Abstract.–Atlantic sturgeon (*Acipenser oxyrinchus*) are a large anadromous fish which is especially vulnerable to overharvesting owing to its late age of maturity and low rate of reproduction. Age determination methods and growth rates are poorly described for this species. Pectoral-fin spine sections and sagittal otolith sections were examined to determine whether one of these structures would be useful in estimating the age and growth of Atlantic sturgeon. Otoliths have been difficult to collect, process, and interpret. Interpretation of annuli in sectioned pectoral spines has proven to be an unbiased method for aging juvenile and adult Hudson River Atlantic sturgeon. Marginal increment analysis has indicated an annual cycle of annulus deposition. Microchemical analysis with an electron microprobe of the periphery of fin spines has shown seasonal patterns of calcium and phosphorus concentrations related to the translucent and opaque zones of the annuli. Formation of yearly annuli was verified in 4-year-old laboratory-reared sturgeon. Von Bertalanffy growth models (based upon fin-spine interpretations) were fitted for the Hudson River population. Models predicted a more rapid growth rate for males than for females (females: K=0.07, L_∞=251 cm; males: K=0.25, L_∞=180 cm). Females, however, attained a greater maximum age (42 yr) and size (TL=277 cm). We believe that exploitation has had a large but unquantifiable bias on growth estimates for male and female Atlantic sturgeon. As the Hudson River population recovers, age structure and growth rate estimates should be refined to predict population recovery rates more accurately in the absence of a directed fishery.

Age determination and growth of Hudson River Atlantic sturgeon, *Acipenser oxyrinchus**

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Atlantic sturgeon (*Acipenser oxyrinchus*) are a large anadromous fish that ranges the East Coast of North America and spawns in rivers from Florida to Canada. Population levels throughout the range of the species declined appreciably in the late 19th century owing to increased harvest of sturgeon for caviar following the Civil War (Murawski and Pacheco, 1977; Secor and Waldman, in press). Overfishing and deterioration of habitat, predominantly the blockage of spawning runs, have contributed to the extirpation of several Atlantic sturgeon populations (Taub, 1990; Waldman and Wirgin[1]). The life history strategy of the anadromous Atlantic sturgeon indicates that age structure and vital rates are especially critical to conservation. Atlantic sturgeon exhibit high maximum age, late maturation (females 14–17, males 10–12; Van Eenennaam et al., 1996), and probable low mortality rates; growth, however, is rapid. These traits, as well as low relative fecundity and less-than-annual spawning frequency, make sturgeon especially susceptible to overexploitation (Boreman, 1997). Therefore, models of Atlantic sturgeon population dynamics may be expected to be sensitive to biases in estimated vital rates and reproductive schedules.

Atlantic sturgeon growth rates have been estimated in several studies, but results are divergent (Table 1). Poorly validated techniques have been employed to estimate age; and rates of growth, reproduction, and mortality have not been developed sufficiently to support resource management models (Taub, 1990).

Studies of acipenserid age have employed annuli in calcified structures including scutes, pectoral-fin spines, otoliths, operculi, and other skeletal parts (Harkness, 1923; Greeley, 1937; Brennan and Cailliet, 1989, 1991; Guenette et al., 1992; Rien and Beamesderfer, 1994). The term "fin ray," previously used to describe the leading (primary) ray of the pectoral fin supporting element, was revised by Feindeis (1997) because this element becomes fully ensheathed with dermal bone early in ontogeny, and therefore should be termed a spine. Pectoral-fin spine sections have been preferred for aging because annuli in sections can be consistently interpreted, and fin spines are easily col-

Table 1

Imprecision in aging studies of various long-lived species, reported as coefficient of variation (CV).

Species	Study	CV	Maximum age observed
Atlantic sturgeon (*Acipenser oxyrinchus*) (fin spines)	This study	4.8	42
White sturgeon (*Acipenser transmontanus*)	Rien and Beamesderfer (1994)	7.8	104
Yellowfin sole (*Pleuronectus asper*)	Kimura and Lyons (1991)	3.2	26
Sablefish	Kimura and Lyons (1991)	12.9	29
Pacific ocean perch (*Sebastes alutus*)	Kimura and Lyons (1991)	4.9	78
Tarpon (*Megalops atlanticus*)	Cyr (1991)	12.0	50

lected and processed without sacrifice of fish. They have been used in the past to age Atlantic sturgeon, but authors have described difficulty in aging older fish (>20 yr; Magnin, 1964; Huff, 1975; Dovel and Berggren, 1983). Aging based upon fin spines has been validated for white sturgeon, *Acipenser transmontanus* (Brennan, 1988; Brennan and Cailliet, 1991) and lake sturgeon, *A. fulvescens* (Rossiter et al., 1995); however, no studies have validated the periodicity of annulus deposition in Atlantic sturgeon.

Otoliths are often preferred for estimating fish age, but rate of otolith annulus formation has not been evaluated in sturgeons. Greeley (1937) enumerated ridges on the external surface of otoliths without examination of an internal section. Subsequent studies have indicated that annuli on an internal section of otoliths do not provide age estimates as precise as those from fin-spine sections (Schneberger and Woodbury, 1944; Brennan and Cailliet, 1991). Otolithic material, however, does not resorb, which is desirable for accurate aging, especially of long-lived fishes.

The objectives of this study were to identify an appropriate calcified structure and develop a precise and unbiased method for determining age of Atlantic sturgeon and to model growth rates of Hudson River Atlantic sturgeon on the basis of juvenile and adult fish collected in 1992–96.

Materials and methods

Adult Atlantic sturgeon were collected during 1992–95 from fishery harvests in the Hudson River and New York Bight, in cooperation with New York State Department of Environmental Conservation and New Jersey Department of Environmental Protection. Fish were collected by using drift and anchored gill nets (25–36 cm stretched mesh) and otter trawls. During the period of collection, a minimum size limit of 152 cm total length (TL) was imposed on the New

York fishery. In New Jersey, the minimum size limit of 107 cm TL was replaced with a 152-cm size limit in 1993.

We collected pectoral-fin spines from sturgeon smaller than the minimum commercial size limit (≤149 cm TL) in the Hudson River during 1993–95, using monofilament anchored gill nets (3–13 cm stretched mesh). Because few fish less than 152 cm were collected, other mid-Atlantic Bight regions were sampled. Fin spines were obtained from sturgeon collected from Chesapeake Bay commercial pound nets and gill nets in 1996 (*n*=11), from National Marine Fisheries Service trawl surveys in the Mid-Atlantic Bight (1994 and 1996; *n*=4), and from U.S. Fish and Wildlife Service gillnet surveys of the Delaware Bay (*n*=8). Because the Hudson River stock is the dominant reproducing stock in the Mid-Atlantic area (Waldman et al., 1996), subadults from areas other than the Hudson River were assumed to be predominantly of Hudson River origin.

Removal and preparation of hard parts

Pectoral-fin spines (*n*=634) were removed at the point of articulation, air-dried, and sectioned less than one centimeter distal to the articulation point. Soft tissue adhering to the fin spines was allowed to decompose through microbial decay. A one-centimeter-wide section of each fin spine was then embedded in a block of Spurr epoxy, sectioned with an Isomet saw (Buehler, Lake Bluff, IL), and mounted on glass slides (see Secor et al., 1991). Some fin spines (64%) were not embedded but were sectioned with a jeweller's saw. All sections were mounted with thermoplastic glue on glass slides and polished with an automated polishing wheel (MINIMET 1000, Buehler, Lake Bluff, IL) with fine grit carborundum paper and a 0.3-μm alumina slurry on a polishing cloth. Final sections were 1–2 mm thick.

Sagittal otoliths were removed from the severed heads of Atlantic sturgeon collected in 1994–95

(*n*=114). Sagittae were cleaned in 10% bleach, rinsed several times with deionized water, and air-dried. One sagittal otolith from each pair was embedded in Spurr epoxy and sectioned as described in Secor et al. (1991). Owing to their fragility, otolith sections were polished by hand with a variety of fine sandpapers and a 0.03-µm alumina slurry.

Annuli in thin sections of fin spines and otoliths were viewed under reflected light at 15× magnification by two experienced readers. An annulus was defined as a bipartite zone comprising an opaque and a translucent zone (Fig. 1). The first translucent zone was counted as the beginning of the first year of life. In some instances, a secondary fin spine was embedded within the primary fin spine (Feindeis, 1997), in which case care was taken to enumerate annuli only in the primary spine. False annuli were consistently observed in fin-spine sections of older individuals and were excluded from annulus counts. These structures were not continuous around the entire circumference of the section and were thus distinguishable from annuli to be counted (Prince et al., 1985).

Precision and bias

Readers counted annuli without knowing collection date, fish size, or previous age determination. They were trained with the aid of an imaging system that permitted simultaneous observation of annular growth zones. Paired difference tests were used to statistically evaluate bias and precision among readers in a single blind test. The coefficient of variation (CV) was used to measure precision; bias was assessed visually using age-bias plots (Fig. 2). An age-bias plot showed paired estimates of age for the same fish (Campana et al., 1995), with the estimates of reader 2 represented as mean age, and 95% confidence intervals corresponding to each of the age classes estimated by reader 1. For example, if reader 1 estimated five fish to be 15 years old, the age-bias plot indicated the mean age of those five fish as estimated by reader 2. Divergence from the equivalence line, where $Age_{Reader\ 1} = Age_{Reader\ 2}$, indicates a systematic difference between readers. Paired age estimates for either fin-
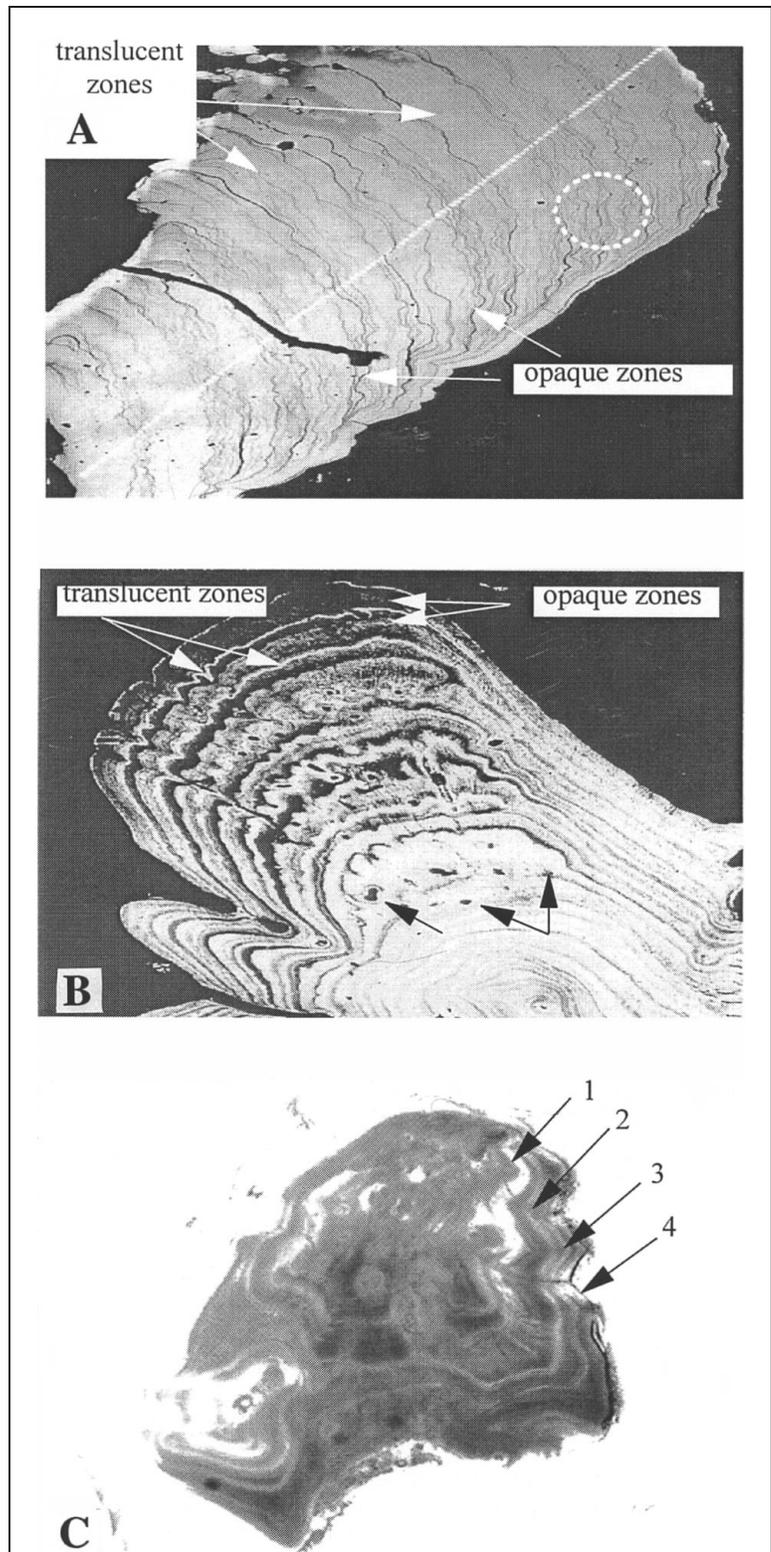

Figure 1

Backscatter electron micrographs show (**A**) a sagittal otolith section; (**B**) a pectoral-fin spine (lower lobe only) from a Hudson River Atlantic sturgeon; and (**C**) a fin-spine section from a hatchery-reared Atlantic sturgeon. White arrows (B) indicate annuli. Organic deposits in the fin-spine section are indicated with dark arrows (B). Pits resulting from chemical microanalysis are visible in the otolith section. Dashed circle in (A) indicates annuli that are difficult to interpret.

spine sections or otolith sections made by two readers were contrasted. In addition, for each reader, ages estimated from fin spine sections were compared with ages estimated from otolith sections from the same fish.

Validation of annulus formation

The periodicity of annulus formation in Atlantic sturgeon fin spines and otoliths was studied by using measurements and chemical microanalysis of marginal increments, and observation of annuli in juvenile hatchery-reared sturgeon marked with oxytetracycline (OTC) at a known age. Efforts were concentrated on fin-spine age validation because annuli were difficult to consistently interpret in otolith sections.

Marginal increment analysis measures the opaque zone deposited after the last identifiable translucent zone at the margin of a structure used for age estimation (Kalish, 1995). Seasonal growth of that opaque zone is used to determine the timing of annulus formation (Cailliet et al., 1986; Beamish and McFarlane, 1987; Brennan and Cailliet, 1989). In our analysis, marginal increments were measured with image analysis software (Optimas, Inc., 1994) to the nearest 0.001 mm. Marginal increment ratio (MIR) was calculated as

$$MIR = MI \times 1/A,$$

where MI = the width of the outermost opaque zone (marginal increment); and
A = the mean width of the three annuli deposited previous to the marginal increment.

Mean MIR was computed for each month separately, with ages and sexes combined. Because very few fish were collected for several months, monthly samples were pooled for four three-month seasons. The winter season (December–February) was eliminated owing to very low sample size.

Microchemical analysis of calcified structures can verify the periodicity of annuli (Jones and Geen, 1977; Casselman, 1983; Radtke and Targett, 1984; Cailliet and Radtke, 1987). Calcium concentration is correlated with optically defined growth zones in the hard part (e.g. calcium is increased in the opaque zone and decreased in the translucent zone; Cailliet and Radtke, 1987; Lai et al., 1996). For instance, the most recently formed material in fin
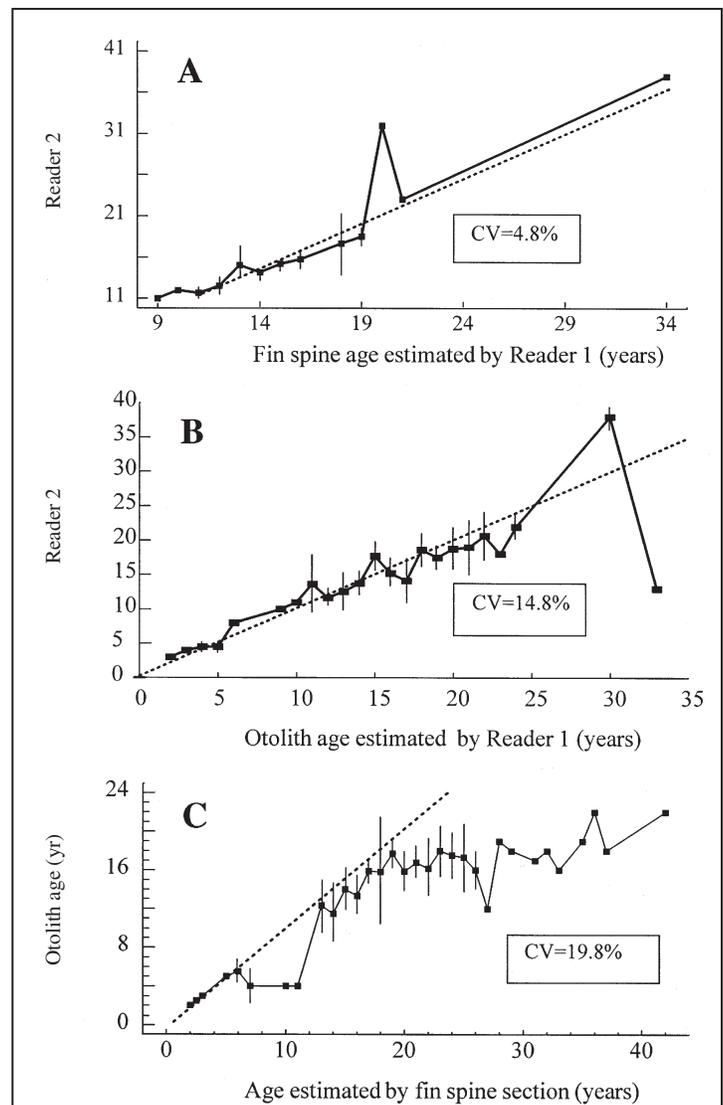

Figure 2
Bias in age estimates for Hudson River Atlantic sturgeon are evaluated by age-bias plots that compare estimates made by two readers interpreting the same (**A**) fin-spine sections and (**B**) otolith sections; and (**C**) made by one reader interpreting fin-spine and otolith sections taken from the same fish. Dashed lines are "equivalence lines" indicating the hypothetical case where both estimates are identical. Error bars represent the 95% confidence interval about the mean age (reader 2) for all fish assigned a given age by reader 1.

spines might contain high or low concentrations of calcium in fish collected during summer (rapid growth) or winter (slower growth), respectively (Cailliet and Radtke, 1987). In this instance, fin-spine microanalysis of calcium across annuli might show nadirs in calcium associated with translucent zones.

Calcium concentration in fin-spine sections was measured using a JEOL JXA-840A wavelength-dis-

persive (WDS) electron microprobe at the Center for Microanalysis, College Park, MD. Phosphorus was also measured because it makes up a large fraction of the fin spine's hydroxyapatite structure (Stevenson, 1997). Accelerating voltage was 25 kV and cup current was 20 nA. Each measurement represented rastering or scanning by the probe over a 5×5 μm area of the hardpart section. Molar weights of calcium and phosphorus were measured in peripheral regions of fin spines for 20 fish aged 3–18 years (fin-spine estimate) collected in March, June, September, and November. The mean of three peripheral points was calculated for each individual, and means were contrasted by month of collection with ANOVA.

Microprobe measurements were used to construct elemental chronologies of 15 fin spine sections taken from sturgeon aged 12–36 years (fin-spine estimate) and 164–236 cm TL. For each chronology, a series of point measurements was taken along an axis that traversed several annuli, with five points per annulus; points were assumed to sample seasons in linear proportion.

A solution of OTC (25 milligrams per kilogram of body weight) was injected into the dorsal musculature of five juvenile laboratory-reared fish of known age (55–65 cm TL) from Hudson River broodstock. Juveniles had been reared in circular fiberglass tanks in a recirculating system and fed a mixture of commercial pellet feeds. They were subjected to a twelve-hour photoperiod; water temperature ranged from 15° to 20°C. Three months after injection, the first fin spine section was removed from three fish with a jeweller's saw, and silver nitrate was applied to encourage clotting of the wound. Fifteen months after injection, a second section was removed from the opposite pectoral-fin spine of one fish only. Fin-spine segments were dried, sectioned, mounted on glass slides, and polished. Thin sections were viewed with epifluorescent microscopy to identify OTC marks. The position of OTC marks with respect to opaque and translucent zones was recorded and a micrograph was taken. In all cases, the reader was aware that the fish had received an injection of OTC but had no knowledge of the date of section collection.

Growth

Reported measurements of dressed carcasses were converted to total length based upon conversion metrics derived for Hudson River Atlantic sturgeon (Stevenson, 1997). Sturgeon included in the conversion metric sample (n=235) were collected during spawning season in the Hudson River; all but five possessed mature gonads. Ages derived from fin-spine and otolith sections were used to fit von Bertalanffy

growth models by using a Marquardt iterative estimation procedure for the three model parameters. Length-at-age relationships were first examined to determine variance structure and progression of modal length with age. Growth parameters were estimated iteratively for males and females with a least-squares method. Because of high variance at the point of growth inflection, it was unlikely that a single growth model would fit all portions of the growth curve. Therefore, the juvenile portion (42–152 cm TL) was modeled separately with a power function based upon the best fit of residuals.

PC-SAS (SAS Institute, Inc., 1994) and Statgraphics Plus (STSC, Inc., 1992) were used for all statistical tests. Data that did not satisfy the assumption of heteroscedasticity (Bartlett's test, α=0.05) were transformed to satisfy this assumption. Transformed data that did not satisfy this assumption were analyzed with a Kruskal-Wallis nonparametric test to examine differences among groups.

Results

Comparison of hard parts

Otoliths were irregularly shaped and their annuli were difficult to interpret. In contrasting several sectioning planes, we observed that annuli on transverse sections yielded the most consistent interpretations. The first three to nine growth zones showed a clear alternation of opaque and translucent zones. Thereafter, translucent zones were irregularly spaced and often appeared to overlap (Fig. 1A). Low optical contrast between opaque and translucent zones reduced the readers' confidence in assigning annuli, especially in sections with more than twenty annuli.

In contrast, fin-spine sections exhibited concentric narrow translucent zones and wide opaque zones when viewed with transmitted light. Fin spines contained a vascularized core and deposits of organic material in lobe regions (Fig. 1B). Interspersed were fibrils that we interpreted as collagen or some other structural protein. Annuli became narrower toward the outer edge in larger (and presumably older) fish. Secondary fin spines (84% of fin-spine sections) and false annuli were observed but were simple to identify and disregard. Belts of two to five narrow annuli were apparent in most female fin-spine sections (96% of a subsample of 48). These belts were not apparent in the juvenile sturgeon examined.

Imprecision (CV) in age estimates was 4.8% between two readers of the same fin-spine section (Fig. 2A). Mean imprecision was 1.2 years (t=–1.97, P>0.05); estimates by the two readers were not significantly

different. Age estimates from otolith sections were less precise than from fin-spine sections (Fig. 2B). Absolute imprecision was 3.3 years and the CV on paired differences was 14.8%. No significant bias occurred in otolith interpretations between readers. In a comparison of ages estimated by a single reader from otolith sections and from corresponding fin-spine sections (i.e. from the same fish), the former were significantly lower than the latter (Fig. 2C; mean difference=5 yr, t=9.01, P<0.05). The bias was most apparent for presumed by older fish.

Validation of the fin-spine aging method

Marginal increment ratios for fish collected in late winter and spring (February–April) were significantly lower than those for summer and fall (Fig. 3; Kruskal-Wallis test; P=0.04). Mean MIR was 18% in spring, 33% in summer, and 36% in fall. The highest rate of marginal increment completion was observed for winter months (December–February), although sample size was very small for these months (n=3).

Readings of annuli from hatchery-reared sturgeon resulted in exact age estimates. The sturgeon were 4+ years old and annuli were clearly defined. There was a distinct difference in the shape of fin spines from hatchery-reared and wild juvenile sturgeon (Fig. 1C). Hatchery-reared fish exhibited irregularly shaped, compressed annuli which could indicate erosion or injury, but were nonetheless easily recognized. In OTC-injected fish, a distinct OTC mark followed by an opaque zone was apparent in all fin spines examined three months after injection. The fish did not show any symptoms of stress following fin-spine removal. The only sample examined at fifteen months after injection exhibited a clear OTC mark that was followed by opaque and translucent zones.

Microchemical analysis

The concentrations of calcium and phosphorus in peripheral regions of fin spines showed significant seasonality (Kruskal-Wallis test, $P \leq 0.04$; Fig. 4). Fin spines collected in November were significantly lower in calcium and phosphorus than those collected in March, June, and September. Calcium-to-phosphorus ratios increased significantly from March through November (Kruskal-Wallis test, P=0.04). Plots of cal-
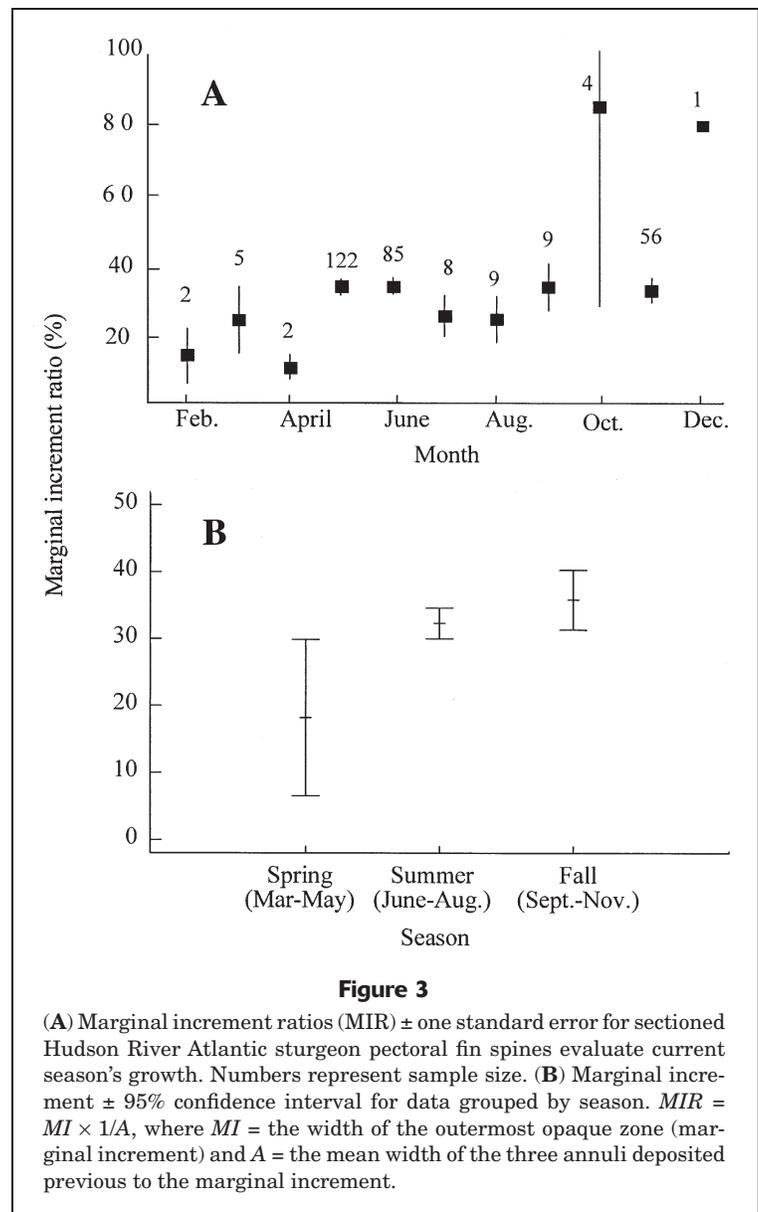
cium and phosphorus in fin spines revealed cyclical trends in both elements, with peaks associated with translucent zones (Fig. 5).

Growth

The size-age relationship for prespawning fish, as judged by interpretations of annuli in fin spines, was best fitted by a power regression (r^2= 0.75; Fig. 6). Von Bertalanffy models for both males and females considerably underestimated length at age for subadults. Over all life history portions, the fit of the von Bertalanffy model was better for females (ages 2–42; r^2=0.56) than for males (ages 4–36; r^2=0.33) owing to the broader range of ages and lengths in our sample

Figure 3

(**A**) Marginal increment ratios (MIR) ± one standard error for sectioned Hudson River Atlantic sturgeon pectoral fin spines evaluate current season's growth. Numbers represent sample size. (**B**) Marginal increment ± 95% confidence interval for data grouped by season. $MIR = MI \times 1/A$, where MI = the width of the outermost opaque zone (marginal increment) and A = the mean width of the three annuli deposited previous to the marginal increment.

of females (Fig. 7A). Males grew faster but reached a smaller asymptotic length at a younger age than did females. Females grew more slowly (K=0.07) toward a significantly larger maximum length (251 ±12.8 cm). The asymptotic growth phase for females and males was 12–42 and 11–28 years, respectively. Estimates of growth coefficients, K, were significantly different between sexes (t=73.2, df=431, P<0.05). Log transformation of the data did not correct for the error structure. Residuals from the models were designated as corresponding either to fish of the size at entry into the fisheries (152 cm TL in New York and after 1993 in New Jersey), or to larger or smaller fish. The resulting residual plots indicated that the faster-growing males were harvested just as they reached size at entry (positive residuals) and that the slower-growing females entered the fishery at much older ages (negative residuals; Fig. 7B). The modeled growth pattern for females appeared more biased than that for males owing to a sharp shift in residuals from positive to negative at about 15 years. At older ages, the von Bertalanffy model underestimated the size of females. These patterns in residuals were also apparent in males, albeit less pronounced.

Discussion

Fin spines or otoliths?

Owing to ease of collection and processing, as well as precision and accuracy in aging, we recommend the use of fin spines rather than otoliths for demographic analysis of Atlantic sturgeon. Preparation techniques used in this study (embedding, sectioning, and polishing) may have improved the visual resolution of annuli in pectoral-fin spines over that reported in earlier investigations.

Annuli in sturgeon otoliths and, as a result, growth rates, have been grossly misinterpreted in the past owing to examination of the external surface of hard parts only (Greeley, 1937). Especially in presumed older individuals, otoliths should not be used to verify age estimates based on fin spines. Annular clarity diminishes towards the distal end of the otolith (more recent growth), which may result in lower age estimates. In addition, individuals must be sacrificed to collect otoliths. Concern over declining sturgeon populations should restrict the size of otolith samples.
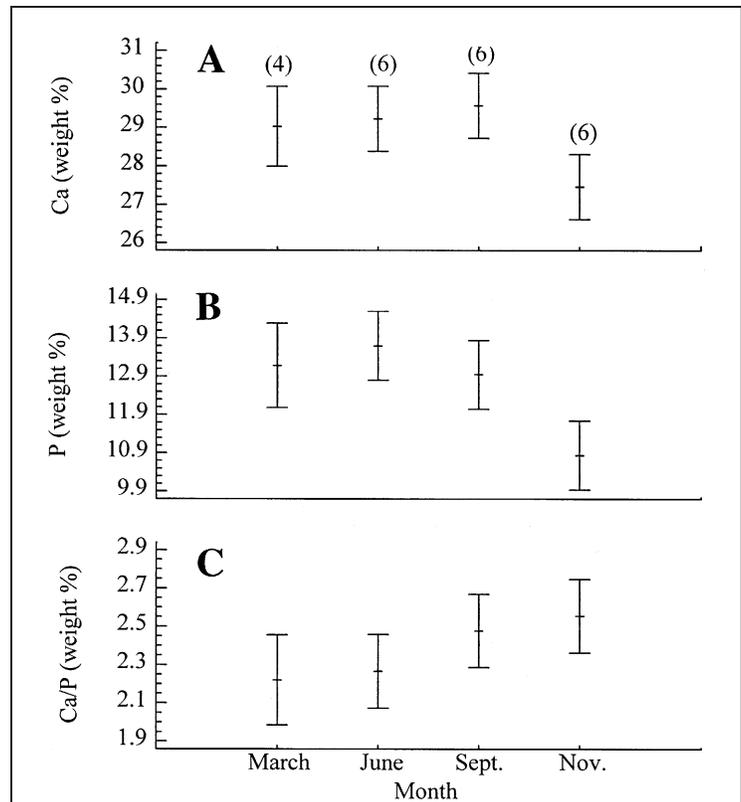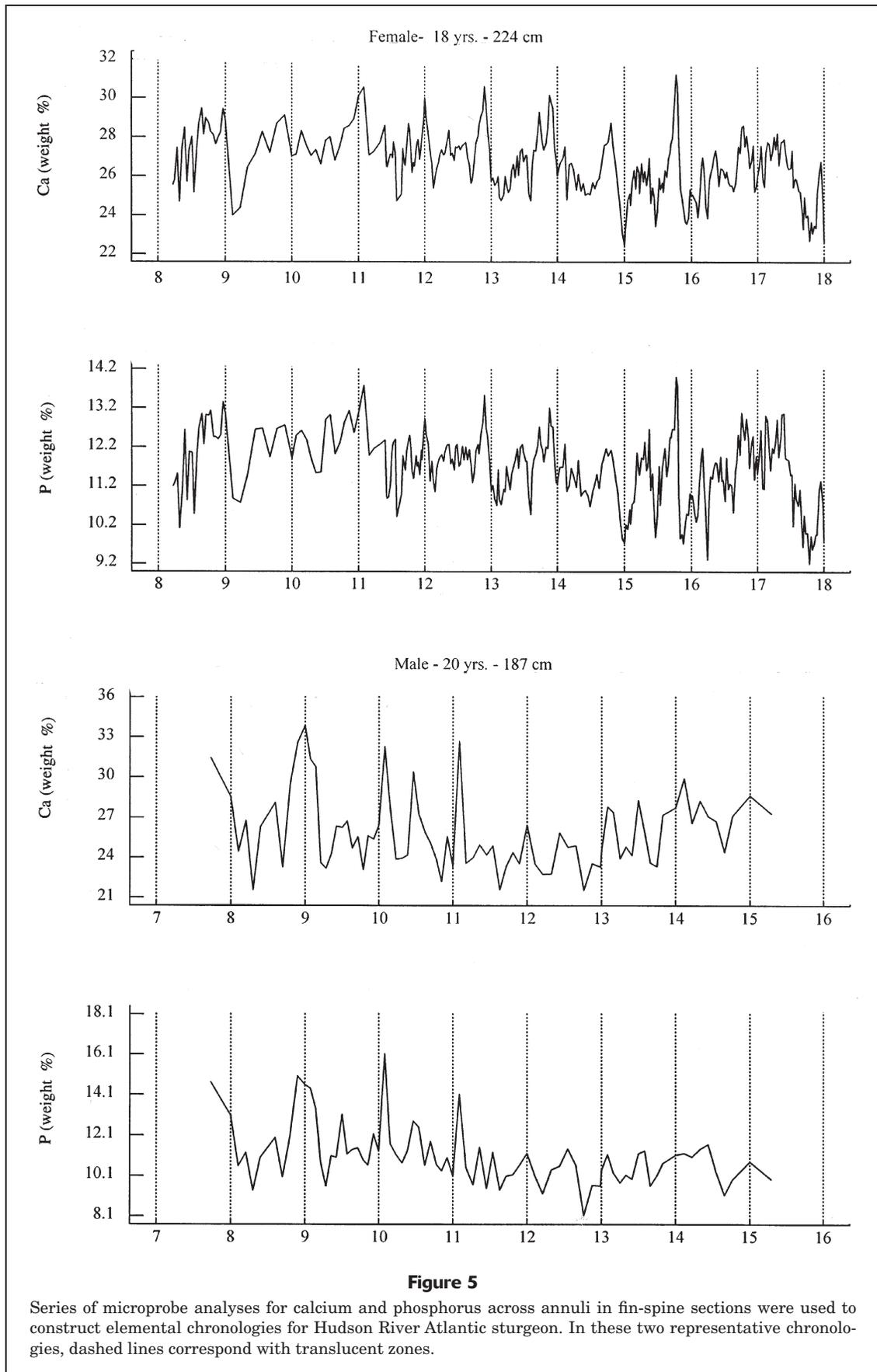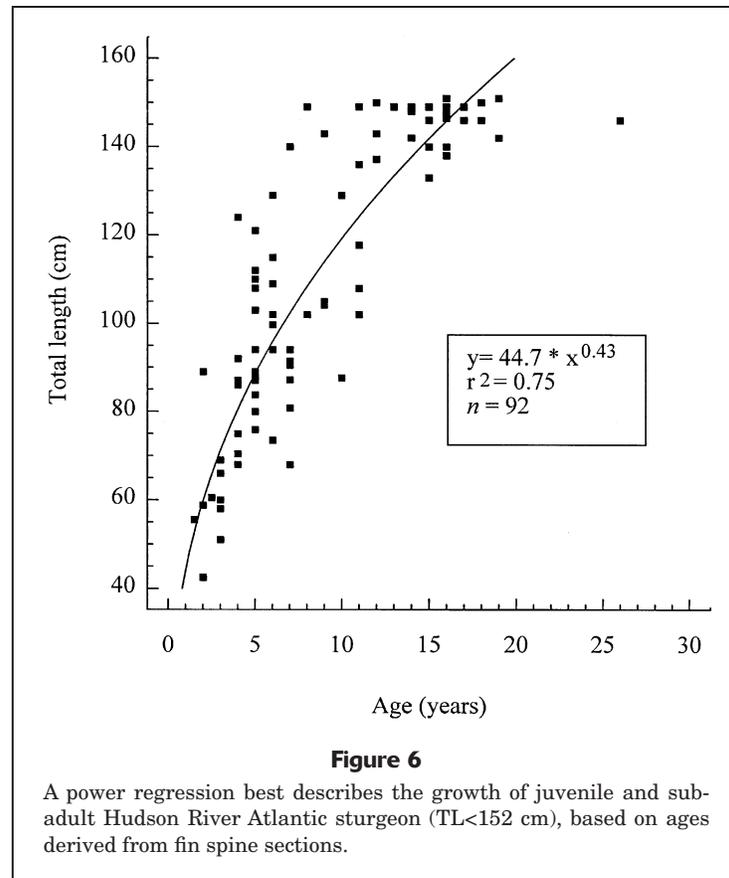

Figure 4

Microchemical analysis of marginal increments of fin spine sections taken from Hudson River Atlantic sturgeon show significant seasonality in (**A**) calcium; (**B**) phosphorus; and (**C**) calcium-to-phosphorus ratio. Means and 95% confidence intervals are depicted. Three points were analyzed per section. Numbers in parentheses indicate how many fin-spine sections were analyzed for fish collected in each of the four months (these apply to all three graphs).

Precision and accuracy

Age estimates based on fin spines were unbiased and precise. Aging imprecision for Atlantic sturgeon was similar or better than imprecision reported for other long-lived (>20 yr) species, for which precision is often affected by narrow annuli, which result from reduced growth rates in older fish (Rien and Beamesderfer, 1994; Table 1). The annual patterns of marginal increment ratio (MIR), observations on fish of known age, and microchemistry have supported the hypothesis that a pair of opaque and translucent zones forms annually in Atlantic sturgeon fin spines. A small sample of OTC-marked juveniles also indicated annual annulus growth (Stevenson, 1997). Results for Atlantic sturgeon were similar to Huff's (1975) analysis of Gulf sturgeon (*Acipenser oxyrinchus desotoi*) fin-spine sections, in which a higher percentage of fin-spine sections showed that a completely formed

Figure 5

Series of microprobe analyses for calcium and phosphorus across annuli in fin-spine sections were used to construct elemental chronologies for Hudson River Atlantic sturgeon. In these two representative chronologies, dashed lines correspond with translucent zones.

Figure 6

A power regression best describes the growth of juvenile and sub-adult Hudson River Atlantic sturgeon (TL<152 cm), based on ages derived from fin spine sections.
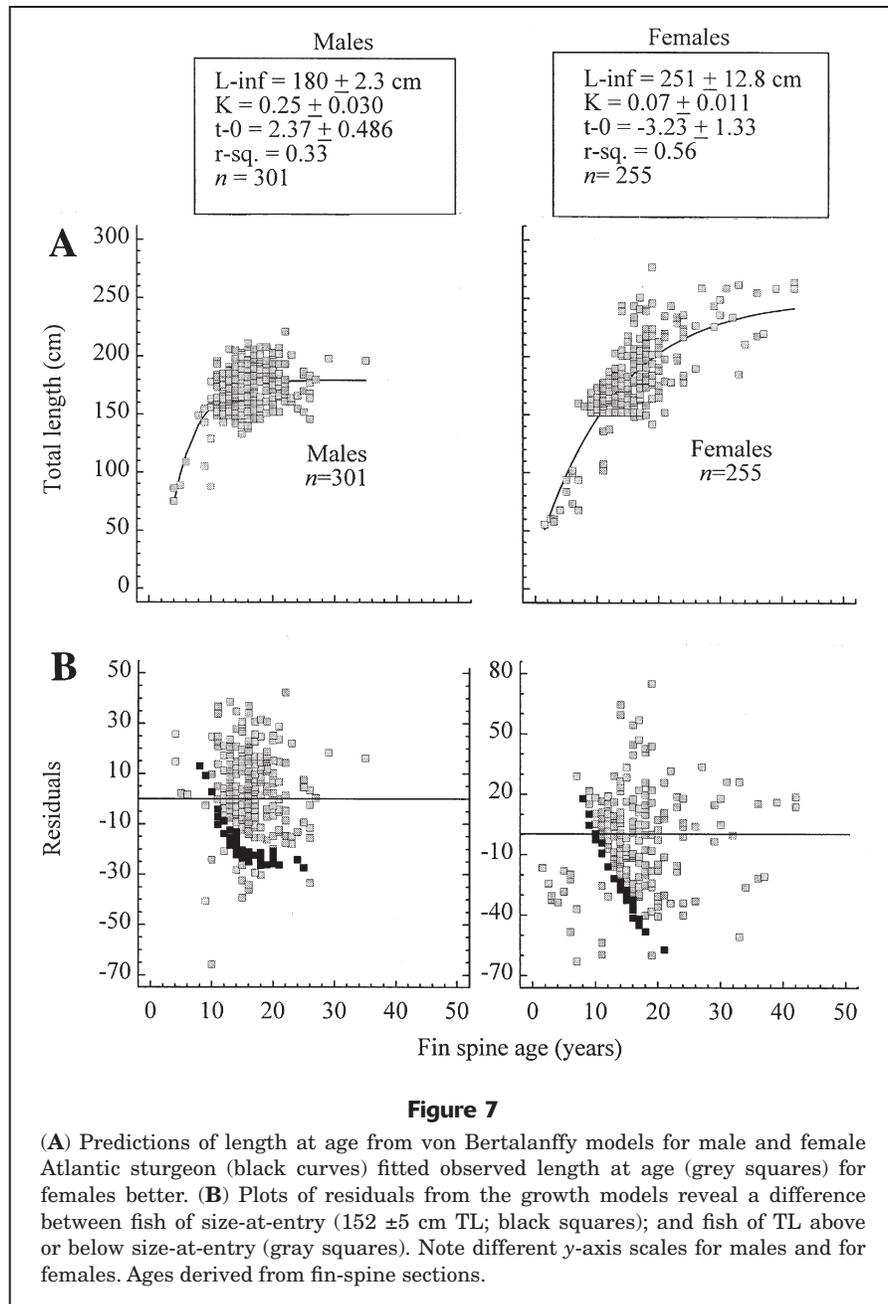
marginal annulus was completely formed in the fall rather than in the spring. Ideally, marginal increment analysis should be performed on separate age classes to ensure that annulus formation occurs for all ages (Casselman, 1983). However, owing to the relative scarcity of older individuals and the unavailability of fish in some seasons and because marginal increments are often difficult to discern in fin-spine sections taken from older individuals, age classes were pooled in our study. Accuracy of age estimation at older ages remains untenable. An attempt to validate longevity estimates of Hudson River Atlantic sturgeon using radiometric ^{210}Pb/^{226}Ra dating was unsuccessful (Burton et al., 1999). Recapture of hatchery-released Atlantic sturgeon (Secor[2]) has provided an opportunity to verify age determinations in older or mature individuals. Fin spines taken from juvenile sturgeon did not exhibit belts of annuli; such belts may provide information about spawning behavior in females.

Chemical microanalysis of hard parts is a promising tool for age verification (Jones and Geen, 1977; Casselman, 1983; Cailliet and Radtke, 1987). However, seasonal cycles were not consistently observed in elemental chronologies of Atlantic sturgeon fin spines. The technique assumes that the hard part is a closed system, and there is no resorption or remodeling. Burton et al. (1999) using radiometric tracers, found that Atlantic sturgeon fin spines appear to be open systems. In our study, we may have observed a corrupted seasonal signal.
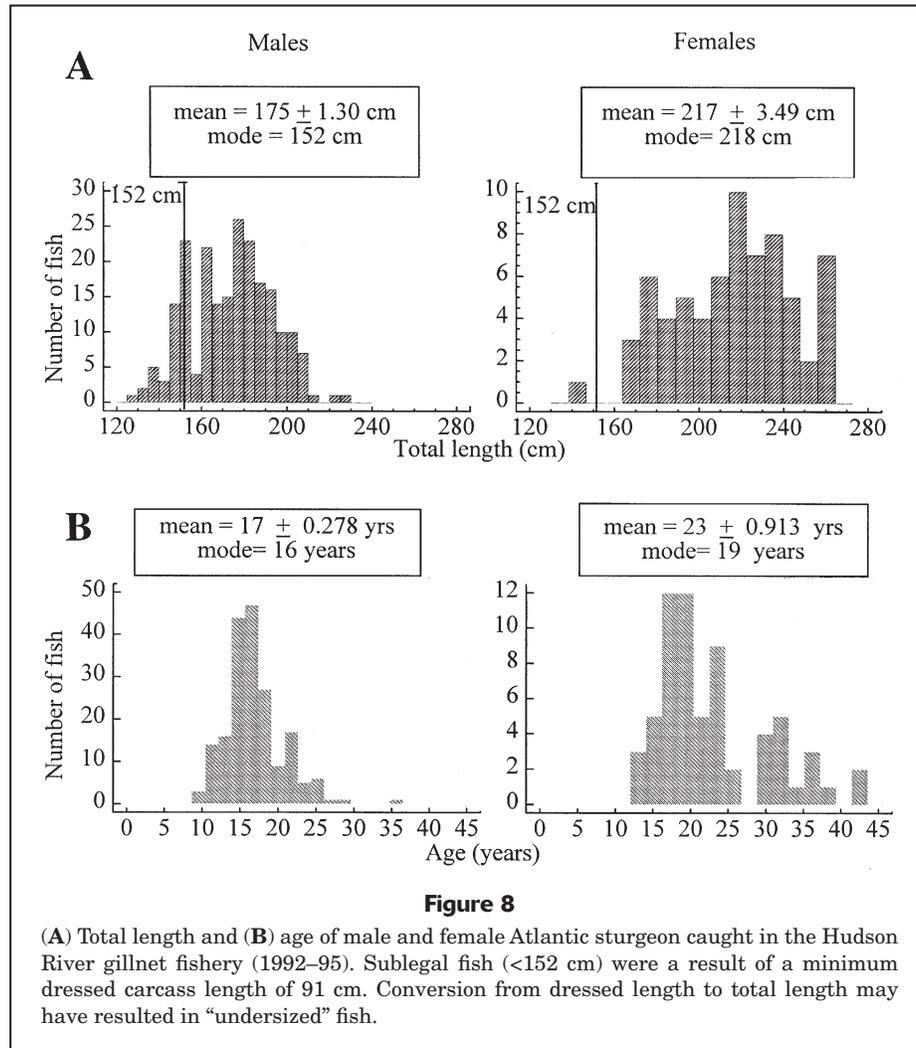
Growth

Sexually dimorphic growth patterns in Atlantic sturgeon may be a result of differential reproductive schedules and migration patterns. The age-length relationship shows substantial variability in both males and females. Males mature earlier (12 yr) and spawn annually. Females mature later at a much larger size and are thought to spawn every 3–5 years (Smith, 1985). Lower growth rates and larger achieved sizes are typical for large, long-lived fish that broadcast numerous offspring (Adams, 1980; Moreau, 1987; Roff, 1988, Winemiller and Rose, 1992).

Figure 7

(**A**) Predictions of length at age from von Bertalanffy models for male and female Atlantic sturgeon (black curves) fitted observed length at age (grey squares) for females better. (**B**) Plots of residuals from the growth models reveal a difference between fish of size-at-entry (152 ±5 cm TL; black squares); and fish of TL above or below size-at-entry (gray squares). Note different y-axis scales for males and for females. Ages derived from fin-spine sections.

Growth is difficult to model accurately in long-lived species (Mulligan et al., 1987). Because little bias was detected in our readings (aging precision was unaffected by age), discrepancies in age estimates should not introduce systematic error in estimates of population parameters such as mortality rate, K, and L_∞. High variability in observed length at age indicates that length may be a poor predictor of age for Atlantic sturgeon. This high variability may result from amplification of early growth differences over a long life span. Variance in size at age may also have resulted from the nature of the

Hudson River Atlantic sturgeon fishery. The imposed minimum size limit on Atlantic sturgeon commercial fisheries (>152 cm TL) may have biased the sample used for growth estimates and could have caused K and L_∞ to be over- and under-estimated, respectively (Fig. 8). The von Bertalanffy curve may have been driven upwards at younger ages by the potential maximum growth rate of the population. For instance, as soon as the fastest growing members of an age class exceeded the minimum size limit, they were harvested. At later ages, the curve is pulled downward as slower growing individuals enter the

Figure 8

(**A**) Total length and (**B**) age of male and female Atlantic sturgeon caught in the Hudson River gillnet fishery (1992–95). Sublegal fish (<152 cm) were a result of a minimum dressed carcass length of 91 cm. Conversion from dressed length to total length may have resulted in "undersized" fish.

fishery (as evidenced by residual patterns), increasing K and decreasing L_∞.

Growth parameter estimates reported here for females are consistent with another study of the same population (Doroshov et al.[3]) but do not agree with an earlier study (with sexes combined) of the population (Dovel and Berggren, 1983). Recent reduction of the accumulated biomass by fishing, and resultant age and size truncation of the population, would cause lower apparent L_∞ and higher K values than in an unexploited population. Maximum length (L_∞) determined for females was substantially smaller than historical records of maximum size for this species (427 cm; Murawski and Pacheco, 1977), which may be a result of increased fishing pressure on the

largest (female) component of the population during the past ten years. The historical longevity of females in the Hudson River also probably exceeded our estimate of 42 years; Magnin (1964) reported a 60-year-old female in the St. Lawrence estuary.

Because the largest male sampled (72 kg) was only 22 years of age, yet much smaller males were older than 30 years, male longevity in the unexploited population was also probably higher than in the population we sampled. Consideration of possible bias in von Bertalanffy growth parameters should direct managers to undertake sensitivity analyses in developing demographic-based stock assessments. Because L_∞ and K are inversely related (Kimura, 1980), age and size truncation would result in an over-estimated K (a lower L_∞ is approached more rapidly).

We found L_∞ values that were relatively low compared with estimates in previous studies of Hudson River Atlantic sturgeons (Greeley, 1937; Dovel and Berggren, 1983). These low values may indicate

[3] Doroshov, S., J. Van Eenennaam, G. Moberg, and G. Waton. 1994. Reproductive conditions of the Atlantic Sturgeon (*Acipenser oxyrinchus*) stock in the Hudson River. Report for year two to Hudson River Foundation. Animal Science Department, University of California, Davis, 65 p.

age truncation of the population by directed fishing effort. However, Dovel and Berggren (1983) reported difficulty in aging fish greater than 153 cm TL and may have misidentified annuli in both juveniles and adults. Greeley's (1937) study was based on enumerating annuli in otoliths. Likewise, K estimates from our study are higher than those estimated previously. Our growth estimates are consistent, however, with those of Doroshov et al.,[3] who aged the same population in the early 1990s.

Comparative studies of fish populations along a latitudinal gradient have shown an inverse relation between latitude and rates of growth and mortality (e.g. Leggett and Carscadden, 1978; Jennings and Beverton, 1991). Among Atlantic sturgeon populations, the most rapid growth was exhibited by fish sampled in southern latitudes. Maximum size increased with increasing latitude, which may indicate postponement of maturation (Magnin, 1964). Values of K for the Hudson River population did not differ significantly from those for any other population ($\alpha=0.05$), whereas L_∞ values estimated for the Hudson River population were statistically different from those estimated for all other populations ($\alpha=0.05$) along a latitudinal gradient (Table 2).

Implications for stock restoration

Growth rates of acipenserid species are apparently affected by migratory behavior (Roff, 1988). Anadromous species of sturgeons exhibit higher growth coefficients than do semi-anadromous or freshwater resident species, although the semi-anadromous

Table 2

Growth parameters have been calculated in various studies of Atlantic sturgeon populations (combined sexes). For Smith (1985), n=number of age classes. Smith's (1985) data were converted from fork length to total length (FL= 1.11×TL; Beamesderfer, 1993) and were presented as mean length by age class in the literature.

Location	Study	n	K	L_∞ (cm)
St. Lawrence River	Magnin, 1964	582	0.03	315
Kennebec, ME	Smith, 1985	7	0.06	236
Hudson River, NY	This study	634	0.08	225
Winyah Bay, SC	Smith, 1985	24	0.12	242
Suwannee River, FLA	Smith, 1985	17	0.14	184

white sturgeon achieves a higher maximum length than do anadromous sturgeons (Table 3). Atlantic sturgeon undergo an ontogenetic habitat shift from estuarine nursery grounds to marine waters (Gilbert, 1989). We believe these species grow rapidly as juveniles (as shown by their high K coefficient) to outgrow predation in marine waters. Unfortunately, rapid growth may affect the timing of juvenile migration and increase their susceptibility to coastal fisheries at an early age.

Estimates of growth traits for Hudson River Atlantic sturgeon indicate that they are extremely vulnerable to overfishing. Slow growth following maturation, high longevity, and presumed low natural mortality indicate that year classes in this population reach their maximum biomass at relatively old ages (Alverson and Carney, 1975). Therefore, maximum fishing yield from sturgeon would be achieved at low

Table 3

Growth parameters (von Bertalanffy parameters unless otherwise indicated) estimated for North American sturgeons. Parameters were estimated for both sexes combined except where otherwise noted.

Species	Study	Location	n	L_∞ (cm TL)	K	t_0
Atlantic sturgeon (*A. oxyrinchus*)	This study[1]	Hudson River, NY	634	256 (female)	0.07	–3.2
				180 (male)	0.25	2.4
White sturgeon (*A. transmontanus*)	DeVore et al., 1995	Unimpounded Columbia River, OR	783	307	0.03	–1.13
Green sturgeon (*A. medirostris*)	USFWS[1]	Klamath River, CA	173	238	0.05	2.0
Shortnose sturgeon (*A. brevirostris*)	Dadswell, 1979	St John's River, Canada	446	144[2]	0.04	2.0
Lake sturgeon (*A. fulvescens*)	Thuemler, 1985[3]	Menominee River, WI–MI	1464	156	0.07	–0.02

[1] Growth parameters estimated for males and females separately.

[2] United States Fish and Wildlife Service. 1982. Klamath River Fisheries Investigation Program annual report, p. 123–141.

[3] Converted from fork length (FL= 1.11 × TL; Beamesderfer, 1993).

[4] Growth parameters derived from plot of mean TL at age.

rates of fishing or harvest of large, mature individuals (Bullock et al., 1992; Stevenson, 1997). A moratorium on commercial sturgeon fishing in the New York Bight was instituted in 1996; however, Atlantic sturgeon continue to be caught incidentally in many coastal fisheries. Continued research and monitoring of recruitment and bycatch mortality will be necessary to ensure the restoration of this population.

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