesh perimeter (Figure 20). Selectivity modifiers yielded a falsely inflated catch adjustment for one fish that fell on the extreme upper limb of the 15.2 cm mesh curve. This sturgeon measured 984 mm TL and was estimated at 30 years old. Due to its large size and subsequent peripheral position on the 15.2 cm selectivity curve, the adjusted catch was scaled up to 20 'fish' (1900\% inflation). Following $\log _{\mathrm{e}}$ transformation, the adjusted catch value of 3.4 fell well above three standard deviations (s.d. $=0.23$ ) of the 30 year age-class catch of 0.06 predicted by the catch curve and was therefore considered a statistical outlier and not included as a valid predictor of recruitment strength.

## Recruitment

Catch data, adjusted for gear selectivity and effort, yielded an adjusted total catch of $\mathrm{C}_{\text {adjust }}=1238$ sturgeon $\left(\mathrm{C}_{\text {actual }}=554\right)($ Table 7$)$. Adjusted catch values represent the number of sturgeon of each size-class that would have been caught if all gear sizes were fished with equal effort and selectivity modifiers were identical across sturgeon sizes. Adjusted catch-at-age peaked at 5 years and remained stable until 7 year before declining; therefore, fish of age $\geq 7$ years were assumed to have fully recruited to the gear and were included in the catch curve analysis. The maximum age included in the catch curve was 23 years. Least-squares linear regression $\left(\mathrm{R}^{2}=\right.$ 0.75 ) yielded a $Z=-0.22 \pm 0.03$ (s.e.) (Figure 21 A ). This implies that $20 \%$ of the standing abundance of each cohort (age 5+) perishes annually, or a survivorship of $80 \%$ cohort $^{-1}$ year $^{-1}$. Based upon the protected status of the shortnose and assuming


Figure 20. Baranov selectivity curves generated for each of the mesh sizes. Optimal capture length $l_{0}$ is denoted by arrows for each mesh size.

Table 7. Catch by age class with mean Total Length (TL), catch per mesh, actual ( $\mathrm{C}_{\text {actual }}$ ) and adjusted ( $\mathrm{C}_{\text {adjusted }}$ ) catches of shortnose sturgeon over the course of field sampling. In the bottom row is estimated mortality, Z , calculated for each mesh, actual, and adjusted values, Z used in calculations, 0.22 , given in boldface.

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



Figure 21. A) Natural log transformed adjusted catch (y-axis) plotted against age for Hudson River shortnose sturgeon. Least-squares linear regression was fitted to filled data given by filled circles only. Above each symbol is the associated subsample size. B) Catch curve residuals plotted against age (abscissa) with four year-class stanzas denoted by the dashed boxes.
negligible poaching/bycatch, the estimate of Z represents the natural mortality rate, M.

Residuals from the catch curve described a slight, curvilinear pattern (Figure 21 B). Significant differences in residuals (1979-1999 cohorts) occurred between age-classes when binned into 5-year stanzas (interval 1984-1979 included only 5 ageclasses though spanning 6 years) (Figure 21 B ). Residuals of 5-9 \& 20-26 year olds were negatively biased in regard to predicted values and both showed a significant difference from the 15-19 year old mean residual value (Table 8).

Observed recruitment strength index (RSI) values indicated that 1988 was the strongest $(\mathrm{RSI}=1.0)$ and 1979 the weakest year-class $(\mathrm{RSI}=0.13)$ during the period 1979-1999 (Figure 22). Unadjusted age structure corroborated RSI results, with 13 year-olds comprising the most numerous age-class ( $\mathrm{n}=95$ ). No recruits were predicted from 1976, 1977 and 1980 due to a lack of capture data from the $24,27 \&$ 28 age classes. Hindcast estimates of yearling cohort abundances varied by up to an order of magnitude among year-classes. The most abundant year-class was spawned in 1988, which resulted in 42,659 yearlings while the most depauperate was the 1994 year-class, which yielded 4,886 yearlings (Figure 23).

## Fall Juvenile Survey

Shortnose bycatch from the Hudson River Utilities Fall Juvenile Survey was significantly correlated with predicted RSI values (Table 9). Iterative lagging of the trawl data yielded progressively increasing correlation values from 2-6 years, though significant correlations were present for each of the 4-8 year lag scenarios $\left(r_{S}>0.46\right.$,

Table 8. Mean catch curve residual values grouped by age-class stanzas. See Figure 21 for catch curve. Means with any identical letters are not significantly different at $\alpha=0.05$ (Tukey-Kramer protected against experimentwise error inflation).

| Age-class | Year-class | Mean residual value |
| :---: | :---: | :---: |
| $5-10$ | $1999-1995$ | $-0.6134^{\mathrm{a}}$ |
| $11-15$ | $1994-1990$ | $0.2551^{\mathrm{ab}}$ |
| $16-20$ | $1985-1989$ | $0.4943^{\mathrm{b}}$ |
| $21-26$ | $1979-1984$ | $-0.6611^{\mathrm{a}}$ |



Figure 22. Index of yearly recruitment success based upon actual catch adjusted for gear selectivity, effort and cumulative mortality. Relative cohort strengths (y-axis) are plotted against hatch year (abscissa).


Figure 23. Estimated age 1 cohort abundance for Hudson River shortnose sturgeon, ages 5-30 years.

Table 9. Correlation of yearling recruitment strength index (RSI) values relative to shortnose sturgeon bycatch from the Hudson River utilities sponsored Juvenile Fall Survey, lagged over yearly increments.

|  |  |  |
| :--- | :---: | :---: |
| Lag scenario | Correlation $\left(\mathrm{r}_{\mathrm{S}}\right)$ | p -value |
| No lag | $-\mathbf{0 . 6}$ | $\mathbf{0 . 0 2}$ |
| 1 year | -0.34 | 0.12 |
| 2 years | -0.05 | 0.85 |
| 3 years | 0.33 | 0.19 |
| $\mathbf{4}$ years | $\mathbf{0 . 4 6}$ | $\mathbf{0 . 0 5}$ |
| $\mathbf{5}$ years | $\mathbf{0 . 4 8}$ | $\mathbf{0 . 0 5}$ |
| $\mathbf{6}$ years | $\mathbf{0 . 5 8}$ | $\mathbf{0 . 0 1}$ |
| $\mathbf{7}$ years | $\mathbf{0 . 5 6}$ | $\mathbf{0 . 0 2}$ |
| $\mathbf{8}$ years | $\mathbf{0 . 5 2}$ | $\mathbf{0 . 0 4}$ |
| $\mathbf{9}$ years | 0.14 | 0.62 |

$\mathrm{p} \leq 0.05$ ). Lagging trawl data by 6 years resulted in the highest correlation ( $\mathrm{r}_{\mathrm{S}}=0.58$, $\mathrm{p}=0.01)($ Figure 24).

## Environment: Flow

Correlation analysis suggested significant correlation between RSI estimates and mean monthly flow volumes (Figure 25). Flow was found to correlate with fall months in the year preceding individual recruitment events (adult effect). November flow ( $443.4 \mathrm{~m}^{3} \mathrm{sec}^{-1}$ ) was positively correlated with RSI of yearlings spawned the following year ( $\mathrm{r}_{\mathrm{S}}=0.51, \mathrm{p}<0.05$ ), as was October flow $\left(328.6 \mathrm{~m}^{3} \mathrm{sec}^{-1}, \mathrm{r}_{\mathrm{S}}=0.44, \mathrm{p}\right.$ $<0.05$ ). Mean fall flow volume (September, October, November) showed a similarly significant correlation $\left(327.7 \mathrm{~m}^{3} \mathrm{sec}^{-1}, \mathrm{r}_{\mathrm{S}}=0.53, \mathrm{p}<0.05\right)$. Correlations between spring flow volume (May, June) and the RSI (egg and/or larval effect) were not evident from the analysis. Analysis of the late juvenile period indicated a weak correlation $\left(\mathrm{r}_{\mathrm{S}}=0.43, \mathrm{p}=0.05\right)$ between yearling recruitment levels and mean fall (September, October, November) flow volume ( $322.1 \mathrm{~m}^{3} \mathrm{sec}^{-1}$ ).


Hatch year
Figure 24. A) Hindcast annual recruitment strengths (open bars) versus shortnose sturgeon CPUE from the Hudson River utilities sponsored Fall Juvenile Trawl Survey. B) Trawl bycatch CPUE lagged by 6 years and overlaid on hindcast recruitment strengths.



Figure 25. Time series of mean monthly flow volume ( $\mathrm{ft}^{3}$ minute ${ }^{-1}$, primary y-axis) collected from Green Island, New York (19462002, USGS) with hindcasted recruitment strength (secondary y-axis) overlaid on flow for corresponding years (Blow-up window) of 1974-1997.

## Discussion

Recovery of shortnose sturgeon in the Hudson River coincided with a series of strong year-classes from 1988-1991 but the demographic analysis did not support my initial expectation of strong year-classes during the early 1980's (Figure 23). Mean recruitment levels (estimated as the subsequent year's abundance of yearlings) from 1988-1991 was 36,331, compared to the preceding and succeeding periods of 1979$1987($ mean $=15,361)$ and 1992-1999 $($ mean $=9,753)$. Yearling abundance estimates varied 10-fold from 1979-1999, reflecting episodic recruitment success often associated with a 'periodic' reproductive strategy (Winemiller \& Rose 1992), which has been associated with long-lived, highly fecund species such as Acipenser (Bain 1997, Bemis \& Kynard 1997, Secor \& Waldman 1999). Counter to the hypothesized response, year-class abundance showed no significant correlations with the magnitude of annual spring freshets, possibly due to a non-linear response and/or the exclusion in the analysis of water temperature, which may act in concert or confound the influence of flow. It was not possible to analyze recruitment success concomitant with the return of system normoxia; yet retrospective analysis of yearclass strength and growth rates based upon my demographic analysis provided circumstantial evidence (e.g., presence of strong year-classes) for improved recruitment, growth rates, and physical condition (no observed malformation or fin rot) during the recent period of system recovery to summertime normoxia.

As a prerequisite to determining population demographics, annuli in pectoral spines were validated as an appropriate ageing structure for Hudson River shortnose sturgeon. The technique yielded age estimates that were found to be non-biased
across ages and over time in repeated trials. The yearly formation of annuli was validated through Marginal Increment Analysis (MIA). The timing of annuli formation typically occurred during the over-wintering period (November-March); presumably a period of low metabolic activity and reduced growth. Growth rate (TL) for the Hudson River population was more rapid than size-at-age data from the late 1970's suggest (Dadswell 1984), though asymptotic size appears to have declined slightly since that time. The recent increase in growth rate (i.e., compared to 1980 population) may be indicative of improvements in ambient water quality mediated by density-dependent factors that in more recent years could be limiting growth rates. Growth rate was intermediate relative to populations at the extremes of the species' range and was similar to those systems in close latitudinal proximity to the Hudson River. The Hudson River population appears to experience a higher than expected annual mortality of $20 \% \mathrm{yr}^{-1}(\mathrm{Z}=-0.22)$, though this estimate is predicated on the assumption of constant recruitment and is likely inflated relative to the actual annual mortality rate.

## Age Determination

Age estimates of wild shortnose sturgeon based upon annuli observed in pectoral fin spines were relatively precise, with precision index values comparing favorably to studies of other Acipenserids and similar moderate to long-lived species (Table 10). Lack of an age bias in CV values indicated that shortnose fin spines can provide precise ages for individuals 5-30 years old. The discrepancy in CV and APE in the literature may be attributed to the disparity in estimated age maxima for each species (Campana 2000). At older ages, CV and APE values are expected to rise due

Table 10. Precision in ageing studies of Acipenser and other fish species of varying longevity, reported as average percent error (APE) and coefficient of variation (CV).

| Species | APE | CV | Maximum estimated age |
| :---: | :---: | :---: | :---: |
| Acipenseridae |  |  |  |
| White sturgeon A. transmontanus ${ }^{\text {a }}$ | 5.9 | 7.8 | 104 |
| Atlantic sturgeon A. oxyrinchus ${ }^{\text {b }}$ | - | 4.8 | 42 |
| Shortnose sturgeon A. brevirostrum | 3.0 | 4.0 | 30 |
| Goldband snapper Pristipomoides mutidens ${ }^{\text {c }}$ | 10.4 | - | 30 |
| Starspotted smoothound Mustelus manazo ${ }^{\text {d }}$ | 6.9-12.7 | - | 20 |
| European eel Anguilla anguilla e | - | 34.0-4.2 | 18.5 |
| Thorny skate Amblyraja radiata ${ }^{\text {f }}$ | - | 2.8 | 16 |
| Common carp Cyprinus carpio ${ }^{\text {g }}$ | - | 7.5-7.9 | 15 |
| Northern pike Esox luscius ${ }^{\text {h }}$ | 1.2 | 1.2 | 11 |
| Monkfish Lophius vomerinus ${ }^{\text {i }}$ | - | 6.3 | 11 |

${ }^{\mathrm{a}-\mathrm{h}}$ Source: (a) Rien \& Beamesderfer (1994); (b) Stevenson \& Secor (1999); (c) Newman \& Dunk (2003); (d) Cailliet et al. (1990); (e) Svedang et al. (1998); (f) Sulikowski et al. (2005); (g) Vilizzi \& Walker (1999); (h) Laine et al. (1991); (i) Maartens et al. (1999)
to increased difficulty in interpreting narrow annuli associated with decreased growth rates as the fish approaches asymptotic size (Casselman 1987, Campana et al. 1995).

Evidence supported seasonal elaboration of an annulus by Hudson River shortnose sturgeon over an annual cycle. Marginal increment analysis indicated that annuli were fully formed sometime between the late fall and early spring months. This timing of annulus formation agrees with a similar study by Stevenson and Secor (1999) on a sympatric population of Atlantic sturgeon. Ideally, here and elsewhere, annulus formation should be verified across many age classes (Campana 2000). Because the shortnose sturgeon is listed as an Endangered Species, we were unable to target a sufficiently large sample to undertake age-class specific marginal increment analysis. Thus, our marginal increment analysis was undertaken for pooled yearclasses, which limits its generality across all ages.

I was unable to accurately estimate the known age of hatchery-raised shortnose sturgeon. Errors in age determination of captive sturgeons (e.g., white sturgeon, Brennan \& Cailliet 1991; pallid sturgeon, Hurley et al. 2004) and of reared individuals of other species (e.g., Atlantic herring Clupea harengus, Lough et al. 1980; starry flounder Platichthys stellatus, Campana 1984; walleye Sander vitreus, Parrish et al. 1994), is well-documented and has been associated with artificial conditions experienced by the fish within the rearing or holding facility. In the wild, reinforced annual cycles related to light, temperature, salinity, feeding, and reproduction are probably critical to annulus timing; these cycles are not well simulated in most hatchery environments.

Limits to precision and accuracy in interpreting annuli in fin spines in hatchery-raised fish included supernumary annuli, bands of narrow annuli, variable widths of annuli, inclusion of embedded rays within the primary spine, resorption or deposition of calcareous material and physical deterioration. Supernumary annuli were especially prevalent across the first three to five annuli of estimated age and may constitute a source of age overestimation if not correctly or consistently interpreted. Variable spacing of annuli has been hypothesized to stem from endogenous and exogenous factors that cause fish to grow slowly (Roussow 1957, Rossiter et al. 1995). The reduction in somatic growth may be recorded in the relative widths of annuli. Spawning bands are thought to chronicle a reduction in somatic growth as energy is shunted to gonadal development over a period of several years prior to a spawning event (Roussow 1957). If annuli are not clearly contrasted or are tightly banded, ages are likely underestimated.

Age validation studies have been reported for Siberian sturgeon (A. baerii) (Sokolov \& Akimova 1976), white sturgeon (Brennan \& Cailliet 1991, Rien \& Beamesderfer 1994, Paragamian \& Beamesderfer 2003), lake sturgeon (A. fulvescens) (Rossiter et al. 1995), Atlantic sturgeon (A. oxyrinchus) (Stevenson 1997, Stevenson \& Secor 1999), pallid sturgeon (Scaphirhynchus albus) (Hurley et al. 2004), and shovelnose sturgeon (S. platorynchus) (Whiteman et al. 2004). These studies have used a suite of validation techniques, including mark-recapture experiments with oxytetracycline markers and traditional tagging or a combination of the two (Brennan \& Cailliet 1991, Rien \& Beamesderfer 1994, Rossiter et al. 1995, Stevenson \& Secor 1999, Paragamian \& Beamesderfer 2003), marginal increment analysis (Stevenson \&

Secor 1999, Whiteman et al. 2004), microchemical analysis (e.g., calcium concentrations) (Stevenson \& Secor 1999), radiometric ageing (Burton et al. 1999), and the use of known-age individuals (Sokolov \& Akimova 1976, Brennan \& Cailliet 1991, Stevenson \& Secor 1999, Hurley et al. 2004). Attempts to validate age estimates have yielded mixed results, with few providing compelling evidence (Sokolov \& Akimova 1976, Rossiter et al. 1995). Some studies support partial validation over a limited range of age-classes (Brennan \& Cailliet 1991, Stevenson \& Secor 1999; this study) and the majority of studies conclude that annulus formation was temporally inconsistent and/or annuli were difficult to interpret (Rien \& Beamesderfer 1994, Burton et al. 1999, Paragamian \& Beamesderfer 2003, Hurley et al. 2004, Whiteman et al. 2004). These problems underscore the importance of validating the relationship between counts of annuli and known age for each species.

## Growth

Age estimates indicate high intra-cohort variability in size for the Hudson River population, a characteristic common to Acipenser spp. (Kolhorst et al. 1980, Nakamoto et al. 1995, Stevenson \& Secor 1999). Sexual dimorphism of shortnose sturgeon probably constitutes a substantial portion of the observed variability in size-at-age. In a review article by Greeley (1937), age and length data are given for male $(n=34)$ and female $(n=47)$ shortnose sturgeon captured from the Hudson River. The largest male was 713 mm TL and 7 years of age, while the largest female was 883 mm TL and 13 years of age. Mean length of males was greater than females for ages $5\left(\delta^{\lambda}: 560 \mathrm{~mm}, ~, q: 513 \mathrm{~mm}\right)$ and $7\left(\delta^{\lambda}: 652 \mathrm{~mm},+, 605 \mathrm{~mm}\right)$, indicating more rapid growth of males during the sub-adult stage. In the St. John River, Dadswell (1979)
observed similar sex-specific growth attributes, with males experiencing higher initial growth rates and attaining a lower maximum length $\left(\mathrm{K}=0.063, \mathrm{FL}_{\infty}=1087 \mathrm{~mm}\right)$ than females $\left(\mathrm{K}=0.047, \mathrm{FL}_{\infty}=1270 \mathrm{~mm}\right)$.

Recapture of tagged Hudson River shortnose sturgeon provided a second source of growth estimates that generally corroborated my age estimates and growth models. Still, without known ages for the marked fish, the accuracy of predicted and estimated ages remains uncertain. Mark-recapture studies of sturgeon spp. have yielded disparate results; an analysis of white sturgeon mark-recapture data from the Kootenai River, ID showed that age estimates derived from fin-spines significantly underestimated true ages (Paramagian \& Beamesderfer 2003). Interestingly, in my study there was a significant difference in the yearly growth increment $\left(\mathrm{mm} \mathrm{yr}^{-1}\right)$ between larger and smaller sturgeon with smaller sturgeon at tagging experiencing lower growth rates than larger fish. This result runs counter to the expectation that smaller sturgeon would demonstrate higher mean growth $\mathrm{yr}^{-1}$ relative to older fish as has been reported in tag-effect studies on other fishes (e.g., northern pike Scheirer \& Coble 1991, Arctic grayling Thymallus arcticus Hughes 1998, tropical goby Coryphopterus glaucofraenum Malone et al. 1999). This discrepancy could indicate that smaller sturgeon were disproportionately stressed by handling and tagging and therefore experienced significant post-capture growth depression. Alternatively, those fish that were larger at the time of tagging may have been predominantly females. The smaller "males" would be constrained by a smaller asymptotic size and evince lower growth. Sexual dimorphism on this scale does not seem unreasonable. Greeley (1937) reported a maximum size for male Hudson River shortnose sturgeon
of 713 mm which is well below the mean tagging TL of 772 mm for the larger size bin. This interpretation is based upon the assumption that the smaller fish at tagging were predominately males and not simply younger females, an assumption that remains speculative due to lack of data.

Growth parameters $\mathrm{L}_{\infty}$ and K were intermediate in relation to the set of values estimated for shortnose sturgeon across their range (Table 11). Shortnose sturgeon populations tend to exhibit, more rapid growth $\left(\mathrm{K}_{\max }=0.149\right)$ and a smaller maximum size $\left(\mathrm{FL}_{\infty \min }=870 \mathrm{~mm}\right)$ in southern estuaries compared to northern systems $\left(\mathrm{K}_{\min }=0.042 \& \mathrm{FL}_{\infty \max }=1300 \mathrm{~mm}\right.$; Figure 26; Dadswell et al. 1984). The Hudson River $\mathrm{FL}_{\infty}(925 \mathrm{~mm})$ was similar to literature values for the proximal Connecticut (1000 mm) and Kennebec (938 mm) Rivers.

Growth parameter values from a previous study of the same Hudson River population reported $\mathrm{TL}_{\infty}=1234 \mathrm{~mm}$ (calculated from 1064 mm FL ) and $\mathrm{K}=0.044$ (Dadswell et al. 1984), which suggests a temporal shift in growth dynamics. In general, shortnose sturgeon are currently attaining a larger size at age than they did 20-40 years ago (Figure 27). Factors that would prompt an increase in growth include improved water quality, increased nursery habitat, and conditions favoring greater forage.

A recent increase in specific growth rates of Hudson River shortnose sturgeon, particularly during the juvenile stage when habitats are limited, may reflect the return of large portions of the river to year-round normoxia. Hypoxia can limit the function of most bioenergetic processes, resulting in reduced growth and/or increased mortality (Fry 1971, Niklitschek \& Secor 2005). Regulations promulgated under the

Table 11. Growth parameters from the von Bertalanffy growth function estimated for shortnose sturgeon across their range. Boldface row indicates parameters derived during this study.

| River System | $\mathrm{FL}_{\infty}$ | K | t | Z | *Source |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Saint John R., FL |  |  |  |  |  |
| Female | 127 | 0.047 | -1.1 |  | Dadswell, 1979 |
| Male | 108.7 | 0.063 | 0.79 |  |  |
| Combined | 130 | 0.042 | -1.96 | 0.12-0.15 |  |
| Kennebec R., ME |  |  |  |  |  |
| Combined | 93.8 | 0.098 | -3.89 |  | *Squiers \& Smith, 1978 |
| Connecticut R. <br> (Holyoke Pool, MA) |  |  |  |  |  |
| Combined | 87.8 | 0.084 | $-2.64$ | 0.12 | *Taubert, 1980b |
| Connecticut. R. <br> (Lower river, CT ) |  |  |  |  |  |
| Combined | 100 | 0.073 | $-2.73$ |  | *Buckley, unpublished |
| Hudson R., NY Combined | 925 | 0.064 | -7.05 | 0.22 | Current study |
| Hudson R., NY |  |  |  |  |  |
| Female | 102.6 | 0.079 | -3.17 |  | *Greely, 1937 |
| Male | 57.9 | 0.305 | -1.8 |  |  |
| Combined | 106.4 | 0.044 | 6.39 |  | *Dovel, 1981 |
| Pee Dee-Winyah, SC |  |  |  |  |  |
| Female | 83.8 | 0.133 | -2.33 |  | *Marchette \& Smiley, |
| Male | 73.9 | 0.114 | -4.5 |  | 1982 |
| Combined | 87 | 0.093 | -6.02 | 0.08-0.12 |  |
| Altamaha R., GA |  |  |  |  |  |
| Combined | 97 | 0.149 | -3.15 |  | *Heidt \& Gilbert, 1978 |

[^1]

Figure 26. Von Bertalanffy growth parameters $\mathrm{FL}_{\infty}$ (primary y -axis) and k (secondary y-axis) plotted against latitude.


Figure 27. Predictions of Fork Length-at-age from von Bertalanffy growth models (combined sex models) for three different estuaries across the latitudinal range of shortnose sturgeon. Sources for each curve: 1) Dadswell et al. 1984, 2) current study, 3) Dadswell et al. 1984, 4) Dadswell 1979.

Clean Water Act (1970) led to increased summertime DO levels across a substantial portion of the Hudson River Estuary (Leslie et al. 1988), from Troy's Federal Dam extending c. 60 km downstream. This area constitutes c. $40 \%$ of the larval/juvenile nursery habitat for shortnose sturgeon as well as summer foraging habitat used by adult fish (Dovel 1980, Bain 1995). Laboratory studies have shown that YOY and yearling shortnose sturgeon are unusually sensitive to hypoxia and demonstrate decreased routine metabolism, consumption, feeding metabolism, growth and survival at DO levels $<40 \%$ saturation (Jenkins et al. 1994, Niklitschek 2001, Secor \& Niklitschek 2001, Campbell \& Goodman 2004).

Older juveniles and sub-adults may experience secondary effects of hypoxia if it limits their distribution to smaller or less profitable foraging and refuge habitats. The cascading effects of seasonal hypoxia can substantially reduce the biomass of benthic macrofauna and diminish an ecosystem's ability to transfer energy to higher trophic levels in estuarine systems (Baird et al. 2004, Eby et al. 2005). Invertebrate benthic macrofauna constitute the principal prey source of the shortnose sturgeon diet (Dadswell 1979, Carlson \& Simpson 1987). With a reduction in chronic seasonal hypoxia, the sturgeon population would experience a simultaneous increase in suitable foraging habitat during the important summer growth period and a concomitant rise in available forage densities. Both of these factors could contribute to the higher growth rates observed for the Hudson River population.

Exposure and uptake of PCBs can initiate an array of physiological responses including disruption of the endocrine system and subsequently irregular growth and development. In conjunction with increased summertime DO levels, reduced
contaminant concentrations may explain increases in sturgeon growth rates during recent decades. Time series data show a $>95 \%$ decline in PCB body burden for white perch (Marone americana,31 $\rightarrow 3 \mathrm{ppm}$ ) and American eel (Anguilla rostrata, $77 \rightarrow 2$ ppm) in the lower Hudson River from 1978-1996 (NYSDEC 2001), two species whose habitats overlap that of shortnose sturgeon. Recent body burdens appear to have stabilized near 3 ppm among sampled fishes (e.g., striped bass M. saxatilis, American shad, largemouth bass Micropterus salmoides, channel catfish Ictalurus punctatus) below the Federal Dam (NYSDEC 2001).

Sublethal levels of bioaccumulated PCB's have been found to retard growth in channel catfish (Ictalurus punctatus, Hansen et al. 1976), larval Atlantic croaker (Micropogonias undulatus, McCarthy et al. 2003) and brook trout (Salvelinus fontinalis, Ndayibagira et al. 1995) and may manifest a similar effect in shortnose sturgeon as has been proposed for white sturgeon (Kolhorst et al. 1980).

Developmental malformations and disease have been documented for PCB-exposed sturgeon populations. Doyon et al. (1999) found that PCB induction of an enzyme (cytochrome P-450) involved in the metabolism of a biologically active form of vitamin A may be associated with limb and craniofacial anomalies in St. Lawrence River lake sturgeon. In Hudson River shortnose sturgeon samples collected from 1975-1980, Dovel et al. (1992) reported the presence of a facial abnormality termed "u-snout" in c. 2\% of the captured sturgeon; a similar facial abnormality to that noted among lake sturgeon sampled from the St. Lawrence River near Montreal (Doyon et al. 1999). No incidents of facial malformation was observed during our field collections ( $\mathrm{n}=596$ ).

## Recruitment

Generating a valid estimate of population age structure and index of recruitment strengths required adjustment of the original catch values. Actual catch $\left(\mathrm{C}_{\text {act }}=597\right)$ was scaled to adjusted catch $\left(\mathrm{C}_{\text {adj }}=1238\right)$ following compensation for size-selectivity and effort. This procedure was similar to that used by Dadswell (1979) for the St. John River population. Subsequent estimates of annual mortality, age structure and recruitment were based on the adjusted catch.

## Gear Selectivity

Application of the Baranov gear selectivity model involves several assumptions, the most important of which is the principle of geometric similarity: selectivity curves for different mesh size are similar because the ratio of mesh and fish profile is similar across mesh sizes (Hamley 1975). One of the corollaries implicit in the principle of geometric similarity is that the ratio of mesh size to optimal capture length, K , is equal across mesh sizes (Hamley 1975). Results from field sampling did not support this corollary; calculated values of K increased progressively from 0.15 to 0.22 for the 10.2 and 17.8 cm mesh nets. These values are often interpreted in terms of body morphology: thin bodied fishes (e.g., northern pike, mackerel Scomber spp.) exhibit K values of $0.10-0.15$, while deep body fishes (e.g., sunfishes Lepomis spp.) typically have values $>0.2$ (Hamley 1975). The observed increase in K corresponds with a positive shift in the girth to length ratio with increased age of sturgeon, a general ontogenetic change observed in many fishes.

Selectivities of different mesh sizes are not necessarily equal in terms of catch efficiency for a single species. Hamley \& Regier (1973), using direct estimates of gill
net selectivity on walleye (S. vitreus), showed increased overall selectivity in larger mesh sizes. The same pattern of increasing catch frequency with increased mesh size was observed by Dadswell (1979) for the St. John River population of shortnose sturgeon. In my study, this bias would tend to amplify observed patterns of stronger year-classes historically than in recent times. Although indirect methods such as those employed here are not preferred and may introduce bias, studies continue to employ indirect methods of estimating gear selectivity (see Milton et al. 1998, Anderson \& Neumann 2000) as a practical and necessary alternative to direct methods.

## Mortality

The total instantaneous mortality rate $\mathrm{Z}=0.22$ for Hudson River shortnose sturgeon was somewhat higher than that reported for other systems. A theoretical estimate of natural mortality $(M)$ based on observed longevity $\left(\mathrm{t}_{\max }=30\right)$ yielded $\mathrm{M}=$ 0.15 (Hoenig 1983). Estimates of total mortality may be viewed as a proxy for M as there is no extant fishery for shortnose sturgeon anywhere in the United States. In the most synoptic demographic shortnose sturgeon study to date, Dadswell (1979) estimated $Z=0.12,0.15(1974,1975)$ for ages $15-55$ years from the Saint John River (Table 11). Dadswell's estimate included a fishing mortality component F (0.07) stemming from bycatch in commercial fisheries for other species. Although a limited American shad (Alosa sapidissima) fishery still exists on the Hudson River in which shortnose have been observed as incidental bycatch (S. Nack, pers. com.), the fishery is small and net deployment time is brief; therefore, shortnose sturgeon bycatch mortality is likely to be negligible. The Hudson River population is considered the
largest (NMFS 1998) and as such could be exhibiting density-dependent mortality not apparent in other systems where shortnose sturgeon occur. Additionally, the catchcurve analysis assumes constant recruitment, yet I have shown that recruitments have substantially varied over the past 25 years. For the presented catch curve (Figure 21 A), higher residuals for ages 12 to 17 and negative residuals for ages $>17$ would result in a shift in slope towards a more negative value than were residuals more homogenously distributed. An overestimation of $Z$ would tend to underestimate of early year-class strengths and overestimate more recent year-class strengths.

## Age-structure

Age-structure for unexploited, long-lived fish populations is typified by a wide range of successive age-classes composed of progressively fewer individuals (Gill \& Weatherley 1987; Secor 2000). Although the distribution of ages was likely influenced by gear selectivity, this pattern agrees with the trend in demographic structure observed for the Hudson population. Juveniles younger than 5 years of age were not captured; reflecting the likely escape of smaller sturgeon from the sampling gear. Also, juveniles do not tend to display the strong aggregating behavior of the adults (Bain 1997, Haley 1999). The oldest sturgeon reported for the Hudson River was 37 years old (Dadswell et al. 1984) and it seems likely that individuals of that age still exist within the population at abundances below the detection level of this study (i.e., a sampling rate of $\mathrm{c} .1 \%$ ).

The recruitment strength index (RSI) highlights a trend in increased recruitment success that occurred 11-18 years ago (1993-1986). This period of enhanced recruitment is corroborated through bycatch of adult shortnose sturgeon
during the Hudson River Utilities Fall Juvenile Survey (Figure 24). Catch rates from the survey showed a temporal pattern of fluctuation similar to that of our hindcast recruitment index. Because survey gear and sampling design are standardized, interannual changes in the trawl survey shortnose CPUE should accurately reflect changes in annual abundance of those fish vulnerable to the gear. Mean size at capture in the trawl survey was 670 mm TL (Bain et al. 1997), which would correspond to 6-8 years old (TL $\sim 650 \mathrm{~mm}$; Figure 16). This suggests a lag of c .6 years between the formation of strong year classes and increased relative abundance in the trawl survey, a prediction that was substantiated through correlation analysis (Table 9).

Predictions of yearling abundances across year-classes indicated that recruitment of Hudson River shortnose sturgeon varied by an order of magnitude. Year-class variability of this magnitude is common among moderately to long-lived estuarine and coastal fishes and reflects a "periodic" life-history strategy that depends on conditions favorable for survival and growth of early life-stages that occur at an interval less than the average life-span of the organism (Winnemiller \& Rose 1992; Warner and Chesson 1995). In the case of the Hudson River shortnose sturgeon, I observed two c. 5-year periods of relatively low recruitments bridged by a 4-year period of high recruitment (Figure 22). Interestingly, in more recent years lower recruitments are coincident with record high abundance levels. Should recruitments become density dependent as the population approaches carrying capacity, variability in year-class strength might be expected to dampen as regulation becomes a more dominant force.

Water pollution is listed as a principal factor in the decline of shortnose populations (NMFS 1998). The return of normoxia to a substantial portion of the tidal freshwater portion (c. 60 km ) of the Hudson River Estuary (Leslie et al. 1988) during the 1970's occurred in a critical habitat for shortnose sturgeon. The location of the former hypoxic zone, adjacent and downstream of the spawning grounds, would have been particularly detrimental to larvae and juveniles. Mortality due to hypoxic-anoxic conditions may result from direct mortality, reduced production resulting from increased metabolic costs (Secor and Niklitschek 2001), and synergistic interactions among stressors (i.e., a "habitat squeeze" sensu Coutant 1985, Niklitschek \& Secor 2005). Therefore, the return of normoxia during a crucial period of growth and development (i.e., summer months) may have eliminated a substantial recruitment bottleneck to the Hudson River population. Slow recovery of the benthic ecosystem could explain the observed lag of c. 10 years (1978-1988) between system return to normoxia and the first measurable strong yearling recruitment.

There is evidence that annual reproduction relies on an environmentallymediated endogenous mechanism in some fishes (de Vlaming 1972, Buckley \& Kynard 1985). The positive correlation of fall flow volume to recruitment success of Hudson River shortnose sturgeon the following year may indicate that flow acts as a primary component of a suite of environmental cues that initiate the final stages of gonadal development. Alternatively, flow may be acting as an indicator of water temperature or other environmental parameter exercising a more direct effect on conditioning of adult sturgeon. Pre-spawn 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 has been shown to be a significant factor in determining the success of subsequent spawning of white sturgeon (Doroshov et al. 1997, Webb et al. 1999). These results support further study into the effects of fall flow on pre-spawn conditioning of ovigerous shortnose sturgeon.

Although spring flow has frequently been implicated in recruitment of anadromous fishes (Creco \& Savoy 1984, Maurice et al. 1987, Stevens et al. 1987, Paragamian \& Wakkinen 2002), there was no correlation between spring flows and year-class strength. This may stem from a non-linear response of spawning activity to ambient flow rate on the spawning beds (Veshchev 1982, Buckley \& Kynard 1985, Kynard 1997). Moderate to swift current velocities ( $0.4-1.8 \mathrm{~m} \mathrm{sec}^{-1}$ ) appear to trigger spawning activity (Dadswell et al. 1984, Kynard 1997, but see Duncan et al. 2004), while periods of extremely high discharge have been shown to deter spawning (Buckley \& Kynard 1985). Also, spring flow is likely to be confounded with temperature effects since shortnose spawning tends to occur within a narrow temperature window, ranging from $9-16^{\circ} \mathrm{C}$ (Taubert 1980, Dadswell et al. 1984, Buckley \& Kynard 1985, Duncan et al. 2004). Further correlative analyses using a long-term data set of water temperature near the spawning grounds may help elucidate the relationship between environmental variables and annual recruitment success.

## Management Implications

The shortnose sturgeon is showing signs of strong recovery in the Hudson River although many population segments, especially in the south, still display low
abundance (or a lack of formal demographic assessment to make such a determination). The Hudson River population appears to satisfy the formal delisting criterion as defined by the Shortnose Sturgeon Recovery Team in which sufficient abundance exists to 1 ) defray extinction risk and 2 ) make the loss of genetic diversity unlikely (NMFS 1998). In addition, this study has shown that the population is composed of a multi-tiered age structure, displays expected growth characteristics for the species and population, and has experienced substantial recruitment $(>4,500$ yearlings) annually for over two decades. Thus, the Hudson River population probably represents an Endangered Species success story, the first of its kind among listed fishes. Though a formal delisting process following recovery does not exist, this population could serve as a template for evaluation and future delisting of other population segments or species. Delisting shortnose sturgeon in the Hudson River could expand opportunities for scientific study of the species, the findings of which could prove beneficial to the species as a whole. Such research could include ecological studies of YOY life stages, telemetry tracking of juvenile-adults, quantification of vital rates across life stanzas, and environmental influences on behavior.

The Hudson River shortnose sturgeon population also offers a unique opportunity to employ physical (e.g., PIT, Floy ${ }^{\circledR}$, Carlin tags) or bio-assimilated labels (i.e., Oxytetracycline) as methods for further validating the yearly formation of annuli. Shortnose sturgeon of the Hudson River are optimal candidates for these procedures because the robust demographic structure of the population equates to ontogenetic stanzas of juveniles to mature adults available for validation of annulus
formation. Capture, marking, release and subsequent resampling requires direct contact between researchers and sturgeon, a scenario with the potential to inflict high stress levels on an Endangered Species. However, the Hudson River supports the largest population of shortnose sturgeon in terms of numerical abundance (Bain 2001) and therefore any stress-induced mortality would likely have trivial effects on this population relative to other, less abundant populations. Use of Hudson River shortnose as brood-stock to produce tagged known-age sturgeon to be released to the river would serve as another powerful method of age validation in this species. Yet, care would be required to avoid genetic swamping and reductions to the effective population size due to the use on insufficient brood numbers.

## Appendix

Shortnose sturgeon sampling data collected from Hudson River, November 2003 November 2004. Sampling locations (Locale): Esopus Meadows area (Esopus), Catskill-Burden Dock area (Burden), and Albany area (Albany). Except for Clip \# 299 (juvenile Atlantic sturgeon), all data entries refer to shortnose sturgeon.

| Clip | Age | $\begin{gathered} \text { FL } \\ (\mathrm{mm}) \end{gathered}$ | $\begin{gathered} \mathrm{TL} \\ (\mathrm{~mm}) \end{gathered}$ | Weight <br> (kg) | $\begin{aligned} & \text { Mesh size } \\ & (\mathrm{cm}) \end{aligned}$ | Sample event | Season | Locale |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 17 | 652 | 737 | 2.3 | 15.2 | 1st | fall | Esopus |
| 2 | 16 | 680 | 771 | 2.8 | 15.2 | 1st | fall | Esopus |
| 3 | 15 | 721 | 840 | 4.5 | 15.2 | 1 st | fall | Esopus |
| 4 | 11 | 598 | 680 | 1.65 | 15.2 | 1st | fall | Esopus |
| 6 | 16 | 683 | 800 | 3 | 15.2 | 1st | fall | Esopus |
| 7 | 15 | 599 | 699 | 1.6 | 15.2 | 1st | fall | Esopus |
| 8 | 13 | 575 | 646 | 1.5 | 15.2 | 1st | fall | Esopus |
| 9 | 9 | 628 | 736 | 2.1 | 15.2 | 1st | fall | Esopus |
| 10 | 12 | 686 | 755 | 2.9 | 15.2 | 1st | fall | Esopus |
| 11 | 19 | 636 | 736 | 2 | 15.2 | 1 st | fall | Esopus |
| 12 | 19 | 721 | 839 | 3.2 | 15.2 | 1st | fall | Esopus |
| 13 | 17 | 642 | 751 | 2.2 | 15.2 | 1st | fall | Esopus |
| 14 | 14 | 751 | 865 | 3.6 | 15.2 | 1st | fall | Esopus |
| 15 | 9 | 635 | 715 | 2.1 | 15.2 | 1st | fall | Esopus |
| 16 | 15 | 655 | 745 | 2.1 | 15.2 | 1st | fall | Esopus |
| 17 | 15 | 706 | 820 | 2.9 | 15.2 | 1st | fall | Esopus |
| 18 | 16 | 632 | 741 | 2.4 | 15.2 | 1st | fall | Esopus |
| 19 | 14 | 602 | 686 | 1.8 | 15.2 | 1st | fall | Esopus |
| 20 | 15 | 682 | 788 | 2.7 | 15.2 | 1st | fall | Esopus |
| 21 | 16 | 632 | 729 | 2.5 | 15.2 | 1st | fall | Esopus |
| 22 | 11 | 552 | 640 | 1.5 | 15.2 | 1st | fall | Esopus |
| 23 | 18 | 662 | 772 | 3.1 | 15.2 | 1st | fall | Esopus |
| 24 | 15 | 680 | 771 | 2 | 15.2 | 1st | fall | Esopus |
| 25 | 22 | 576 | 672 | 2 | 15.2 | 1st | fall | Esopus |
| 26 | 15 | 551 | 749 | 2.9 | 15.2 | 1st | fall | Esopus |
| 27 | 14 | 638 | 734 | 2.3 | 15.2 | 1st | fall | Esopus |
| 28 | 13 | 610 | 710 | 2 | 15.2 | 1 st | fall | Esopus |
| 29 | 14 | 649 | 748 | 2.6 | 15.2 | 1st | fall | Esopus |
| 30 | 17 | 621 | 717 | 2.5 | 15.2 | 1st | fall | Esopus |
| 31 | 9 | 665 | 782 | 3 | 15.2 | 1st | fall | Esopus |
| 32 | 16 | 580 | 700 | 2.3 | 15.2 | 1 st | fall | Esopus |
| 33 | 16 | 667 | 775 | 3 | 15.2 | 1st | fall | Esopus |
| 34 | 15 | 706 | 820 | 2.9 | 15.2 | 1st | fall | Esopus |
| 35 | 14 | 630 | 746 | 2.7 | 15.2 | 1st | fall | Esopus |







| 258 | 13 | 664 | 788 | 2.5 | 15.2 | 2nd | spring | Esopus |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 259 | 14 | 712 | 830 | 3.4 | 15.2 | 2nd | spring | Esopus |
| 260 | 11 | 644 | 759 | 2.5 | 15.2 | 2nd | spring | Esopus |
| 261 | 15 | 828 | 916 | 4.8 | 15.2 | 2nd | spring | Esopus |
| 262 | 10 | 656 | 781 | 2.1 | 15.2 | 2nd | spring | Esopus |
| 263 | 11 | 670 | 775 | 2.8 | 15.2 | 2nd | spring | Esopus |
| 264 | 13 | 727 | 845 | 3.2 | 15.2 | 2nd | spring | Esopus |
| 265 | 11 | 625 | 733 | 1.8 | 15.2 | 2nd | spring | Esopus |
| 266 | 12 | 689 | 798 | 2.8 | 15.2 | 2nd | spring | Esopus |
| 267 | 12 | 660 | 766 | 2.9 | 15.2 | 2nd | spring | Esopus |
| 268 | 11 | 651 | 749 | 2.7 | 15.2 | 2nd | spring | Esopus |
| 269 | 9 | 544 | 636 | 1.2 | 15.2 | 2nd | spring | Esopus |
| 270 | 13 | 735 | 833 | 4.6 | 15.2 | 2nd | spring | Esopus |
| 271 | 18 | 668 | 775 | 2.7 | 15.2 | 2nd | spring | Esopus |
| 272 | - | 751 | 850 | 3.1 | 15.2 | 2nd | spring | Esopus |
| 273 | 10 | 705 | 803 | 2.6 | 15.2 | 2 nd | spring | Esopus |
| 274 | 13 | 700 | 817 | 2.8 | 15.2 | 2nd | spring | Esopus |
| 275 | 17 | 639 | 749 | 2.4 | 15.2 | 2nd | spring | Esopus |
| 276 | 14 | 722 | 837 | 3.4 | 15.2 | 2 nd | spring | Esopus |
| 277 | 17 | 754 | 880 | 4.3 | 15.2 | 2nd | spring | Esopus |
| 278 | 10 | 655 | 778 | 2.3 | 15.2 | 2nd | spring | Esopus |
| 279 | 11 | 706 | 805 | 3.2 | 15.2 | 2nd | spring | Esopus |
| 280 | 19 | 682 | 784 | 2.4 | 15.2 | 2nd | spring | Esopus |
| 281 | 13 | 658 | 769 | 2.6 | 15.2 | 2nd | spring | Esopus |
| 282 | 16 | 660 | 763 | 2.6 | 15.2 | 2nd | spring | Esopus |
| 283 | 13 | 623 | 732 | 2.3 | 15.2 | 2nd | spring | Esopus |
| 284 | 12 | 673 | 797 | 2.8 | 15.2 | 2nd | spring | Esopus |
| 285 | 18 | 715 | 841 | 3.3 | 15.2 | 2nd | spring | Esopus |
| 286 | 11 | 629 | 726 | 2.4 | 15.2 | 2 nd | spring | Esopus |
| 287 | 9 | 690 | 779 | 2.7 | 15.2 | 2nd | spring | Esopus |
| 288 | 16 | 670 | 786 | 2.8 | 15.2 | 2nd | spring | Esopus |
| 289 | - | 702 | 815 | 2.5 | 15.2 | 2nd | spring | Esopus |
| 290 | 14 | 664 | 773 | 2.6 | 15.2 | 2nd | spring | Esopus |
| 291 | 10 | 621 | 711 | 2.7 | 15.2 | 2nd | spring | Esopus |
| 292 | 12 | 685 | 798 | 3 | 15.2 | 2nd | spring | Esopus |
| 293 | 12 | 625 | 721 | 2.6 | 15.2 | 2nd | spring | Esopus |
| 294 | 17 | 740 | 843 | 3.7 | 15.2 | 2nd | spring | Esopus |
| 295 | 13 | 674 | 787 | 3 | 15.2 | 2nd | spring | Esopus |
| 296 | 14 | 618 | 715 | 1.9 | 10.2 | 2 nd | spring | Esopus |
| 297 | - | 571 | 666 | 1.2 | 10.2 | 2nd | spring | Esopus |
| 298 | 13 | 779 | 892 | 3.8 | 10.2 | 2nd | spring | Esopus |
| *299 | 8 | 476 | 552 | 0.7 | 10.2 | 2nd | spring | Esopus |
| 300 | 8 | 483 | 571 | 0.9 | 10.2 | 2nd | spring | Esopus |
| 301 | 14 | 595 | 685 | 1.9 | 10.2 | 2nd | spring | Esopus |
| 302 | 14 | 728 | 830 | 3.3 | 10.2 | 2nd | spring | Esopus |
| 303 | 5 | 477 | 562 | 0.7 | 10.2 | 2nd | spring | Esopus |





| 442 | 15 | 685 | 800 | 3 | 15.2 | 3rd | spring | Albany |
| :---: | :---: | :---: | :---: | :---: | :---: | :--- | :--- | :--- |
| 443 | 18 | 822 | 940 | 4.9 | 15.2 | 3rd | spring | Albany |
| 444 | 15 | 725 | 835 | 4 | 15.2 | 3rd | spring | Albany |
| 445 | 17 | 750 | 865 | 3.6 | 15.2 | 3rd | spring | Albany |
| 446 | - | 802 | 942 | 4.5 | 15.2 | 3rd | spring | Albany |
| 447 | 10 | 577 | 662 | 1.5 | 10.2 | 3rd | spring | Albany |
| 448 | 12 | 684 | 801 | 2.6 | 10.2 | 3rd | spring | Albany |
| 449 | 11 | 661 | 760 | 2.1 | 10.2 | 3rd | spring | Albany |
| 450 | 11 | 641 | 755 | 1.7 | 10.2 | 3rd | spring | Albany |
| 451 | 9 | 669 | 777 | 1.9 | 10.2 | 3rd | spring | Albany |
| 452 | 14 | 697 | 805 | 2.6 | 10.2 | 3rd | spring | Albany |
| 453 | 14 | 596 | 685 | 1.4 | 10.2 | 3rd | spring | Albany |
| 454 | 15 | 667 | 780 | 3.7 | 10.2 | 3rd | spring | Albany |
| 455 | 12 | 574 | 660 | 1.5 | 10.2 | 3rd | spring | Albany |
| 456 | 7 | 550 | 632 | 1.5 | 10.2 | 3rd | spring | Albany |
| 457 | 6 | 575 | 660 | 1.7 | 10.2 | 3rd | spring | Albany |
| 458 | 16 | 724 | 838 | 3 | 10.2 | 3rd | spring | Albany |
| 459 | 9 | 573 | 649 | 1.5 | 10.2 | 3rd | spring | Albany |
| 460 | 14 | 632 | 741 | 1.9 | 10.2 | 3rd | spring | Albany |
| 461 | 14 | 733 | 865 | 3.7 | 10.2 | 3rd | spring | Albany |
| 462 | - | 520 | 590 | 0.9 | 10.2 | 3rd | spring | Albany |
| 463 | 15 | 675 | 800 | 3.1 | 10.2 | 3rd | spring | Albany |
| 464 | 5 | 450 | 530 | 0.8 | 10.2 | 4th | summer | Burden |
| 465 | 16 | 745 | 860 | 4.8 | 15.2 | 4th | summer | Burden |
| 466 | 13 | 610 | 693 | 2.3 | 15.2 | 4th | summer | Burden |
| 467 | 8 | 568 | 686 | 1.5 | 15.2 | 4th | summer | Burden |
| 468 | 15 | 725 | 831 | 2.6 | 15.2 | 4th | summer | Burden |
| 469 | - | 745 | 850 | 3.6 | 15.2 | 4th | summer | Burden |
| 470 | 17 | 775 | 895 | 4.1 | 15.2 | 4th | summer | Burden |
| 471 | - | 750 | 875 | 3.3 | 15.2 | 4th | summer | Burden |
| 472 | 13 | 710 | 805 | 2.8 | 15.2 | 4th | summer | Burden |
| 473 | 15 | 655 | 772 | 2.2 | 15.2 | 4th | summer | Burden |
| 474 | 12 | 695 | 807 | 2.8 | 15.2 | 4th | summer | Burden |
| 475 | 18 | 705 | 815 | 2.7 | 15.2 | 4th | summer | Burden |
| 476 | 11 | 605 | 695 | 1.7 | 15.2 | 4th | summer | Burden |
| 477 | 10 | 725 | 850 | 3.8 | 15.2 | 4th | summer | Burden |
| 478 | 13 | 700 | 805 | 2.8 | 15.2 | 4th | summer | Burden |
| 487 | 16 | 750 | 880 | 3.8 | 15.2 | 4th | summer | Burden |


| 488 | 16 | 665 | 770 | 2 | 15.2 | 4th | summer | Burden |
| :---: | :---: | :---: | :---: | :---: | :---: | :--- | :--- | :--- |
| 489 | 15 | 655 | 770 | 2.4 | 15.2 | 4th | summer | Burden |
| 490 | 11 | 580 | 683 | 1.4 | 15.2 | 4th | summer | Burden |
| 491 | 16 | 675 | 760 | 2.5 | 15.2 | 4th | summer | Burden |
| 492 | 16 | 740 | 865 | 3.4 | 15.2 | 4th | summer | Burden |
| 493 | 12 | 710 | 795 | 2.5 | 15.2 | 4th | summer | Burden |
| 494 | 11 | 700 | 810 | 2.7 | 15.2 | 4th | summer | Burden |
| 495 | 5 | 580 | 665 | 1.2 | 15.2 | 4th | summer | Burden |
| 496 | 9 | 526 | 605 | 1 | 15.2 | 4th | summer | Burden |
| 497 | 16 | 655 | 745 | 2.4 | 15.2 | 4th | summer | Burden |
| 498 | 17 | 475 | 775 | 3.3 | 15.2 | 4th | summer | Burden |
| 499 | - | 640 | 725 | 2.2 | 15.2 | 4th | summer | Burden |
| 500 | 14 | 665 | 770 | 2.1 | 15.2 | 4th | summer | Burden |
| 501 | 11 | 705 | 805 | 2.8 | 15.2 | 4th | summer | Burden |
| 502 | 12 | 610 | 712 | 1.7 | 15.2 | 4th | summer | Burden |
| 503 | 13 | 660 | 755 | 3.4 | 15.2 | 4th | summer | Burden |
| 504 | 10 | 705 | 815 | 2.9 | 15.2 | 4th | summer | Burden |
| 505 | 20 | 770 | 905 | 5 | 15.2 | 4th | summer | Burden |
| 506 | 14 | 755 | 890 | 3.8 | 15.2 | 4th | summer | Burden |
| 507 | 12 | 680 | 760 | 2.5 | 15.2 | 4th | summer | Burden |
| 508 | 14 | 670 | 780 | 2.9 | 15.2 | 4th | summer | Burden |
| 509 | 16 | 675 | 755 | 2.8 | 15.2 | 4th | summer | Burden |
| 510 | 12 | 650 | 755 | 2.3 | 15.2 | 4th | summer | Burden |
| 511 | 14 | 695 | 785 | 3.8 | 15.2 | 5th | summer | Burden |
| 512 | 23 | 925 | 1045 | 9 | 15.2 | 5th | summer | Burden |
| 513 | 17 | 710 | 805 | 3.2 | 15.2 | 5th | summer | Burden |
| 514 | 13 | 735 | 845 | 3.2 | 15.2 | 5th | summer | Burden |
| 515 | 15 | 720 | 835 | 2.8 | 15.2 | 5th | summer | Burden |
| 516 | 16 | 695 | 785 | 2.6 | 15.2 | 5th | summer | Burden |
| 517 | 13 | 775 | 895 | 4.5 | 15.2 | 5th | summer | Burden |
| 518 | 17 | 745 | 845 | 4.2 | 15.2 | 5th | summer | Burden |
| 519 | 15 | 735 | 855 | 3.8 | 15.2 | 5th | summer | Burden |
| 520 | 15 | 690 | 790 | 2.9 | 15.2 | 5th | summer | Burden |
| 521 | 16 | 670 | 795 | 2.8 | 15.2 | 5th | summer | Burden |
| 522 | 12 | 695 | 795 | 2.5 | 15.2 | 5th | summer | Burden |
| 523 | 14 | 685 | 780 | 3 | 15.2 | 5th | summer | Burden |
| 524 | 13 | 700 | 815 | 2.9 | 15.2 | 5th | summer | Burden |
| 535 | 16 | 760 | 860 | 4.2 | 15.2 | 5th | summer | Burden |
| 535 | 14 | 820 | 955 | 3.7 | 15.2 | 5th | summer | Burden |


| 534 | 17 | 790 | 925 | 4 | 15.2 | 5th | summer | Burden |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 535 | 18 | 790 | 920 | 4.4 | 15.2 | 5th | summer | Burden |
| 536 | 14 | 695 | 820 | 2 | 15.2 | 5th | summer | Burden |
| 537 | 13 | 640 | 735 | 2.5 | 15.2 | 5th | summer | Burden |
| 538 | 16 | 745 | 840 | 3.4 | 15.2 | 5th | summer | Burden |
| 539 | 19 | 845 | 955 | 5.5 | 15.2 | 5th | summer | Burden |
| 540 | 12 | 730 | 845 | 2.6 | 15.2 | 5th | summer | Burden |
| 541 | 13 | 760 | 895 | 3 | 15.2 | 5th | summer | Burden |
| 542 | 16 | 765 | 865 | 2.8 | 15.2 | 5th | summer | Burden |
| 543 | 15 | 610 | 725 | 2 | 15.2 | 5th | summer | Burden |
| 544 | 22 | 690 | 795 | 2 | 15.2 | 5th | summer | Burden |
| 545 | 14 | 860 | 990 | 5.2 | 15.2 | 5th | summer | Burden |
| 546 | 13 | 635 | 705 | 1.1 | 15.2 | 5th | summer | Burden |
| 547 | - | 595 | 660 | 1.5 | 10.2 | 6th | fall | Esopus |
| 548 | 13 | 670 | 763 | 2.8 | 10.2 | 6th | fall | Esopus |
| 549 | - | 675 | 740 | 2.3 | 10.2 | 6th | fall | Esopus |
| 550 | 13 | 695 | 771 | 2.25 | 10.2 | 6th | fall | Esopus |
| 551 | 7 | 520 | 558 | 1 | 10.2 | 6th | fall | Esopus |
| 552 | - | 563 | 640 | 1.55 | 10.2 | 6th | fall | Esopus |
| 553 | 12 | 648 | 707 | 2.15 | 10.2 | 6th | fall | Esopus |
| 554 | 14 | 755 | 834 | 3.75 | 10.2 | 6th | fall | Esopus |
| 555 | 13 | 647 | 758 | 2.7 | 10.2 | 6th | fall | Esopus |
| 556 | 8 | 505 | 592 | 1.15 | 10.2 | 6th | fall | Esopus |
| 557 | 11 | 580 | 680 | 2 | 10.2 | 6th | fall | Esopus |
| 558 | 10 | 673 | 790 | 2.6 | 15.2 | 6th | fall | Esopus |
| 559 | 23 | 704 | 780 | 3.2 | 15.2 | 6th | fall | Esopus |
| 560 | 13 | 715 | 832 | 3.05 | 15.2 | 6th | fall | Esopus |
| 561 | 12 | 710 | 805 | 3.3 | 15.2 | 6th | fall | Esopus |
| 562 | 14 | 615 | 710 | 2.45 | 15.2 | 6th | fall | Esopus |
| 563 | - | 660 | 768 | 2.55 | 15.2 | 6th | fall | Esopus |
| 564 | 10 | 668 | 765 | 2.3 | 15.2 | 6th | fall | Esopus |
| 565 | 13 | 570 | 680 | 1.95 | 15.2 | 6th | fall | Esopus |
| 566 | 13 | 660 | 770 | 2.1 | 15.2 | 6th | fall | Esopus |
| 567 | 22 | 760 | 885 | 3.8 | 15.2 | 6th | fall | Esopus |
| 568 | 14 | 665 | 770 | 2.85 | 15.2 | 6th | fall | Esopus |
| 569 | 11 | 640 | 730 | 2.2 | 15.2 | 6th | fall | Esopus |
| 570 | 17 | 790 | 940 | 4.4 | 15.2 | 6th | fall | Esopus |
| 571 | 15 | 700 | 834 | 2.7 | 15.2 | 6th | fall | Esopus |
| 572 | 12 | 636 | 720 | 2.1 | 15.2 | 6th | fall | Esopus |
| 573 | 15 | 705 | 804 | 3.05 | 15.2 | 6th | fall | Esopus |
| 574 | 12 | 640 | 724 | 2.2 | 15.2 | 6th | fall | Esopus |
| 575 | 13 | 588 | 663 | 1.65 | 15.2 | 6th | fall | Esopus |
| 576 | 13 | 645 | 750 | 2.3 | 15.2 | 6th | fall | Esopus |
| 577 | 14 | 700 | 760 | 2.7 | 15.2 | 6th | fall | Esopus |
| 578 | 11 | 700 | 812 | 2.75 | 15.2 | 6th | fall | Esopus |
| 579 | 8 | 495 | 583 | 1.05 | 15.2 | 6th | fall | Esopus |


| 580 | 15 | 740 | 850 | 3.45 | 15.2 | 6 th | fall | Esopus |
| :---: | :---: | :---: | :---: | :---: | :---: | :--- | :--- | :--- |
| 581 | 15 | 680 | 780 | 2.6 | 15.2 | 6th | fall | Esopus |
| 582 | 13 | 680 | 775 | 2.55 | 15.2 | 6 th | fall | Esopus |
| 583 | 13 | 450 | 630 | 1.35 | 15.2 | 6 th | fall | Esopus |
| - | - | 575 | 665 | 1.6 | 15.2 | 6th | fall | Esopus |
| - | - | 620 | 730 | 2.4 | 15.2 | 6th | fall | Esopus |
| - | - | 660 | 740 | 2.4 | 15.2 | 6th | fall | Esopus |
| - | - | 675 | 770 | 3.55 | 15.2 | 6th | fall | Esopus |
| - | - | 695 | 778 | 3.3 | 15.2 | 6th | fall | Esopus |
| - | - | 685 | 790 | 2.7 | 15.2 | 6th | fall | Esopus |

## References

Anderson, M. R., and R. M. Neumann. 2000. Indirect estimate of gill net mesh size selectivity for landlocked alewives. Journal of Freshwater Ecology 15(4):491496.

Bain, M. B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48:347358.

Bain, M. B., S. Nack, W. Dovel. 1997. Trends in the abundance of Hudson River sturgeons. In Sturgeon Notes \#4. Department of Natural Resources, Cornell University. (previously available at http://www.dnr.cornell.edu/hydro2/sturgeon/sn4/sn4 1-17.htm\#senescence)

Bain, M. B., N. Haley, D. L. Peterson, K. K. Arend, K. E. Mills, and P. J. Sullivan. 2000. Shortnose sturgeon in the Hudson River: an Endangered Species recovery story. Biology, Management and Protection of Sturgeon Symposium Pre-Print. EPRI, Palo Alto, CA.

Baird, D., R. R. Christian, C. H. Peterson, and G. A. Johnson. 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. Ecological Applications 14:805-822.

Baranov, F.I. 1914. The capture of fish by gillnets. Materialy Poznaniyu Russ. Rybolov. 3(6):56-99 (as referenced by Hamley 1975).

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determination. Canadian Journal of Fisheries and Aquatic Sciences. 38:982-983.

Bemis, W. E., and B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. Environmental Biology of Fishes 48:167-183.

Bertalanffy, L. v. 1938. A quantitative theory on organic growth. Human Biology 10:181-213.

Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environmental Biology of Fishes 48:399-405.

Boyle, R. H. 1979. The Hudson River: A natural and unnatural history. W.W. Norton
\& Company. New York.

Brennan, J. S., and G. M. Cailliet. 1989. Comparative age-determination techniques for white sturgeon in California. Transactions of the American Fisheries Society 118:296-310.

Brennan, J. S., and G. M. Cailliet. 1991. Age determination and validation studies of white sturgeon, Acipenser transmontanus, in California. Pages 209-234 in P. Williot, editor. Acipenser. Centre National du Machinisme Agricole du Genie Rural des Eaux et des Forets, Bordeaux.

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 Publishers, Dordercht.

Burton, E. J., A. H. Andrews, K. H. Coale, and G. M. Cailliet. 1999. Application of Radiometric age determination to three long-lived fishes using $210 \mathrm{~Pb}: 226 \mathrm{Ra}$ disequilibria in calcified structures: A review. Pages 77-87 in J.A. Musick editor. Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals. American Fisheries Society, Symposium 23, Bethesda, Maryland

Campana, S. E. 1984. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder, Platichthys stellatus. Canadian Journal of Zoology 62:1507-1512.

Campana, S. E., M. C. Annad, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131-138.

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.

Campbell, J. G., and L. R. Goodman. 2004. Acute sensitivity of juvenile shortnose sturgeon to low dissolved oxygen concentrations. Transactions of the American Fisheries Society 133:772-776.

Carlson, D. M., and K. W. Simpson. 1987. Gut contents of juvenile shortnose sturgeon in the upper Hudson estuary. Copeia 3:796-802.

Casselman, J. M. 1987. Determination of age and growth. Pages 209-242 in A. H.

Weatherley and H. S. Gill, editors. The Biology of Fish Growth. Academic Press, Inc. Orlando, FL.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39:12081210.

Collins, M. R., and T. I. J. Smith. 1996. Sturgeon fin ray removal is nondeleterious. North American Journal of Fisheries Management 16:939-941.

Collins, M. R., and T. I. J. Smith. 1997. Distributions of shortnose and Atlantic sturgeons in South Carolina. North American Journal of Fisheries Management 17:995-1000.

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(3):917-928.

Coutant, C. C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Transactions of the American Fisheries Society 114: 31-61.

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 Science 41:1216-1223.

Cuerrier, J. P. 1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. Canadian Fish Culturist 11:10-18.

Dadswell, M. J. 1979. Biology and population characteristics of the shortnose sturgeon, Acipenser brevirostrum LeSueur 1818 (Osteichythyes:
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 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. 1981. The endangered shortnose sturgeon of the Hudson estuary: Its life history and vulnerability to the activities of man. The Oceanic Society. FERC Contract No. DE-AC 39-79 RC-10074.

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, NY.

Doyon, C., R. Fortin, and P. A. Spear. 1999. Retinoic acid hydroxylation and teratogenesis in lake sturgeon (Acipenser fulvescens) from the St. Lawarence River and Abitibi region, Quebec. Canadian Journal of Fisheries and Aquatic Sciences 56:1428-1436.

Duncan, M. S., J. J. Isley, and D. W. Cooke. 2004. Evaluation of shortnose sturgeon spawning in the Pinopolis Dam tailrace, South Carolina. North American Journal of Fisheries Management. 24: 932-938.

Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. 2005. Marine Ecology Progress Series 291:249-261.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1-98 in W. S. Hoar, and D. J. Randall, editors. Fish Physiology, Volume IV. Academic Press, New York.

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, NY.

Gross, M. R., J. Repka, C. T. Robertson, D. H. Secor, and W. van Winkle. 2002. Sturgeon Conservation: Insights from Elasticity Analysis. American Fisheries Society Symposium 28:13-30.

Guenette, S., and coauthors. 1992. La périodicité de la croissance chez la femelle de l'esturgeon jaune (Acipenser fulvescens) du fleuve Saint-Laurent est-elle reliée a la périodicité de la reproduction? Canadian Journal of Fisheries and Aquatic Science 49:1336-1341.

Greeley, J. R. 1937. XI. Fishes of the area with annotated list. Pages 45-103 in A Biological Survey of the Lower Hudson Watershed. Supplement to $26^{\text {th }}$

AnnualReport,1936. New York State Conservation Department, Albany, New York.

Gulland, J. A. 1983. Fish Stock Assessment: A Manual of Basic Methods. FAO Wiley Series on Food and Agriculture, Rome.Volume 1.

Haas, R. E., and C. W. Recksiek. 1995. Age verification of winter flounder in Narragansett Bay. Transactions of the American Fisheries Society 124:103111.

Haley, N. J. 1999. Habitat characteristics and resource use patterns of sympatric sturgeons in the Hudson River estuary. Masters Thesis, University of Massachusetts. Amherst.

Hamley, J. M., and H. A. Regier. 1973. Direct estimates of gillnet selectivity to walleye (Stizostedion vitreum vitreum). Journal of Fisheries Resources Board of Canada 30:817-830.

Hamley, J. M. 1975. Review of gillnet selectivity. Journal of Fisheries Resources Board of Canada 32(11):1943-1969.

Hansen, L. G., W. B. Wiekhorst, and L. Simon. 1976. Effects of dietary Aroclor 1242 on channel catfish (Ictalurus punctatus) and the selective accumulation of PCB components. Journal of Fisheries Resources Board of Canada 33:13431352.

Hilborn, R., and C. J. Walters. 2001. Quantitative Fisheries Stock Assessment:
Choice Dynamics and Uncertainty, $3^{\text {rd }}$ edition. Kluwer Academic Publishers, Norwell, MA.

Holt, S. J. 1963. A method for determining gear selectivity and its application. ICNAF Special Publication 5:106-115.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fisheries Bulletin 82:898-903.

Hovgard, H. 1996. A two-step approach to estimating selectivity and fishing power of research gillnets used in Greenland waters. Canadian Journal of Fisheries and Aquatic Science 53:1014-1117.

Hovgard, H., and H. Lassen. 2000. Manual on estimation of selectivity for gillnet and longline gears in abundance surveys, volume 397. FAO, Rome.

Hughes, N. F. 1998. Reduction in growth due to electrofishing and tagging may
change interannual movement behavior of stream salmonids: evidence from Arctic grayling in an interior Alaskan stream. Transactions of the American Fisheries Society 127:1072-1077.

Hurley, K. L., R. J. Sheehan, and R. C. Heidinger. 2004. Accuracy and precision of age estimates for pallid sturgeon from pectoral fin rays. North American Journal of Fisheries Management 24:715-718.

Jenkins, W. E., T. I. J. Smith, L. D. Heyward, and D. M. Knott. 1993. Tolerance of shortnose sturgeon, Acipenser brevirostrum, juveniles to different salinity and dissolved oxygen concentrations. Proceedings of the $47^{\text {th }}$ Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:476-484.

Jung, S., and E. D. Houde. 2003. Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. Estuarine, Coastal and Shelf Science 58:335-351.

Kohlhorst, D. W., L. W. Miller, and J. J. Orsi. 1980. Age and growth of white sturgeon collected in the Sacramento-San Joaquin Estuary, California: 19651970 and 1973-1976. California Fish and Game 66(2):83-95.

Kynard, B. 1997. Life history, latitiudinal patterns, and status of the shortnose sturgeon, Acipenser brevirostrum. Environmental Biology of Fishes 48:319334.

Kynard, B., and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic stgurgeon, Acipenser oxyrinchus oxyrinchus, and shortnose sturgeon, A. brevirostrum, with notes on social behavior. Environmental Biology of Fishes 63:137-150.

Leslie, J. A., K. A. Abood, E. A. Maikish, and P. J. Keeser. 1988. Recent dissolved oxygen trends in the Hudson River. Pages 287-303 in C. L. Smith, editor. Fisheries Research in the Hudson River. State University of New York Press, Albany.

Lough, R. G., M. Pennington, G. R. Goltz, and A. A. Rosenberg. 1982. Age and growth of larval Atlantic herring, Clupea harengus L., in the Gulf of MaineGeorges Bank region based on otolith gorwth increments. Fishery Bulletin 80(187-199).

Maartens, L., A. J. Booth, and T. Hecht. 1999. The growth of monkfish Lophius vomerinus in Nambian waters, with a comparison of otolith and illicia methods of ageing. Fisheries Research 44:139-148.

Malone, J. C., G. E. Forrester, and M. A. Steele. 1999. Effects of subcutaneous
microtags on the growth, survival, and vulnerability to predation of small reef fishes. Journal of Experimental Marine Biology and Ecology 237:243-253.

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. American Fisheries Society Symposium (1):79-88.

McCarthy, I. D., L. A. Fuiman, and M. C. Alvarez. 2003. Aroclor 1254 affects growth and survival skills of Atlantic croaker Micropogonias undulatus larvae. Marine Ecology Progress Series 252:295-301.

Milton, D. A., D. Die, C. Tenakanai, and S. Swales. 1998. Selectivity for barramundi (Lates calcarifer) in the Fly River, Papua New Guinea: implications for managing gill-net fisheries on protandrous fishes. Marine and Freshwater Research 49:499-506.

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-18:1-18.

Nack, S. Personal Communication. Columbia County Soil and Water Conservation District. Ghent, New York. November 2004.

Nakamoto, R. J., T. T. Kisanuki, and G. H. Goldsmith. 1995. Age and growth of Klamath River green sturgeon (Acipenser medirostris). U.S. Fish and Wildlife Service, 93-FP-13, Yreka.

Ndayibagira, A., M. J. Cloutier, P. D. Anderson, and P. A. Spear. 1995. Effects of 3, $3^{\prime}, 4,4^{\prime}$-Tetrachlorobiphenyl on the dynamics of vitamin-A in brook trout (Salvelinus fontinalis) and intestinal retinoid concentrations in lake sturgeon (Acipenser fulvescens). Canadian Journal of Fisheries and Aquatic Sciences 52: 512-520.

Niklitschek, E. J. 2001. Bioenergetics modeling and assessment of suitable habitat for juvenile Atlantic and shortnose sturgeons (Acipenser oxyrinchus and A. brevirosturm) in the Chesapeake Bay. Doctoral dissertation. University of Maryland, College Park.

Niklitschek, E. J., and D. H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic surgeon in the Chesapeake Bay. Estuarine, Coastal and Shelf Science 64:135-148.

Nilo, P., P. Dumont, and R. Fortin. 1997. Climatic and hydrological determinants of
year-classs strength of St. Lawrence River lake sturgeon (Acipenser brevirostrum). Canadian Journal of Fisheries and Aquatic Science 54:774780.

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, MD.

NYSDEC (New York State Department of Environmental Conservation) 2001. Injuries to Hudson River fishery resources: fishery closures and consumption restrictions, Hudson River natural resource damage assessment. NYSDEC Final report.

Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data anlaysis, $5^{\text {th }}$ edition. Duxbury-Thompson Learning, Pacific Grove, CA.

Paragamian, V. L., and V. D. Wakkinen. 2002. Temporal distribution of Kooteni River white sturgeon spawning events and the effect of flow and temperature. Journal of Applied Ichthyology 18:542-549.

Paragamian, V. L., and R. C. Beamesderfer. 2003. Growth estimates from tagged white sturgeon suggest that ages from fin rays underestimate true age in the Kootenai River, USA and Canada. Transactions of the American Fisheries Society 132:895-903.

Parrish D. L., B. Vondracek, and W. J. Eckmayer. 1994. Accuracy and precision of daily age estimates for walleyes from Ohio hatcheries and Lake Erie. Transactions of the American Fisheries Society 123:601-605.

Richmond, A. M., and B. Kynard. 1995. Ontogenetic behavior of shortnose sturgeon, Acipenser brevirostrum. Copeia 1:172-182.

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. American Fisheries Society Symposium 28:45-54.

Rossiter, A., D. L. G. Noakes, and F. W. H. Beamish. 1995. Validation of age
estimation for the lake sturgeon. Transactions of the American Fisheries Society 124:777-781.

Roussow, G. 1957. Some considerations concerning sturgeon spawning periodicity. Journal of the Fisheries Resource Board of Canada 14:553-572.

Salvanes, A. G. V. 1991. The selectivity for cod (Gadus morhua L.) in two experimental trammel-nets and one gillnet. Fisheries Research 10:265-285.

Scheirer, J. W., and D. W. Coble. 1991. Effects of Floy FD-67 anchor tags on growth and condition of northern pike. North American Journal of Fisheries Management 11:369-373.

Secor, D. H., and T. E. Gunderson. 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic strugeon, Acipenser oxyrinchus. Fishery Bulletin 96:603-613.

Secor, D. H., and J. R. Waldman. 1999. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. American Fisheries Society Symposium 23:203-216.

Secor, D. H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass. ICES Journal of Marine Sciences 157:403-411.

Secor, D. H., and E. J. Niklitschek. 2001. Hypoxia and sturgeons. Chesapeake Biological Laboratory, TS-314001-CBL, Solomons, MD.

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. American Fisheries Society Symposium 28:3-10.

Sokolov, L. I., and N. V. Akimova. 1976. Age determination of the Lena River sturgeon. Journal of Ichthyology 16(5):773-778.

Stevens, D. E., H. K. Chadwick, and R. E. Painter. 1987. American shad and striped bass in California's Sacramentro-San Joaquin River system. Pages 66-78 in. American Fisheries Society.

Stevenson, J. T. 1997. Life history characteristics of Atlantic sturgeon (Acipenser oxyrinchus) in the Hudson River and a model for fishery management. Master's thesis. University of Maryland, College Park.

Stevenson, J. T., and D. H. Secor. 1999. Age determination and growth of Hudson River Atlantic sturgeon, Acipenser oxyrinchus. Fishery Bulletin 97:153-166.

Taubert, B. D. 1980. Reproduction of shortnose sturgeon (Acipenser brevirostrum) in Holyoke Pool, Connecticut River, Massachusetts. Copeia 1:114-117.

US Geological Survey (USGS). 2005. Monthly/annual flow data. Green Island, NY monitoring station \# 01358000. Available: http://nwis.waterdata.usgs.gov (May 2005).

Veinott, G. I., and R. D. Evans. 1999. An examination of elemental stability in the fin ray of the white sturgeon with Laser Ablation Sampling-Inductively Coupled Plasma-Mass Spectrometry (LAS-ICP-MS). Transactions of the American Fisheries Society 128:352-361.

Veshchev, P. V. 1982. Reproduction of sterlet, Acipenser ruthenus (Acipenseridae), in the Lower Volga. Journal of Ichthyology 22(4):40-47.

Vladykov, V. D., and J. R. Greeley. 1963. Order Acipenseroidei. Pages 24-60 in V. H. Olsen, editor. Fishes of the Western North Atlantic, Part III. Memoirs of the Sears Foundation for Marine Research, New Haven, CT.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist 125:769-787.

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 surgeon, Acipenser transmontanus. Aquaculture 201:137-151.

Weatherley, A. H., and H. S. Gill. 1987. The Biology of Fish Growth. Academic Press, Inc. Orlando, FL.

Winnemiller, 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 49:2,196-2,218.

Whiteman, K. W., V. H. Travnichek, M. L. Wildhaber, A. DeLonay, D. Papoulias, and D. Tillett. 2004. Age estimation for shovelnose sturgeon: a cautionary note based on annulus formation in pectoral fin rays. North American Journal of Fisheries Management 24:731-734.

Zar, J. H. 1999. Biostatistical Analysis $4^{\text {th }}$ edition. Pearson Education, Inc. Dehli, India.


[^0]:    *No mortality observed, all fish released alive in apparent good condition, ${ }^{\dagger}$ Kingston area sampled due to logistic constraints.

[^1]:    * Growth parameters as given by Dadswell et al. 1984

