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Habitat Utilization and Biological Characteristics of Adult Atlantic Sturgeon in Two South Carolina Rivers

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Abstract.—Thirty-nine adult Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* (136–234 cm total length) were caught in gill nets fished at historical sturgeon-fishing locations in the Combahee and Edisto rivers (South Carolina) during spring and fall 1998. All fish were tagged (with passive integrated transponders and darts), and radio and acoustic transmitters were surgically implanted in 29 fish. When possible, gonad biopsies were taken for sex and maturity-stage determination. Locations of telemetered fish were determined several times per week from airplanes (radio) and boats (radio and acoustic). Nominal ages, based on microscopic examination of pectoral spine cross-sections, ranged from 7 to 20 years. Of the 28 fish for which sex was definitively ascertained, 21 (aged 7–15) were male and 7 (aged 15–20) were female. All fish moved out of the rivers during the period extending from October to November. Twelve fish returned the following spring (most in March), and many took up residence at the same sites utilized the previous year. Fall and spring spawnings were documented based on histological examination of gonad biopsies and directed upriver movements of fish during both seasons. Habitats used during summer were diverse and included the lower and upper estuaries, tidal freshwater, river, and perhaps even the ocean, as some fish left the system entirely. One male was captured in two successive springs and was in spawning condition (running ripe) both years.

The Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* is an anadromous species inhabiting the Atlantic coast of North America from Labrador to Florida. Recorded exploitation dates prior to 2198 BC (Ritchie 1969). By 1860, major commercial fisheries were established in a number of states from Georgia through New York (Smith 1990). Because of the high value of these fish, the fisheries were vigorously pursued, and within a decade, all fisheries suffered drastic declines or total collapse (Murawski and Pacheco 1977).

After the collapse of the more northerly fisheries, South Carolina became a major producer of sturgeon. In 1976, South Carolina produced 55% of the total U.S. landings of Atlantic sturgeon (Smith et al. 1984). As a result of increased fishing pressure following the embargo on Iranian caviar, landings continued to increase in South Carolina, but catch per unit effort was steadily declining. By 1984, it became apparent that the fishery was being overexploited, and in 1985 the South Carolina sturgeon fishery closed indefinitely until systems for estimating abundance and monitoring the fishery could be implemented. Recently the Atlantic States Marine Fisheries Commission (ASMFC 1998) implemented a long-term moratorium on all U.S. Atlantic sturgeon fisheries.

Little is known about the ecology of adult Atlantic sturgeon in the southeastern United States. The ASMFC conducted an information survey while developing a Fishery Management Plan and noted that research on habitat use and reproduction/recruitment should be considered a high priority (ASMFC 1990, 1998). To date, however, no spawning areas have been identified in any southeastern river, nor have specific spawning conditions been defined. Further, habitat use by adult Atlantic sturgeon during nonspawning seasons is unknown. Age-distribution and sex-ratio information are also unavailable for most southern populations. Thus, a broad range of biological data is needed to facilitate restoration and management of this valuable species (Smith 1985; Smith and Clugston 1997). To address these issues, a study was conducted to provide information on habitat use, age distribution, reproductive status, and seasonal movements of adult Atlantic sturgeon in two South Carolina rivers.

Methods

With assistance from three former sturgeon anglers who were familiar with the study areas, sturgeon gill nets were deployed in the Combahee and Edisto rivers of the Ashepoo, Combahee, and Edisto rivers (ACE) basin (South Carolina) during

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spring and fall 1998. Gill nets were 11–23 m long, with 29.2–45.7-cm stretch mesh. Nets were anchored perpendicular to the bank at previously productive fishing locations and were checked during morning and evening. The same locations were sampled and the same gear was used during spring and fall. Fish were brought into the boat and placed upside down in a V-shaped trough with the anterior portion of the fish positioned in a tank that was receiving flow-through river water. Total length (TL) and fork length (FL) were measured, and a marginal pectoral spine was removed for age estimation. Sturgeon were tagged at the base of the dorsal fin with a passive integrated transponder (PIT) tag and a dart tag. Individuals suitable for telemetry studies (i.e., those that were not injured or highly stressed) received a 5-cm incision just off the midline of the abdomen, about 10 cm anterior to the vent, for insertion of radio and acoustic transmitters and for sex determination. Radio (Advanced Telemetry Systems, Inc., model 12AA) and acoustic (Sonotronics, Inc., model CHP-87-L) transmitters were sterilized with betadine and inserted anteriorly through the incision. Sex was initially determined by gross examination, but later an Eppendorfer biopsy punch was used to take a small sample of gonad. The incision was closed using Ethicon Ethibond Excel 2/0 braided polyester sutures, and the fish was released. In one instance the acoustic transmitter was attached externally at the base of the dorsal fin, and in another instance both transmitters were attached externally, one on each side of the dorsal fin.

Gonad biopsy specimens were preserved in 10% formalin. After a 1–2-week fixation, they were transferred to 50% isopropanol, processed, vacuum-infiltrated in a modular vacuum tissue processor, and embedded in paraffin. Blocked samples were sectioned at 7 μm, stained with double-strength gill hematoxylin, and counterstained with eosin-y. Sections were examined microscopically, and sex and maturity stages were assigned using histological criteria modified from Wallace and Selman (1981; see also West 1990; Amiri et al. 1996a, 1996b; Van Eenennaam and Doroshov 1998; Vorobyova and Markov 1999) (Table 1). Ripe and running ripe fish of both sexes and females with ovaries containing postovulatory follicles were classified as being "in spawning condition."

Pectoral fin spines were sectioned with a low-speed diamond-blade saw. Three sections from the base of each spine were cut to a thickness of 0.5 mm and mounted on glass slides. Each section was

TABLE 1.—Histological criteria used to establish maturity stages of male and female Atlantic sturgeon from microscopic examination of sectioned and stained gonad samples.

Stage	Characteristics
	Males
Immature	Predominance of spermatogonia, some cysts of primary spermatocytes may be present, no evidence of previous spawning
Developing	
Early	Nearly equal amounts of cysts with spermatogonia and cysts with primary and secondary spermatocytes, some spermatids may be present
Mid	Lobules contain approximately equal amounts of cysts with spermatogonia, spermatocytes and spermatids, some spermatozoa may be present in lobular lumina
Late	Ripe; predominance of cysts with spermatids, and spermatozoa more abundant, some cysts with spermatogonia and spermatocytes
Running ripe	Lobules filled with spermatozoa, little or no spermatogenesis; spermiation
Spent	Only residual spermatozoa present in lobules that have contracted, proliferation of interstitial tissue and phagocytosis of germ cells
Resting	Predominance of interstitial tissue, small empty lobules evident, spermatogonial proliferation at the end of this stage
	Females
Immature	No evidence of atresia, predominance of chromatin-nucleolar oocytes, abundant oogonia along periphery of lamellae, perinucleolar oocytes present at the end of this stage
Developing	
Early	Cortical alveoli appear in the peripheral cytoplasm of the largest oocytes
Mid	Predominance of primary (yolk-granular) and secondary (yolk-globular) vitellogenic oocytes
Late	The most advanced oocytes are in tertiary vitellogenic stage (yolk globules fuse into yolk platelets), with two-layered zona radiata
Ripe	Nucleus at the animal pole in the most advanced oocytes
Running ripe	Mature oocytes ovulated into the abdominal cavity and spawning takes place
Recently spawned	Postovulatory follicles (POF) present indicating that fish spawned during previous few hours to 2 d (dependent upon water temperatures)
Spent	Unshed advanced oocytes atretic, POF no longer present
Resting	Predominance of perinucleolar oocytes, traces of atresia may be present

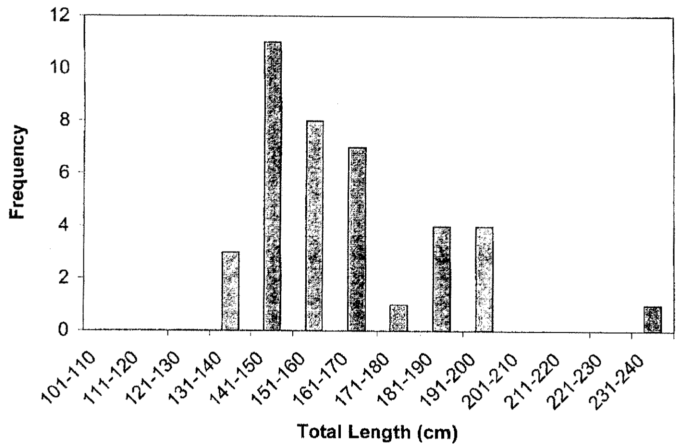

FIGURE 1.—Length frequency for adult Atlantic sturgeon captured in the Combahee and Edisto rivers (South Carolina).

examined microscopically, and the fish were assigned nominal ages based on the number of annuli observed (see Cuerrier 1951; Brennan and Cailliet 1989).

Overflights were used to survey the freshwater segments of the rivers for telemetered fish, and fish locations were pinpointed by boat. Egg collectors, which consisted of anchored plastic matrix pads (floor buffing pads; see Sulak and Clugston 1998) and which provided an artificial substrate to which sturgeon eggs would adhere, were deployed at possible spawning locations. Varying numbers of these collectors were placed in the vicinities of telemetered fish, and collectors were checked every 2 d. Habitats utilized regularly were characterized in terms of depth, substrate, water temperature, dissolved oxygen, and salinity. When fish used brackish water habitats, acoustic tracking was utilized because of attenuation of radio signals.

Results

Thirty-nine adult Atlantic sturgeon, ranging in size from 136 to 234 cm TL, were captured in the Edisto and Combahee rivers (Figure 1). Most fish were caught at night and removed when the nets were checked in the morning. Catch per unit effort (CPUE) of three cooperating former sturgeon anglers in the Combahee and Edisto rivers was 0.0–0.456 fish/net-day (1 net-day = 91 m of gill net fished for 1 d) during spring 1998. The CPUE was greater for two of the three anglers in fall 1998, with a range of 0.288–0.408 fish/net-day.

Nominal ages were determined for 38 fish, as one spine was considered unreadable. Nominal ages were 7–20, with a modal age of 9 and a mean age of 10.8 (Figure 2). The oldest, and also the largest, fish captured was a female taken in spring 1998. Females were aged 15–20, and males were aged 7–15.

Sex information obtained by gross examination was not used, except for fish that were running ripe. Of the 28 sturgeon for which sex was determined, 21 were male (139–195 cm TL), and 7 were female (180–234 cm TL), providing a 3:1 sex ratio. In the spring, running ripe males were captured as early as 2 March, and a running ripe female (at Edisto River river kilometer [RKM] 56) was captured on 7 March, when the water temperature was 13.6°C. One male that was captured in March 1998 and recaptured in March 1999 was in spawning condition (running ripe) both years. Spent males were captured as early as late March, and spent females were captured as late as mid-May.

Running ripe males began reappearing at the end of August. During September, ripe and running ripe males were present in approximately equal numbers, and during October, only one of seven males captured was not running ripe. A late-developing female was captured on 2 June, and histological examination indicated that this female had not spawned in the spring. This fish moved upriver to RKM 105 in late September. Spent females, including one that had spawned very recently (postovulatory follicles still present), were captured in late September and October, when the water temperature was 17–18°C.

Adult Atlantic sturgeon were present in the Edisto River from March through October 1998. In early 1999, 12 telemetered fish returned to the

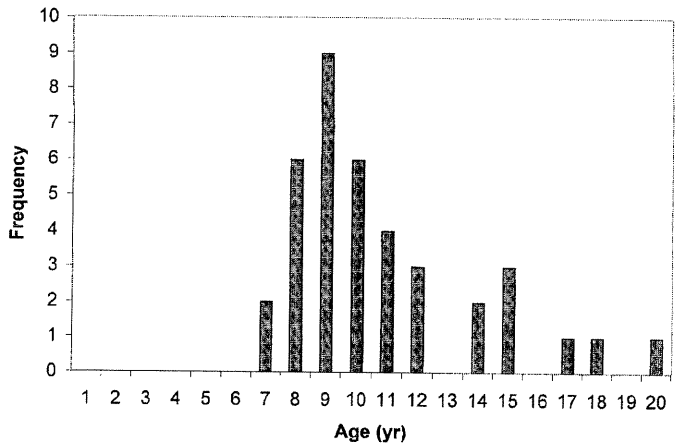

FIGURE 2.—Nominal age frequency from microscopic examination of pectoral spine sections for adult Atlantic sturgeon captured in the Combahee and Edisto rivers (South Carolina).

river, primarily during the month of March. Only one fish, a male that was ripe in spring 1998, moved upriver. The rest remained in the lower river and estuary, many of them using the same locations that they had utilized the previous summer.

Movements of three males suggest that Atlantic sturgeon may not differentiate among ACE basin rivers. All were initially captured at RKM 53 in the Combahee River, one in the spring and two in the fall of 1998. The fish caught in the spring was recaptured after 13 d at large at RKM 56 on the Edisto River. The recapture allowed for examination of the incision and sutures. The incision had entirely closed, and the sutures were gone. The two fish captured in the fall left the Combahee River in October 1998 and were located in the lower Edisto River in early June 1999.

Movements of two fish were strongly indicative of a fall spawning migration. Both fish were telemetered in late May 1998. They spent the summer in the lower Edisto River, then in October moved upriver to RKM 190. No sturgeon eggs were collected with the artificial substrates, so spawning sites were not confirmed. However, a running ripe female that may have been in the process of spawning was captured in the spring at Edisto RKM 56, and a very recently spawned female was captured at the same location in fall. The substrate in that area is limestone. Fish were located during spawning seasons in three other areas that had hard substrates: RKM 55–60 in the Combahee River and the areas of RKM 105 and 190 in the Edisto River. In the Combahee River, no movements upriver of RKM 60 were noted during spring or fall.

A wide variety of habitats was utilized by adult Atlantic sturgeon during summer. In the Edisto River, habitats included locations in the vicinities of RKM 90–105, RKM 64–72, RKM 40 in the upper fresh/brackish interface zone, RKM 18–29 in the lower interface zone, and RKM 8–10 in the high-salinity section of the estuary. Salinities at locations inhabited by fish varied from 0.0 to 28.6 ppt, dissolved oxygen was 3.4–8.3 mg/L, and temperatures were as high as 33.1°C. Substrates included fine mud, sand, pebbles, and shell hash. Depths utilized varied from 1.5 to 13.0 m, but in nearly all cases, fish were in the greatest depth available in the immediate area. No telemetered fish remained in the Combahee River during summer.

Discussion

The CPUE of the three former sturgeon anglers in fall 1998 and the CPUE of two of the anglers (one caught no sturgeon) in spring 1998 were apparently greater than that recorded from the commercial fishery in the same rivers in 1981–1982. Smith et al. (1984) reported CPUE in terms of weight (15.8 and 13.2 kg/net-day for 1981 and 1982, respectively), but they also gave the mean weight of fish landed in 1982 (73.3 kg). Thus, CPUE in numbers of individuals was approximately 0.216 and 0.180 fish/net-day for 1981 and 1982, in comparison with 0.0–0.456 fish/net-day during spring 1998 and 0.288–0.408 fish/net-day in fall 1998. This suggests that the abundance of adult Atlantic sturgeon may have increased and, therefore, that the population(s) may be recovering because of the closure of the fishery. However, it is possible that the anglers who participated in this study chose the most productive of all historical fishing sites and that additional nets in other locations would produce fewer fish per net-day, thus reducing the overall CPUE.

The youngest mature male caught in the ACE basin was age 7, although Smith (1985) reported that males mature as early as age 5 in South Carolina. Van Eenennaam and Doroshov (1998) reported that the youngest mature male they encountered in the Hudson River (New York) was age 12, supporting Smith's (1985) assertion that Atlantic sturgeon mature at younger ages in the south. Atlantic sturgeon from northern populations reportedly achieve much greater ages than those observed in this study (e.g, age 60; Magnin 1964). Smith (1985) reported a maximum nominal age of 30 for fish sampled from the Winyah Bay, South Carolina commercial fishery, and the oldest fish in the present study was age 20. Similarly, Sulak and Clugston (1999) found a maximum age of 25 among 5,000 Gulf sturgeon *Acipenser oxyrinchus desotoi* in the Suwannee River (Florida).

Smith et al. (1984) reported a mean nominal age of 15 for fish landed in South Carolina during 1978–1980; this represents an age that is substantially greater than the mean of 10.8 years that we observed in the present study. It is not known whether the age distribution observed is "normal" for this region or whether it is a result of intense fishing pressure prior to the fishery's closure. Assuming that the assigned ages are accurate, only eight fish were from year-classes spawned prior to the closure of South Carolina's commercial fishery in 1985. It is possible that only a few fish in this population avoided harvest and that the population is now slowly rebuilding. It should be noted that full age-growth studies have not been conducted for southern populations of Atlantic sturgeon, and the annual nature of marks on hard parts of adult Atlantic sturgeon has not been validated.

There have been reports of fall runs or migrations of Atlantic sturgeon, but they are generally considered to represent postspawning downriver migrations (Smith 1985). Dovel and Berggren (1983) found no convincing evidence for fall migrations in the Hudson River. Smith et al. (1984) reported indications of both spring and fall runs of Atlantic sturgeon in the ACE basin rivers, but they did not confirm that the runs were related to spawning. That spawning takes place in both seasons, at least in this system, has now been histologically verified. Spring and fall spawning are reported to occur in a number of Eurasian sturgeons. Berg (1959) reported that most of these species consist of separate races, which he termed "vernal" and "hiemal." The former commercial sturgeon anglers who participated in the present study stated their belief that fall spawners and spring spawners are separate stocks or races. They based this belief primarily on an assertion that fish of both sexes caught in spring were larger than those caught in fall, as pointed out by Smith et al. (1984). We compared the lengths of males (too few females) captured in the two seasons during 1998. The number of spring spawners was insufficient for statistical comparison, but the length ranges (spring: 189–194 cm TL; fall: 139–152 cm TL) do not overlap.

Group-synchronous development of oocytes in ovaries of migrating female Atlantic sturgeon (only three modes of oocytes present: tertiary vitellogenic, cortical alveoli, and perinucleolar), along with the fish size differences between seasons, suggest that the same females do not spawn twice in the same year. Moreover, the large separation between clutches of mature and previtellogenic oocytes within the same ovary of females in spawning condition (no primary or secondary vitellogenic oocytes) indicates that after mature eggs are released, a long period is required for another clutch to mature. In South Carolina, examination of presumed spawning marks on pectoral rays indicated that intervals between spawnings is 3–5 years for females and 1–5 years for males (Smith 1985). However, it was not verified that the marks were actually the result of spawning. The capture of a running ripe male during consecutive springs (1998 and 1999) verifies that some males may spawn in consecutive years, but there was no indication that the same individuals participate in both spring and fall spawns.

Spawning locations were not verified by collection of eggs. Achieving this goal will likely require substantial additional effort, especially if spawning activity is restricted to a very small area at each site, as appears to be the case for Gulf sturgeon (Sulak and Clugston 1999). However, inferences concerning spawning sites can be drawn from telemetry, histology, and substrate data. It is likely that spawning occurs at several locations in the Comabahee and Edisto rivers, as is the case for Gulf sturgeon in the Suwanee River (Sulak and Clugston 1998, 1999) and the Choctawhatchee River (Florida–Alabama) (Fox and Hightower 2000). The running ripe female captured in the vicinity of limestone outcrops at RKM 56 in the Edisto River may have been in the process of spawning. Similar substrate has been identified as being typical of spawning sites for a number of sturgeon species (Foltz and Meyers 1985; Parsley et al. 1993; Kieffer and Kynard 1996; Sulak and Clugston 1999).

Other areas that the data suggest might have been spawning sites were RKM 105 and 190 in the Edisto River and RKM 55 in the Combahee River. To reach the two upriver sites in the Edisto River, fish had to cross several very shallow (~0.5 m) stretches of river as a result of the low-flow conditions that prevailed during fall 1998. In spring, movements upriver of RKM 56 on the Edisto River were not observed, and no movement above RKM 60 was detected in the Combahee River. Dovel and Berggren (1983) suggested that Atlantic sturgeon in the Hudson River spawn between RKM 55 and 136, although the salt wedge extends as far upriver as RKM 98. Based on histological examination of gonads, Van Eenennaam et al. (1996) concluded that spawning did not take place below RKM 196 in the Hudson River. They also pointed out that based on the sensitivity of sturgeon embryos and larvae to even low salinities, it is doubtful that successful spawning takes place below, or even immediately above, the salt wedge. The proposed spawning sites in the Edisto and Combahee rivers were all more than 12 km upriver of the maximum intrusion of the salt wedges, and they are substantially farther upriver when the salt wedges are displaced downriver during typical flow conditions. Shortnose sturgeon *Acipenser brevirostrum* in general (Kynard 1997), Gulf sturgeon in the Suwannee River (Sulak and Clugston 1999), and Atlantic sturgeon in the Hudson River migrate more than 200 km upriver to spawn. However, this may not always be the case for Atlantic sturgeon in southern rivers, as some spawning in South Carolina may take place relatively close to the coast (but probably well above the salt wedge). This hypothesis is further supported by the recent capture (April 1998) of two very early larval *Acipenser* sp., tentatively identified as Atlantic sturgeon, at RKM 42 in the Savannah River (T. Reinert, Georgia Cooperative Fish and Wildlife Research Unit, personal communication). Sulak and Clugston (1999) hypothesized that Gulf sturgeon spawning sites are determined primarily by a specific topographical, hydrological, and chemical milieu, and such conditions may occur lower in the Edisto, Combahee, and Savannah rivers than in other rivers in which Atlantic sturgeon have been studied.

Migration patterns and general behavior of adult Atlantic sturgeon in the ACE basin closely parallel those of Gulf sturgeon (Sulak and Clugston 1998, 1999), perhaps to a greater extent than those of Atlantic sturgeon in the northern portion of their range. In general, both overwinter in the ocean, migrate into the river in early spring and move upriver to spawn, inhabit the river throughout the summer, and migrate out of the river in the fall. Maximum observed ages for Gulf and southern Atlantic sturgeons are much younger than those reported for northern Atlantic sturgeon. There is also some evidence of fall spawning for Gulf sturgeon (Sulak and Clugston 1998; Ken Sulak, U.S. Geological Survey, Biological Resources Division, personal communication) as well as for ACE basin Atlantic sturgeon. In contrast to Gulf sturgeon, however, Atlantic sturgeon in the ACE basin utilized a broad range of estuarine and riverine habitats during the summer.

This study provides new information on the movements and habitats of adult Atlantic sturgeon in the southeastern United States as well as evidence to substantiate a fall spawning period. However, significant data gaps still remain. For example, a number of sites were identified as probable spawning areas, but collection of eggs for final verification was not achieved. Nominal age structure and catch data suggest that the population in the ACE basin is rebuilding following the closure of the fishery, but population size estimates were not possible. It is not known whether the surprisingly diverse habitats used form a pattern that occurs in other rivers in the region. Atlantic sturgeon spend a substantial portion of their lives in the ocean and have been captured in depths of up to 40 m off the coast of South Carolina (Collins and Smith 1997), but little is known of their movements or specific habitats. Future efforts should focus on addressing these issues as well as on determining the status of Atlantic sturgeon populations in other rivers.

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References

Amiri, B. M., M. Maebayashi, S. Adachi, and K. Yamauchi. 1996a. Testicular development and serum sex steroid profiles during the annual sexual cycle of the male sturgeon hybrid, the bester. Journal of Fish Biology 48:1039–1050.

Amiri, B. M., M. Maebayashi, A. Hara, S. Adachi, and K. Yamauchi. 1996b. Ovarian development and serum sex steroid and vitellogenin profiles in the female cultured sturgeon hybrid, the bester. Journal of Fish Biology 48:1164–1178.

ASMFC (Atlantic States Marine Fisheries Commission). 1990. Fishery management plan for Atlantic sturgeon. ASMFC, Fisheries Management Report 17, Washington, D.C.

ASMFC (Atlantic States Marine Fisheries Commission). 1998. Amendment #1 to the interstate fishery management plan for Atlantic sturgeon. Report of the ASMFC to National Oceanic and Atmospheric Administration, NA87FG0025 and NA77FG0029, Washington, D.C.

Berg, L. S. 1959. Vernal and hiemal races among anadromous fishes. Journal of the Fisheries Research Board of Canada 16:515–537.

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.

Collins, M. R., S. G. Rogers, T. I. J. Smith, and M. L. Moser. In press. Primary factors impacting sturgeon populations in the southeastern U.S.: fishing mortality and degradation of essential habitats. Bulletin of Marine Science.

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.

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

Dovel, W. L., and T. J. Berggren. 1983. Atlantic sturgeon of the Hudson estuary, New York. New York Fish and Game Journal 30:139–172.

Foltz, D. J., and L. S. Meyers. 1985. Management of the lake sturgeon, *Acipenser fulvescens,* populations in the Lake Winnebago system, Wisconsin. Pages 135–146 *in* F. P. Binkowski and S. I. Doroshov, editors. North American sturgeons. Dr. W. Junk, Dordrecht, The Netherlands.

Fox, D. A., and J. E. Hightower. 2000. Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama–Florida. Transactions of the American Fisheries Society 129:811–826.

Kieffer, M., and B. Kynard. 1996. Spawning of shortnose sturgeon in the Merrimack River, Massachussetts. Transactions of the American Fisheries Society 125:179–186.

Kynard, B. 1997. Life history, latitudinal patterns, and status of shortnose sturgeon, *Acipenser brevirostrum.* Environmental Biology of Fishes 48:319–334.

Magnin, E. 1964. Croissance en longeur de trois esturgeons d'Amerique du Nord: *Acipenser oxyrhynchus* Mitchill, *Acipenser fulvescens* Raffinesque, et *Acipenser brevirostris* LeSueur. Internationale Vereinigung für theoretische und angewandte Limnologies Verhandlungen 15:968–974.

Murawski, S. A., and A. L. Pacheco. 1977. Biological and fisheries data on the Atlantic sturgeon, *Acipenser oxyrhynchus* (Mitchill). National Marine Fisheries Service, Technical Series Report 10, Highlands, New Jersey.

Parsley, M. J., L. G. Beckman, and G. T. McCabe, Jr. 1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Transactions of the American Fisheries Society 122:217–227.

Ritchie, W. A. 1969. The archaeology of Martha's Vineyard. National History Press, Garden City, New York.

Smith, T. I. J. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrhynchus,* in North America. Environmental Biology of Fishes 14:61–72.

Smith, T. I. J. 1990. Culture of North American sturgeons for fishery enhancement. NOAA Technical Report NMFS 85:19–27.

Smith, T. I. J, and J. P. Clugston. 1997. Status and management of Atlantic sturgeon, *Acipenser oxyrinchus,* in North America. Environmental Biology of Fishes 48:335–346.

Smith, T. I. J., D. E. Marchette, and G. F. Ulrich. 1984. The Atlantic sturgeon fishery in South Carolina. North American Journal of Fisheries Management 4:164–176.

Sulak, K. J., and J. P. Clugston. 1998. Early life history stages of Gulf sturgeon in the Suwannee River, Florida. Transactions of the American Fisheries Society 127:758–771.

Sulak, K. J., and J. P. Clugston. 1999. Recent advances in life history of Gulf of Mexico sturgeon, *Acipenser oxyrinchus desotoi,* in the Suwannee River, Florida, USA: a synopsis. Journal of Applied Ichthyology 15:116–128.

Van Eenennaam, J. P., and S. I. Doroshov. 1998. Effects of age and body size on gonadal development of Atlantic sturgeon. Journal of Fish Biology 53:624–637.

Van Eenennaam, J. P., S. I. Doroshov, G. P. Moberg, J. G. Watson, D. S. Moore, and J. Linares. 1996. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries 19:769–777.

Vorobyova, E. I., and K. P. Markov. 1999. Specific ultrastructural features of eggs of Acipenseridae in relation to reproductive biology and phylogeny. Journal of Ichthyology 39:157–169.

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. American Zoologist 21:325–343.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. Australian Journal of Marine and Freshwater Research 41:199–222.