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Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes

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Synopsis

The Hudson River estuary supports substantial number of Atlantic sturgeon, *Acipenser oxyrinchus*, and shortnose sturgeon, *Acipenser brevirostrum*. Both species have complex life cycles that have been studied sporadically in the past 50 years. The life cycle of the shortnose sturgeon may be divided into four life intervals: non-spawning adults, spawning adults, eggs and larvae, and juveniles. The life cycle of the Atlantic sturgeon is reviewed in six intervals: non-spawning adults, female spawners, male spawners, eggs and larvae, early juveniles, and late juveniles. Both species are long-lived, mature at advanced age, have rapid and similar growth during the first few years of life, feed on generally similar taxa, use deep channel habitats for all life intervals, and have complex migratory patterns with distinct, seasonal, concentration areas. Atlantic and shortnose sturgeons differ, however, in ages and sizes at maturity, maximum size, timing and location of spawning, migratory behaviors, and management. Use of marine habitats and long-distance coastal migrations are restricted to Atlantic sturgeon, but some evidence indicates that large Atlantic sturgeon juveniles reside in riverine habitats along the Atlantic coast during warm months. Movements and habitat use by both sturgeons in the Hudson River estuary contrasts with the spatial segregation of the species reported in other river systems. Juvenile shortnose sturgeon and early juvenile Atlantic sturgeon have almost the same distributions in the Hudson River estuary during all seasons. During this period of co-occurrence, both species are very similar in size, grow at about the same rate, feed on similar foods, and share deep, channel habitats. Adult shortnose sturgeon distribution overlaps with the distribution of juvenile Atlantic sturgeon, and the latter commence river emigration at a size comparable to co-occurring adult shortnose sturgeon. Life history information on the Hudson River sturgeons substantiates the need to carefully conserve these species because of vulnerability to exploitation and habitat disruption.

Introduction

The Hudson River supports substantial populations of Atlantic sturgeon, *Acipenser oxyrinchus*, and shortnose sturgeon, *Acipenser brevirostrum*. The Atlantic sturgeon is one of North America's

largest fishes, and an important commercial species in the Hudson River and Atlantic coast waters (species reviewed in Smith & Clugston 1997, this volume). In contrast, the shortnose sturgeon is the smallest species of *Acipenser* in North America, and a charter member (included in the original US

Endangered Species Act, 1973) of the U. S. endangered species list (species reviewed in Kynard 1997 this volume).

Observations of sturgeon in the Hudson River date back to the earliest historical accounts of human settlement in the region. Both species were very abundant, often captured for food, and easily observed by people during some part of the year. The first scientific accounts of the Hudson River sturgeons emerged from the New York State Biological Survey conducted in the mid-1930s (Curran & Ries¹, Greeley 1937², Townes³. These studies documented some basic life history attributes such as distribution in the river, sizes and ages of mature fish, and diet. Almost no additional information was collected on the Hudson River sturgeons for 40 years, but then in the 1970s major concerns emerged about the effect of electric generating stations on fish resources of the Hudson River (Barnthouse et al. 1984). William Dovel led extensive studies (Dovel & Berggren 1983, Dovel et al. 1992) which provide most of our current knowledge on the Hudson River sturgeons. Electric utilities that operate power plants along the Hudson River initiated comprehensive environmental monitoring programs that continue today. Some biologists (Carlson & Simpson 1987, Geoghegan et al. 1992, Hoff et al. 1988, Young et al. 1988) working with monitoring program samples and data provided relatively recent reports of sturgeon distributions and life history attributes.

Understanding the complex life cycles of the sturgeons has challenged biologists for more than 50 years. Until recently, the shortnose sturgeon was believed to be an anadromous fish, and therefore the responsibility for recovering this endangered

species was assigned to the National Marine Fisheries Service⁴. Dadswell (1979) provided the first thorough study of the life history of shortnose sturgeon, and a comparably detailed analysis of the biology of any Atlantic sturgeon population has not been reported. Despite numerous and varied reports on the biology of both Hudson River sturgeons, life history reviews within the last 10 years have concluded that important life cycle attributes remain poorly known or unknown (Gilbert 1989, T.I.J. Smith 1985). In only one case (Saint John River and estuary, New Brunswick, Canada) has abundant populations of both species been studied (Dadswell 1979), and they were found to segregate on the basis of habitat, presumably to minimize competition.

In this paper, I review the knowledge of Atlantic and shortnose sturgeon in the Hudson River estuary by summarizing information from biologists going back to 1937. This summary is organized around distinct life intervals of each sturgeon in an effort to present a complete picture for both species. Finally, the potential interactions between the two species will be considered because the Hudson River has sizable populations of both species, and some evidence (Dadswell 1979, Dadswell et al.⁵, Dovel et al. 1992) suggests that competition between them may influence habitat use.

Sturgeon are limited to the lower 246 km of the Hudson River (Figure 1) where habitats range from a typical freshwater river channel to a brackish water fjord (for physicochemical and morphological reviews see Coch & Bokuniewicz 1986 and others in the same volume, Limburg et al. 1989, Smith 1992). This estuary system is nearly straight and oriented in a north-south direction from the New York City harbor (southern tip of Manhattan Island; km 0 [km for river location in kilometers above mouth]) to the Troy Dam (Federal Green Island Dam; km 246) near Albany, New York. The normal tidal ampli-

¹ Curran, H.W. & D.T. Ries. 1937. Fisheries investigations in the lower Hudson River. pp. 124-145. In: A Biological Survey of the Lower Hudson Watershed, Supplement to the 26th Annual Report of the New York State Conservation Department, Albany.

² Greeley, J.R. 1937. Fishes of the area with annotated list. pp. 45-103. In: A Biological Survey of the Lower Hudson Watershed, Supplement to the 24th Annual Report of the New York State Conservation Department, Albany

³ Townes, H.K., Jr. 1937. pp. 217-230. In: A Biological Survey of the Lower Hudson Watershed. Supplement to the 26th Annual Report of the New York State Conservation Department, Albany.

⁴ U.S. Federal Register Vol. 39, No. 230, Pages 41367-41377; 27 November 1974.

⁵ Dadswell, M.J., B.D. Taubert, T.S. Squires, D. Marcette & J. Buckley. 1984. Synopsis of biological data on the shortnose sturgeon, *Acipenser brevirostrum* LeSueur, 1818. NOAA Technical Report NMFS 14, National Marine Fisheries Service, Washington, D.C.

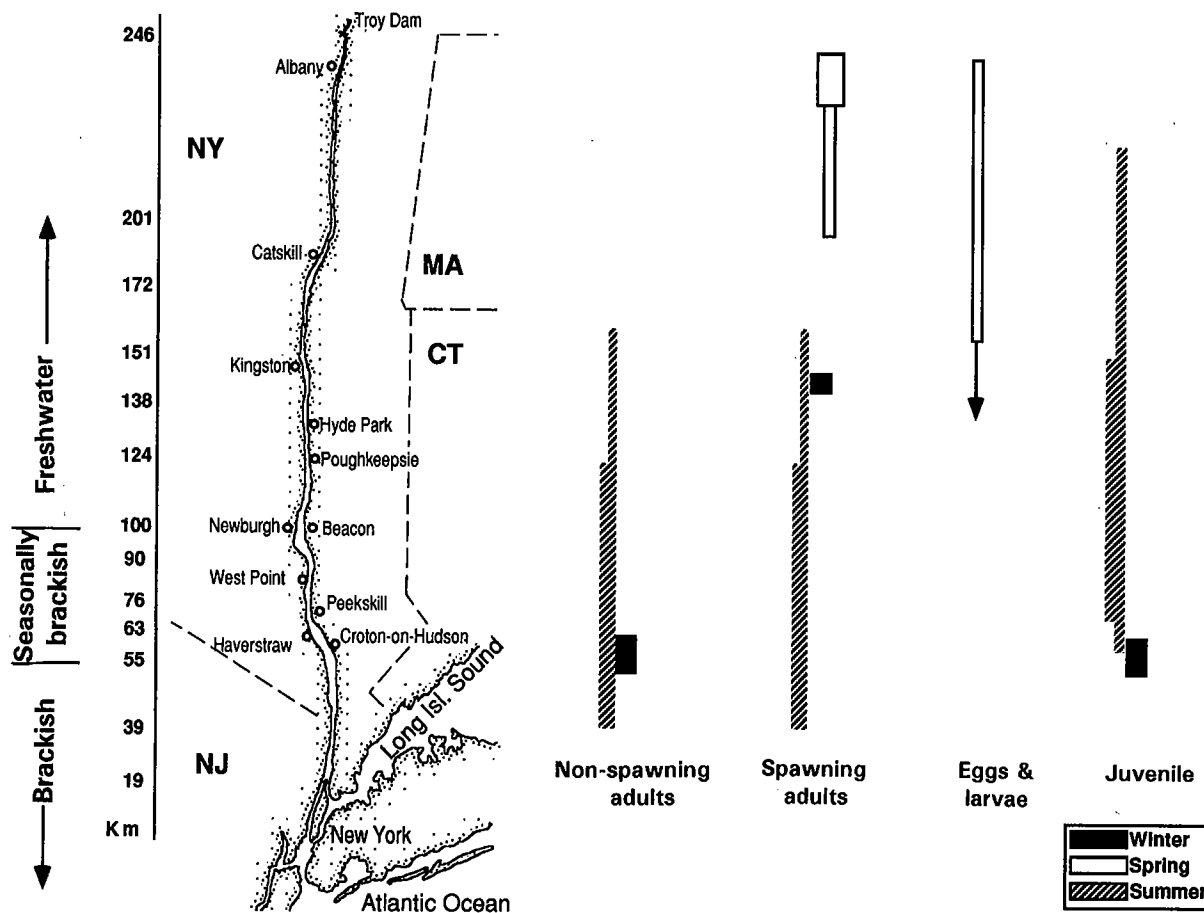


Figure 1. Life intervals and seasonal distribution of shortnose sturgeon in the Hudson River estuary relative to river features, river distances upstream of upper New York City bay, and salinity. Fall and sometimes spring distributions are not shown because these seasons are transitional periods. Width of the distribution lines and symbols indicates relative density of individuals.

tude ranges from 0.82 to 1.43 m causing a tidal volume (mean 5 670 - 8 500 m³ s⁻¹ depending on location) from 10 to 100 times river discharge (mean 623 m³ s⁻¹; Limburg et al. 1989). The Hudson River channel is large (mean width 1280 m) and generally deep (mean depth 10 m), but lacking any significant gradient. However, channel morphology varies with sections averaging as much as 5.5 km wide and 34 m deep (maximum depth = 53 m). Much of the river channel is shaped by rock with fine grain (e.g., sand and clay) sediments composing the substrate. The lower 100 km of the Hudson River estuary is saline (>0.1 ppt salt) during seasons of low freshwater discharge with salinity generally below 10 ppt.

Shortnose sturgeon

Shortnose sturgeon is best described as an amphidromous (defined in McDowall 1987, see also Bemis & Kynard 1997 this volume) species since use of marine waters is limited to the estuaries of their natal rivers (see Kynard 1997 this volume). On one occasion, shortnose sturgeon were reported in waters of coastal New Jersey adjacent to the mouth of the Hudson River (Dovel et al. 1992). Within the Hudson River Estuary, shortnose sturgeon display complex migratory behavior that has been inconsistently described in past investigations. The life history for Hudson River shortnose sturgeon will be reviewed in four intervals that vary in characteristics

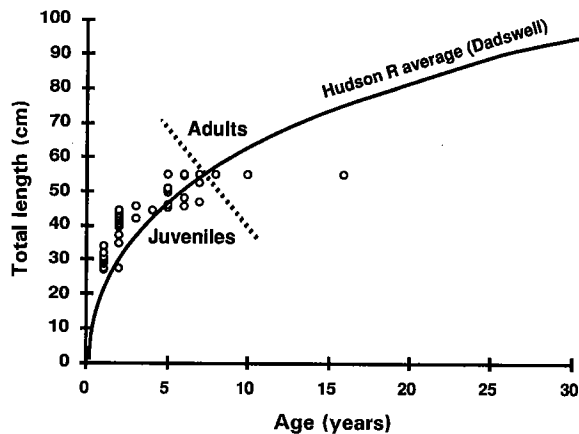


Figure 2. Shortnose sturgeon sizes and ages reported for the Hudson River from Dadswell et al.⁵ using their compilation of unpublished data in modified form, and the total length of shortnose sturgeon aged by Dovel et al. (1992; open circles). The dashed line separates juvenile and adult life intervals at 55 cm total length or about 50 cm fork length.

(Figure 1; also see the species review by Kynard 1997 this volume).

Non-spawning adult interval

In many or all populations of shortnose sturgeon, adult fish do not spawn every year. Dadswell (1979)

reported that females spawn every third to fifth year, and males every second year in the Saint John River, New Brunswick. This pattern may differ in the Hudson River because Dovel et al. (1992) reported the occurrence of tagged shortnose sturgeon at the spawning grounds in successive years. Non-spawning adults appear to use different habitats and display different migratory behavior than adults within a year of spawning.

The maximum sizes reported (Dadswell et al.⁵) for Hudson River shortnose sturgeon were a female weighing 7.2 kg (94.5 cm fork length [FL], 105 cm total length [TL]) and a male weighing 5.3 kg (89 cm FL, 99 cm TL). However, Dovel et al. (1992) documented an even larger but unsexed shortnose sturgeon from the Hudson River: 107 cm TL and 10.7 kg. The age record for shortnose sturgeon is 67 years with the oldest Hudson River specimen aged at 37 years (Dadswell et al.⁵). Most shortnose sturgeon captured in the Hudson River estuary in research and monitoring programs (1983-1988) were adults ranging in size from about 45 to 80 cm TL (Geoghegan et al. 1992) or about 8 to 20 years of age (Figure 2). Pooled across the sexes, maturity criteria that can be used for the Hudson population of shortnose sturgeon would be 50 cm FL (Table 1) and about 6 years of age (sexes pooled, Figure 2). The 50 cm FL criteria (55 cm TL) is useful for field handled

Table 1. Ages and sizes of the life intervals of shortnose and Atlantic sturgeons in the Hudson River. Data reported are generalized because of minor variations in specific values reported in other studies (see text for discussion of specific data).

Life interval	Age range (yr)	Fork length ^a (cm)	Total length ^a (cm)
Shortnose sturgeon			
Larva	< 0.08		≤ 2
Male juveniles	0.08–≥ 3	~ 2–50	2–55
Female juveniles	0.08–≥ 6	~ 2–50	2–55
Male adults	≥ 3	> 50	> 55
Female adults	≥ 6	> 50	> 55
Atlantic sturgeon			
Larva	< 0.08		≤ 3
Early juveniles	0.08–2	~ 2–44	~ 3–49
Intermediate juveniles	3–6	45–63	50–70
Late juveniles	6–11	> 63–134	> 70–149
Non-spawning adults	≥ 12	≥ 135	≥ 150
Female spawners	≥ 15	≥ 180	≥ 200
Male spawners	12–20	≥ 135–190	≥ 150–210

^a Fork length and total length sizes were made to fit the conversion formulae reported by Dadswell et al.⁵ for shortnose sturgeon: FL = 0.9 × TL; TL = 1.1 × FL.

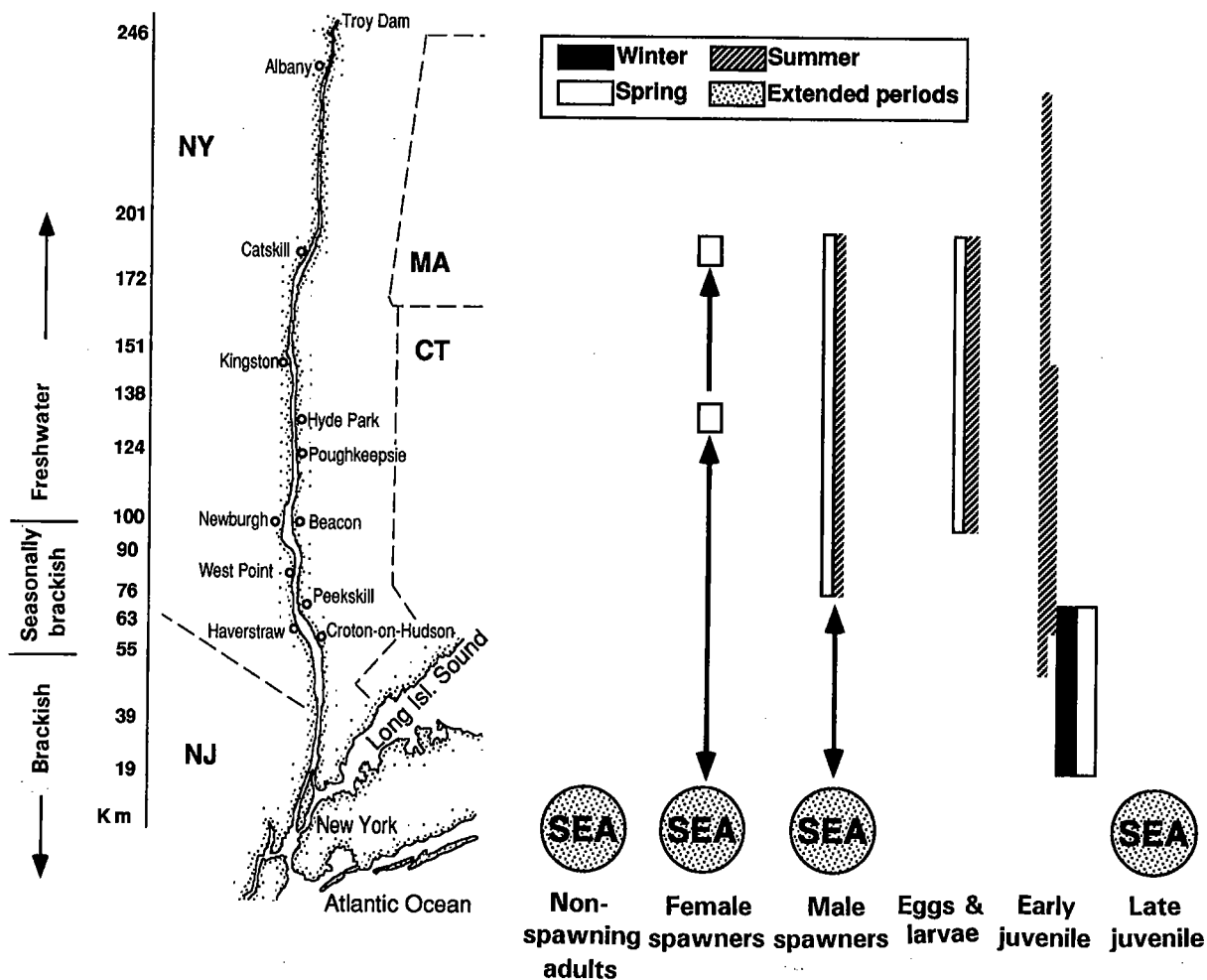


Figure 3. Life intervals and seasonal distribution of Atlantic sturgeon in the Hudson River estuary relative to river features, river distances upstream of upper New York City bay, and salinity. Fall distributions are not shown because this season is transitional. Width of the distribution lines and symbols indicates relative density of individuals. Sea distributions includes long-distance migrations to waters outside the Hudson River estuary.

fish because sex cannot be determined except at the time of spawning by observation of sperm or eggs.

From late spring through early fall, adult shortnose sturgeon are distributed in deep, channel habitats of the freshwater and brackish reaches of the Hudson River estuary. River monitoring (1969–1980) of fish distributions by the Hudson River electric utilities (Hoff et al. 1988) recorded adult shortnose sturgeon from a large portion of the estuary (Figure 1): most captures occurred between km 38 through 122, and no captures upstream of km 166. Later river monitoring (Geoghegan et al. 1992) showed a similar pattern. During this apparent

growth and feeding period, the diet of shortnose sturgeon in the Hudson River likely includes insects and crustaceans with molluscs being a major component (25 to 50% of the diet; Curran & Ries¹, Townes³).

As water temperature declines in the late fall, adult shortnose sturgeon typically concentrate in a few overwintering areas. Dovel et al. (1992) concluded that most or all adults form an overwinter concentration near Kingston (approximately km 140). However, river monitoring in late fall indicates another concentration near Haverstraw (km 54–61). Life history studies for some shortnose stur-

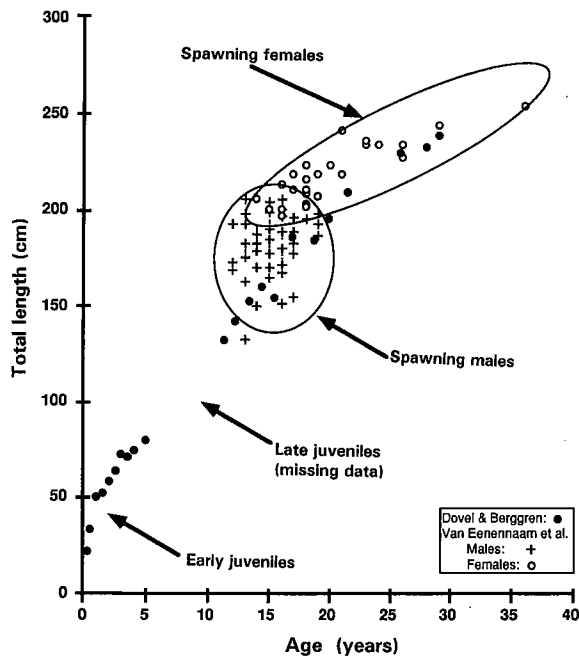


Figure 4. Individual Atlantic sturgeon sizes and ages reported for the Hudson River by Dovel & Berggren (1983; solid dots) and Van Eenennaam et al. (1996; open dots for females, + symbols for males). The circled points indicate individuals determined to be in spawning condition by Van Eenennaam et al. (1996). The arrow for late juveniles indicates a gap in the age and size series corresponding with an absence of fish from the Hudson River.

geon populations (Dadswell et al.⁵) and observations in the Hudson River (Geoghegan et al. 1992) indicate that non-spawning adults behave differently from adults entering reproductive condition. Adults that will not be in reproductive condition the following spring concentrate in brackish waters. In the Hudson, this overwintering area appears to be located between km 54 and 61 (Figure 1). In the spring, these fish migrate upstream and disperse through the tidal portion of the river.

Spawning adult interval

Shortnose sturgeon spawn once in spring, usually at a single location as far upriver as the population ranges. Pre-spawning adults overwinter in one large concentration widely separated from those adults that will not spawn the following spring. Females and males have the same migratory and habitat use

behavior so I treat them as one life history interval (Figure 1).

Growth rates for shortnose sturgeon vary by region and sex but all fish mature at approximately the same size throughout their range: 45–55 cm FL (50–60 cm TL) for males and females (Dadswell et al.⁵). For the Hudson River population, Greeley² reported that males first spawn at 3 to 4 years of age (average 44.5 cm FL), and females first spawn at 6 to 8 years of age (average 51.5 cm FL, Table 1). However, Dadswell (1979) concluded from fin ray interannular increments that first spawning may follow maturation by 1 to 2 years in males and as much as 5 years in females. Therefore, Greeley² may have overestimated the age at maturity.

From late spring through early fall, all adult shortnose sturgeon have a dispersed distribution as described above for non-spawning adults. Adult shortnose sturgeon that will spawn the following spring congregate in an overwintering site near the spawning grounds. In the Hudson, a single large overwintering concentration of pre-spawning adults is well documented to form annually in deep, channel habitats a few kilometers downstream of Sturgeon Point (km 139). Many fish were readily captured at this site by Dovel et al. (1992), and it was known as a productive fishing area prior to protection of the species. From information on other populations (Dadswell 1979), females at the overwintering site may not feed prior to spawning, but males do feed during this period. Food items are probably similar to those reported above for non-spawning adults. In mid-April, adult fish move upstream to the spawning grounds extending from below the Federal Dam at Troy to about Coxsackie (km 239–190; Dovel et al. 1992, Hoff et al. 1988). Spawning occurs from late-April to early May. Afterward, the adults disperse downriver into the summer range.

Egg, embryo and larva interval

Eggs of shortnose sturgeon adhere to solid objects on the river bottom, and newly hatched embryos remain on the bottom (Buckley & Kynard 1981, Taubert 1980). Hatching size ranges from 7 to 11 mm TL

(Buckley & Kynard 1981, Taubert 1980), with Hudson River embryos ranging in size from 15 to 18 mm TL at 10 to 15 days of age (Pekovitch⁶). After hatching, embryos gradually disperse downstream over much of the Hudson River estuary (Hoff et al. 1988). Shortnose sturgeon larvae captured in the Hudson River were associated with deep waters and strong currents (Pekovitch⁶, Hoff et al. 1988). At 20 mm TL, shortnose sturgeon in the Hudson River had fully developed external characteristics indicating a transition to the juvenile interval (Pekovitch⁶; Table 1). No further information is available on this interval of the shortnose sturgeon life cycle.

Juvenile interval

Juvenile shortnose sturgeon (2–55 cm TL; Table 1), use a large portion of the tidal reach of the Hudson River. Dovel et al. (1992) indicated that yearling juvenile sturgeon grow rapidly (to 30 cm TL in first year, Figure 2) and disperse downriver to about km 55 by fall. Juveniles have been captured in the same deep channel habitats used by adults. During mid-summer, the juvenile distribution centers on the mid-river region (Geoghegan et al. 1992). By late fall and early winter, most juveniles occupy the broad region of the Hudson River near Haverstraw (km 55–63; Dovel et al. 1992, Geoghegan et al. 1992). However, there is no evidence that juveniles move out of the lower river into coastal marine waters.

Juvenile shortnose sturgeon feed on smaller and somewhat different organisms than do adults (Carlson & Simpson 1987). Common prey items are aquatic insects (chironomids), isopods, and amphipods. Unlike adults, molluscs do not appear to be an important part of their diet (Dadswell 1979).

Atlantic sturgeon

Atlantic sturgeon are anadromous. Spawning occurs in freshwater, but male and female fish reside for many years in marine waters. Atlantic sturgeon undertake long-distance migrations along the Atlantic coast. Atlantic sturgeon marked in the Hudson River by Dovel & Berggren (1983) were recaptured in marine waters and river mouths from just south of Cape Hatteras, North Carolina to just north of Cape Cod, Massachusetts. In addition to these marine movements, Atlantic sturgeon display complex migratory behavior within the Hudson River. Here, I review the life cycle for Atlantic sturgeon in the Hudson River in six intervals that vary by habitat, migratory behavior, and size (Figure 3). Also see Smith & Clugston (1997 this volume) for a general review of Atlantic sturgeon life history and fishery.

Non-spawning adult interval

The inter-spawning period for Atlantic sturgeon is thought to range from 3 to 5 years depending on sex (discussed below). During non-spawning years, adults use marine waters either all year or seasonally. Little is known about their behavior in marine waters except that adult-size fish (≥ 150 cm TL, Table 1) marked in the Hudson River have been recaptured in coastal waters and river mouths from North Carolina to Massachusetts. The largest commercial harvest of adult Atlantic sturgeon from the Hudson River population occurs in marine waters throughout the New York Bight (Waldman et al. 1996). Female Atlantic sturgeon apparently grow in marine waters, whereas males appear to grow little after maturity (Figure 4). In marine habitats, Atlantic sturgeon eat amphipods, isopods, shrimps, molluscs, and fish (Scott & Crossman 1973).

The maximum age for the species is 30 years (Scott & Crossman 1973) with a similar estimate for the Hudson River (T.I.J. Smith 1985). The largest known Atlantic sturgeon was a female 427 cm TL, and 368 kg (Saint John River, New Brunswick; Van

⁶ Pekovitch, A.W. 1979. Distribution and some life history aspects of the shortnose sturgeon (*Acipenser brevirostrum*). Hazleton Environmental Sciences Corp., Northbrook. 23 pp.

Den Avyle⁷). Large Atlantic sturgeon are likely to be females because of marked sexual dimorphism (Figure 4).

Female spawning interval

Adult female Atlantic sturgeon differ sharply from adult males in size, growth, migratory behavior, and age structure (Figure 3). Spawning female sturgeon are age 15 or older, weigh more than 34 kg, and are greater than 200 cm TL (Van Eenennaam et al. 1996, Table 1). Dovel & Berggren (1983) reported a slightly older age at first spawning (18 years) but the same minimum size. Age and growth data (Van Eenennaam et al. 1996) clearly indicate steady growth in females (Figure 4), and data from Dovel & Berggren (1983) are consistent with this pattern.

Adult females enter the Hudson River Estuary for spawning beginning in mid-May. They migrate directly to the spawning grounds which are deep, channel or off-channel habitats (Dovel & Berggren 1983). The female sturgeon return to marine waters quickly after spawning (C.L. Smith 1985). The spawning period ranges from May through July or possibly August in the Hudson River estuary (Dovel & Berggren 1983, Van Eenennaam et al. 1996). Female sturgeon do not appear to feed on the spawning run in freshwater (T. I. J. Smith 1985).

Dovel & Berggren (1983) report that spawning occurs near the salt wedge (km 55) early in the season (late May), moving upstream to km 136 during June and early July. However, Van Eenennaam et al. (1996) collected spawning Atlantic sturgeon only at two historically important fishing sites known to be spawning areas (Figure 3): near Hyde Park (km 130) and Catskill (km 182). Van Eenennaam et al. (1996) argue that spawning is unlikely to occur near brackish water because sturgeon eggs, embryos and larvae are intolerant of saline conditions, and some significant length of river habitat is needed down-

stream of a spawning site to accommodate dispersal of embryos and larvae.

Male spawning interval

Mature, male Atlantic sturgeon enter the Hudson River starting in April and at least some remain in the Hudson River as late as November (Dovel & Berggren 1983). Spawning males are 12 or more years old and from 150 to 210 cm TL (Van Eenennaam et al. 1996, Table 1). Van Den Avyle⁷ reported that the maximum size for males is 213 cm TL which is similar to the sizes recorded in the Hudson River spawning stock (Figure 4). No spawning males over 20 years old have been recorded in the Hudson River. Male Atlantic sturgeon may not spawn annually, and the period between spawnings has been estimated to range from 1 to 5 years (T.I.J. Smith 1985).

From limited sturgeon telemetry by Dovel & Berggren (1983), males appear to move upstream on incoming tides and then remain stationary for several hours. During their upstream migration, male sturgeon meander back and forth across the channel, but stay in water greater than 7.6 m deep. Van Eenennaam et al. (1996) observed that adult male sturgeon appear at spawning sites in association with females, indicating that they search for females while moving about in the river.

Egg, embryo and larva interval

Eggs of Atlantic sturgeon are adhesive and the embryos remain on the bottom in deep channel habitats. Atlantic sturgeon embryos have been recorded in the Hudson River from km 60 through 148 (Dovel & Berggren 1983); a range including some brackish waters. Sturgeon embryos and larvae have limited salt tolerance, so their habitat must be well upstream of the salt front (Van Eenennaam et al. 1996; as illustrated in Figure 3). No further information is available on this interval of the Atlantic sturgeon life cycle.

Atlantic sturgeon embryos are about 7 mm TL at hatching, and in hatcheries, they reached 19.9 mm TL in 20 days (Smith et al. 1980). The transition

⁷ Van Den Avyle, M.J. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) – Atlantic sturgeon. U.S. Fish and Wildlife Service FWS/OBS-82/11.25, Washington, D.C. 17 pp.

from larva to juveniles appears to occur at about 30 mm TL (Table 1) based on Hudson River specimens (Bath et al. 1981).

Juvenile riverine interval

The juvenile period of the Atlantic sturgeon life cycle is marked by major ecological changes, and it can be divided into two life history intervals: early and late juvenile (Figure 3). The precise division between these intervals is unclear because changes are gradual, although growth is very rapid (Figure 4). Consequently, I added a third intermediate interval for age and growth statistics shown in Table 1. The first juvenile interval is limited to riverine habitats. Relatively good information is available for this interval due to research in the Hudson River estuary.

Juvenile Atlantic sturgeon are well distributed over much of the Hudson River from July through September, and they use deep channel habitats as in other life intervals (Figure 3). The largest numbers of juveniles appear to be located from km 63 to 140 (Dovel & Berggren 1983). As water temperature drops below 20° C in the fall, juveniles form an overwintering distribution in brackish water between km 19 to 74 (Dovel & Berggren 1983). From October through June, this region of the Hudson River contains many juveniles and they appear to move little during the period. Upstream dispersion of juveniles begins in late spring. Some juvenile Atlantic sturgeon have been recorded in the overwintering area used by pre-spawning, adult shortnose sturgeon (Esopus Meadows, km 134) as early as mid-April which indicates some variation in the general migration pattern.

Juvenile Atlantic sturgeon grow quickly in the first three years of life (70 cm TL at age 3, Figure 3) but growth slows considerably if they remain in the Hudson River estuary (Dovel & Berggren 1983). Riverine juveniles feed on aquatic insects, amphipods, isopods, and small molluscs (Scott & Crossman 1973).

Juvenile marine interval

After 2 to 6 years of residence in the Hudson River, juvenile Atlantic sturgeon migrate to marine waters. Dovel & Berggren (1983) reported that some males leave the river in year 2, while females may stay in the river until year 5 or 6. This migration to marine waters marks a major change in ecology, behavior, and growth for Atlantic sturgeon. Table 1 shows approximate ages and sizes for early (riverine) juveniles, late (sea migrant) juveniles, and intermediate juveniles because the later includes the group that gradually emigrates from the river during a period of rapid growth. After about 10 years at sea, juvenile sturgeon reach adult size (about 150 cm TL, Table 1 for sexes pooled).

Little is known about Atlantic sturgeon in marine waters except that large juveniles are often captured in Long Island Sound and off the Long Island and New Jersey coasts in commercial fishing gear. Reviews of Atlantic sturgeon life history (e.g., Van Den Avyle⁷) and information specific to the Hudson River estuary (Dovel & Berggren 1983, C.L. Smith 1985) describe post-emigration juveniles as inhabitants of marine waters. However, large juveniles (50–150 cm TL) may reside in riverine habitats along the Atlantic coast during warm months. Atlantic sturgeon sampling in the Hudson River has documented the occurrence of large juveniles (sometimes called pre-adults; Dovel & Berggren 1983, Van Eenennaam et al. 1996). Data of Dovel & Berggren (1983) on tag recaptures show that most fish were reported from river mouths and the lower sections of coastal rivers from Cape Cod to Chesapeake Bay. Murawski & Pacheco⁸ described a similar pattern for tagging and recaptures in the St. Lawrence River, Quebec. Late juvenile Atlantic sturgeon often enter and reside in rivers that lack active spawning sites (e.g. Merrimack River, Massachusetts; Kieffer & Kynard 1993). Most Atlantic sturgeon in rivers of the central US Atlantic coast are probably from the Hudson River population

⁸ Murawski, S.A. & A.L. Pacheco. 1977. Biological and fisheries data on Atlantic sturgeon, *Acipenser oxyrinchus* (Mitchell). National Marine Fisheries Service Technical Series 10, Highlands. 69 pp.

(Waldman et al. 1996). Consequently, late juvenile Atlantic sturgeon from the Hudson River may annually use other riverine habitats during warm months before returning to the Hudson for spawning.

Discussion

Sturgeon (family Acipenseridae) are the modern descendants of the original ray-finned fish that achieved greatest abundance and diversity 280 to 345 million years ago. Atlantic, shortnose, and all other sturgeon retain many ancestral body characteristics and ways of living that distinguish them as relict fishes (see Bemis et al. 1997 this volume). Among North American fishes, sturgeons exhibit a unique combination of life history attributes: advanced age and large size at maturity, eggs that are numerous and small in relation to body size, and spawning that is episodic and seasonal (Winemiller & Rose 1992). Beyond being unique, these characteristics make sturgeon especially vulnerable to population collapse due to overfishing (Boreman 1997 this volume). Life history information on the Hudson River sturgeons fits these generalizations and it substantiates the need to carefully conserve these species. In addition, life history details such as seasonal areas of concentration, migration times and routes, and specific spawning locations highlight the vulnerability of both shortnose and Atlantic sturgeon to easy exploitation and habitat disruption. Fortunately, in the case of the Hudson River estuary, key habitats for spawning, rearing, and overwintering are intact and suitable for the species. Also, both species of sturgeon are managed through either endangered species protection (shortnose sturgeon; US Endangered Species Act) or fishery restrictions (Smith & Clugston 1997 this volume), even though the latter may not be adequate to sustain the current population (Young et al. 1988, Boreman 1997 this volume).

The two sturgeons in the Hudson River share many common life history attributes. Both are long-lived and mature at advanced age compared to almost all other fishes in the Hudson River. Both species have rapid and similar growth rates during the

first few years of life. In general, sturgeon are characterized as indiscriminate bottom-feeding carnivores, and specific information on diet indicates they feed on generally the same food items in the Hudson River. Both sturgeon have complex migratory patterns in the Hudson River with distinct, seasonal, and predictable concentration areas. Finally, both sturgeons primarily use deep channel habitats for all life intervals.

Despite many similarities in life history, Atlantic and shortnose sturgeons differ in some obvious ways. Adult sizes are greatly different, and the sizes and ages at maturity diverge. The timing and location of spawning is so different that it appears impossible that the two species behaviorally interact during this key life interval. Use of marine habitats and long-distance coastal migrations are restricted to Atlantic sturgeon. With respect to management, one species is heavily exploited while the other is fully protected under the US Endangered Species Act.

Widespread occurrence of Atlantic and shortnose sturgeons in many Atlantic Coast rivers of North America raises questions as to how two species can co-exist with so many shared life history attributes. The prevailing view (e.g., Dadswell et al.⁵, Dovel et al. 1992, Kieffer & Kynard 1993) has been that the two species are spatially segregated in rivers in association with salinity; with shortnose sturgeon oriented to freshwater, and Atlantic sturgeon concentrated in brackish water except at spawning and very early life. However, a review of the movements and habitat use of both species in the Hudson River estuary conflicts with these interpretations.

Juvenile shortnose sturgeon and early juvenile Atlantic sturgeon have virtually identical distributions in the Hudson River estuary during all seasons. During this period of co-occurrence, both species are very similar in size, grow at about the same rate, feed on similar foods, and share deep channel habitats. Furthermore, the distribution of adult shortnose sturgeon overlaps with that of juvenile Atlantic sturgeon. Interestingly, the period of river emigration of juvenile Atlantic sturgeon closely corresponds with the age (intermediate juveniles in Table 1) when they reach a size (ca. 55 cm TL) equal to the minimum adult size of shortnose sturgeon.

The protracted period of Atlantic sturgeon emigration (4 years) indicates that the two species overlap considerably in space, food, and habitat. Also, the pattern of emigration in conjunction with comparability in size and habits between the species suggests that co-exploitation of space and food resources may be important in the migratory behavior of juvenile Atlantic sturgeon.

The apparently extensive co-occurrence of the two sturgeons in the Hudson River estuary has not been clearly identified in previous investigations on the Hudson River. Although sturgeon biologists working on the Hudson River undoubtedly captured both species simultaneously in their work, analyses and reports have always been oriented to a single-species. This review is the first to simultaneously report details of the life history of both sturgeons in the Hudson River. The conclusion that the two species are not spatially segregated for large parts of their life histories indicates that the Hudson River estuary may be unique within the joint ranges of the two species.

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References cited

- Barnhouse, L.W., J. Boreman, S.W. Christensen, C.P. Goodyear, W. Van Winkle & D.S. Vaughan. 1984. Population biology in the courtroom: the Hudson River controversy. *BioScience* 34: 14-19.
- Bath, D.W., J.M. O'Connor, J.B. Alber & L.G. Arvidson. 1981. Development and identification of larval Atlantic sturgeon (*Acipenser oxyrinchus*) and shortnose sturgeon (*A. brevirostrum*) from the Hudson River estuary. *Copeia* 1981: 711-717.
- Bemis, W.E. & B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Env. Biol. Fish.* (this volume).
- Bemis, W.E., E.K. Findeis & L. Grande. 1997. An overview of Acipenseriformes. *Env. Biol. Fish.* (this volume).
- Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. *Env. Biol. Fish.* (this volume).
- Buckley, J. & B. Kynard. 1981. Spawning and rearing of shortnose sturgeon from the Connecticut River. *Prog. Fish-Cult.* 43: 74-76.
- Carlson, D.M. & K.W. Simpson. 1987. Gut contents of juvenile shortnose sturgeon in the upper Hudson estuary. *Copeia* 1987: 796-802.
- Coch, N.K. & H.J. Bokuniewicz. 1986. Oceanographic and geologic framework of the Hudson system. *Northeastern Geol.* 8: 96-108.
- Dadswell, M.J. 1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur, 1818 (Osteichthyes: Acipenseridae), in the Saint John River estuary, New Brunswick, Canada. *Can. J. Zool.* 57: 2186-2210.
- Dovel, W.L. & T.J. Berggren. 1983. Atlantic sturgeon of the Hudson Estuary, New York. *New York Fish and Game J.* 30: 140-172.
- Dovel, W.L., A.W. Pekovitch & T.J. Berggren. 1992. Biology of the shortnose sturgeon (*Acipenser brevirostrum* Leseur, 1818) in the Hudson River estuary, New York. pp. 187-216. *In: C. L. Smith (ed.) Estuarine Research in the 1980s*, State Univ. New York Press, Albany.
- Geoghegan, P., M.T. Mattson & R.G. Keppel. 1992. Distribution of the shortnose sturgeon in the Hudson River estuary, 1984-1988. pp. 217-277. *In: C. L. Smith (ed.) Estuarine Research in the 1980s*, State Univ. New York Press, Albany.
- Hoff, T.B., R.J. Klauda & J.R. Young. 1988. Contribution to the biology of shortnose sturgeon in the Hudson River estuary. pp. 171-189. *In: C.L. Smith (ed.) Fisheries Research in the Hudson River*, State Univ. New York Press, Albany.
- Kieffer, M.C. & B. Kynard. 1993. Annual movements of shortnose and Atlantic sturgeons in the Merrimack River, Massachusetts. *Trans. Amer. Fish. Soc.* 122: 1088-1103.
- Kynard, B. 1997. Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Env. Biol. Fish.* (this volume).
- Limburg, K.E., S.A. Levin & R.E. Brandt. 1989. Perspectives on management of the Hudson River ecosystem. pp. 265-291. *In:*

- D.P. Dodge (ed.) Proceedings of the International Large River Symposium, Can. Spec. Publ. Fish. Aquat. Sci. 106.
- McDowall, R.M. 1987. The occurrence and distribution of diadromy among fishes. Amer. Fish. Soc. Symp. 1: 1-13.
- Scott, W.B. & E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184. 966 pp.
- Smith, C.L. 1985. The inland fishes of New York State. The New York State Department of Environmental Conservation, Albany. 522 pp.
- Smith, C.L. 1992. Estuarine research in the 1980s. State Univ. New York Press, Albany.
- Smith, T.I.J. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrinchus*, in North America. Env. Biol. Fish. 14: 61-72.
- Smith, T.I.J. & J.P. Clugston. 1997. Status and management of Atlantic sturgeon, *Acipenser oxyrinchus*, in North America. Env. Biol. Fish. (this volume).
- Smith, T.I.J., E.K. Dingley & D.E. Marchette. 1980. Induced spawning and culture of the Atlantic sturgeon, *Acipenser oxyrinchus* (Mitchell). Prog. Fish-Cult. 42: 147-151.
- Taubert, B., 1980. Reproduction of shortnose sturgeon (*Acipenser brevirostrum*) in Holyoke Pool, Connecticut River, Massachusetts. Copeia 1980: 114-117
- Young, J.R., T.B. Hoff, W.P. Dey & J.G. Hoff. 1988. Management recommendations for a Hudson River Atlantic sturgeon fishery based on an age-structured population model. pp. 353-365. In: C.L. Smith (ed.) Fisheries Research in the Hudson River, State Univ. New York Press, Albany.
- Van Eenennaam, J.P., S.I. Doroshov, G.P. Moberg, J.G. Watson, D.S. Moore & J. Linares. 1996. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries (in press).
- Waldman, J.R., J. Hart & I. Wirgin. 1996. Stock composition of the New York Bight Atlantic sturgeon fishery, based on analysis of mitochondrial DNA. Trans. Amer. Fish. Soc. 125: 364-371.
- Winemiller, K.O & K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49: 2196-2218.