Harvest and habitats of Atlantic sturgeon *Acipenser* oxyrinchus Mitchill, 1815 in the Hudson River estuary: Lessons for sturgeon conservation

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ABSTRACT

Conservation of the Hudson River population of the sturgeon Acipenser oxyrinchus Mitchill, 1815 has benefitted from the most intensive research programme on any population of the species. We review the history of the fishery for A. oxyrinchus in the Hudson River, and concisely summarise diverse research findings on its life history and habitat use. The fishery for A. oxyrinchus from the Hudson River had one period of very high harvest (pre-1900s), a long period (1900-1979) of minimal harvest and slow population recovery, a period (1980-1992) of restored abundance and high harvest, and finally another decline and suspension of fishing (1996). Sturgeon spawning and early juvenile development occurs in the freshwater portion of the Hudson River, whereas adult and large juvenile sturgeon occupy marine waters, and some of these fish will annually occupy low salinity sites in the Hudson River and other coastal rivers in summer. A. oxyrinchus of the Hudson River are genetically distinct from other populations associated with rivers along the Atlantic coast. Eight different habitats are used during the life cycle of Hudson River A. oxyrinchus, and these are described in physical and temporal terms. The history and biology of the Hudson River A. oxyrinchus suggest three lessons for sturgeon restoration: basic life history knowledge is essential, fishery management is difficult, and regular population monitoring will be needed from the start.

Key words: Fishery, life history, recovery.

RESUMEN

Explotación y hábitats del esturión atlántico Acipenser oxyrinchus Mitchill, 1815 en el estuario del río Hudson: lecciones para la conservación de los esturiones

La conservación de la población del río Hudson de esturión Acipenser oxyrinchus Mitchill, 1815 se ha beneficiado del programa de investigación más intensivo de los proyectados en la preservación de cualquier otra población de la especie. Se revisa aquí la historia de la pesca de A. oxyrinchus en el río Hudson y se resumen concisamente diversos hallazgos de investigación sobre su historia natural y uso del hábitat. La pesca de A. oxyrinchus en el río Hudson tuvo un periodo de muy alta explotación (antes de 1900), un largo periodo de mínima explotación y lenta recuperación poblacional (1900-1979), un periodo de restauración de abundancia y alta explotación (1980-1992) y, finalmente, otro declive y suspensión de la pesca (1996). La puesta del esturión y el desarrollo temprano de los juveniles tienen lugar en el tramo de agua dulce del río Hudson, mientras los adultos y los juveniles grandes ocupan aguas marinas; algunos de estos peces ocuparán anualmente, en verano, lugares de baja salinidad en el Hudson y en otros ríos costeros. La población de

A. oxyrinchus del río Hudson es distinta genéticamente de otras poblaciones asociadas con ríos a lo largo de la costa atlántica. Durante su ciclo vital, el A. oxyrinchus del río Hudson utiliza ocho diferentes hábitats, que son descritos en términos físicos y temporales. La historia y la biología de esta especie del río Hudson sugieren tres lecciones para la restauración de los esturiones: es imprescindible el conocimiento básico de la historia natural, la gestión de la pesca es difícil y el seguimiento regular de la población será necesario desde el principio.

Palabras clave: Pesca, historia natural, recuperación.

INTRODUCTION

Many sturgeon species throughout the world are threatened with extinction by overfishing and habitat loss (Birstein, 1993; Waldman, 1995; Birstein, Bemis and Waldman, 1997), and restoration efforts are being initiated to reverse some species declines and population losses. The sturgeon Acipenser oxyrinchus Mitchill, 1815 was once abundant in large rivers, estuaries, and marine waters along most of the Atlantic coast of North America. This valuable sturgeon has been greatly reduced by overfishing and alteration of essential habitat, such as the loss of spawning site access due to dams (Smith, 1985; Smith and Clugston, 1997; Waldman and Wirgin, 1998). A. oxyrinchus is now protected under one of the most complete and long-term management plans ever implemented for a fish species. The management goal is to restore the species to a safe level of abundance throughout its range. While the Hudson River population of A. oxyrinchus has been relatively abundant in the past, there is now good cause for concern about the status of this population.

The conservation of the Hudson River A. oxyrinchus population has benefitted from the most intensive research programme on any population of this species. Little stock-specific information was available until life history studies were performed in the 1970s and early 1980s. In the mid-1990s, a broad research effort by several university teams was funded and co-ordinated by the Hudson River Foundation for Science and Environmental Research. This research effort covered major aspects of the biology and management of Hudson River Atlantic sturgeon, including reproductive physiology, genetics, age structure and demographics, habitat use, behaviour, and fishery attributes. Our purpose in this paper is to review the history of the fishery for A. o. oxyrinchus in the Hudson River, and concisely summarise knowledge on its life history and habitat. This range of new and historic information is then used to identify key aspects of Atlantic sturgeon biology and management that should be considered when designing restoration efforts.

THE FISHERY

By the 1880s, the fishery for A. oxyrinchus had become well established in the Hudson River and along the Atlantic coast of New York and New Jersey. The total weight of sturgeon (A. oxyrinchus and the shortnose sturgeon Acipenser brevirostrum LeSueur, 1818) harvested was collected by each state for most years starting about 1880. The large size of commonly used gear (33-cm stretched mesh gill nets; Cobb, 1900) indicates that most of the harvest would have been adult A. oxyrinchus. The coastwide A. oxyrinchus fishery from 1880 through 1900 was large, with the total New York and New Jersey harvest reaching approximately 1 350 000 kg in 1890. Much of the total peak harvest for New Jersey should be attributed to the Delaware River stock (Secor and Waldman, 1999) but overall exploitation of Hudson River A. oxyrinchus was also high between 1880 and 1900 (table I). This large fishery for Hudson River fish apparently resulted in the removal of a major portion of the adults from the population, because the fisheries of New York, New Jersey, and all other coastal states with A. oxyrinchus populations collapsed after 1900 (Smith, 1985).

For eight decades after 1900, the *A. oxyrinchus* harvest was steady but very low (1 % of peak harvest) along the US Atlantic coast (table I). Fishery harvest data for the Hudson River population are lacking, but the total New York and New Jersey harvest from 1900 through 1979 suggests little effort

Table I. History of the fishery for *A. oxyrinchus* in the coastal waters of New York, New Jersey, and the Hudson River, based on statistics and plans of national and state fishery agencies. ⁽¹⁾: Atlantic States Marine Fisheries Commission (1990). ⁽²⁾: The New Jersey fishery closure was not implemented until 1997, due to the time needed to administer the regulatory action. ⁽³⁾: Atlantic States Marine Fisheries Commission (1998)

Years	Annual weight harvested (kg)	Composition of catch by life stage	Description of fishery and management Period of a developing fishery, peak harvest, and no fishery regulations. A substantial but unknown portion of the reported harvest includes fish from the Delaware River population and <i>A. brevirostrum</i> that occupied coastal sections of large rivers			
1880-1900	900 000-1 350 000	Primarily large adults				
1900-1979	6 500-13 500	Presumably adults and juveniles	Extended period of very low but stable harvest. Harvest is expected to have been largely Hudson Rive fish			
1980-1992	10 000-125 000	Largely juveniles	Period of a redeveloping fishery focused entirely on Hudson River fish. Fishery restrictions were a minimum total length of either 107 or 122 cm (New Jersey, New York) with some gear restrictions			
1993-1995	13 600-23 000	Largely juveniles	Three years of varied fishery restrictions aimed at reducing harvest to meet targets of the <i>A. oxyrinchus</i> fishery management plan ⁽¹⁾ that had a goal of halting the continued decline of the species in US waters			
1996-present	O (1)	None ⁽²⁾	The Atlantic States Marine Fisheries Commission requested an emergency moratorium on harvest of <i>A.</i> <i>oxyrinchus</i> and New York and New Jersey ⁽²⁾ closed their sturgeon fisheries. Later, the fishery moratorium were changed to a long-term closure for all <i>A. oxyrinchus</i> fisheries in US waters ⁽³⁾			

was devoted to catching sturgeon or there were few fish available for harvest. The low catches (table I) for New York and New Jersey likely reflected a persistent but small Hudson River population, because the Delaware River would have contributed few, if any, fish to the catch. The Delaware River fishery of southern New Jersey had collapsed by 1900 (Secor and Waldman, 1999) and very few Atlantic sturgeon were being recorded from that river. Therefore, the period from 1900 through 1979 appears to be a time when Hudson River Atlantic sturgeon attracted little commercial interest, and the reported catch likely came from a variety of gears targetting many species and as bycatch landing a mix of adults and juveniles.

The first good evidence of a recovery of the Hudson River population came one century after the initial pronounced exploitation of the population. Interestingly, Secor and Waldman (1999) predicted from the analysis of the Delaware River fishery and *A. oxyrinchus* population characteristics that recovery from overexploitation would likely require a century. During the 1980s, the *A. oxyrinchus* harvest in New York and New Jersey increased to a

level about 10 times the longterm harvest of the 1900s. Fishery regulation was weak, and permitted the harvest of juvenile fish (table I); again, records of harvest were limited to total weight landed. Harvest of *A. oxyrinchus* in the State of Delaware remained negligible during the 1980s, indicating that the Delaware River contributed little or nothing to the increased New York and New Jersey harvests. By the early 1990s, fishing for *A. oxyrinchus* clearly became a significant activity, and the increased harvest attracted the serious attention of fishery management agencies.

In 1990, the Atlantic States Marine Fisheries Commission (Anon., 1990) developed an *A. oxyrinchus* sturgeon fishery management plan that aimed to restore the species to a level that could support a fishery with a coastwide harvest totaling 10 % of the peak harvest, in 1890. The 10 %-of-peak goal was a management criteria, and not a product of population analyses. The Hudson River population appears to have been producing a harvest at about this 10 % level. The highest landings of the late 1980s (125 000 kg for New York and New Jersey combined, table I) approached 10 % of the peak 1890 harvest, and this regional-scale harvest is known to have included primarily Delaware River fish. To achieve the fishery management goal for all US populations, the A. oxyrinchus management plan specified that each state adopt one of three options: halt all A. oxyrinchus harvest, impose a minimum harvest size of 213 cm total length to restrict harvest to adults, or implement fishery restrictions expected to be equivalent to a 213 cm minimum total length. Both New York and New Jersey selected the latter option, and proposed fishery management restrictions aimed at controlling harvest to about 7 000 kg per year, or 229 fish for each state. All other states banned A. oxyrinchus fishing. In 1993, New York and New Jersey attempted to meet their harvest target with a 152 cm total length minimum size and limited fishing seasons. Harvest was reduced by these regulations in 1993, but in 1994, the New York harvest was 16 201 kg and 895 fish: more than double the intended harvest by weight and about four times the target number of fish (Anon., 1995). The New Jersey fishery harvest was similarly excessive (B. Andrews, pers. comm.) (New Jersey Department of Environmental Protection). Also, the fishermen were harvesting mostly juvenile A. oxyrinchus, since almost all of the catch was under 213 cm total length. Additional fishery restrictions were imposed in 1995 by both states; however that year, research findings for the Hudson River population clearly indicated that recruitment failure had occurred (Peterson, Bain and Haley, 2000).

In December 1995, the Atlantic States Marine Fisheries Commission convened a meeting of sturgeon researchers and fishery managers to assess the situation. This meeting resulted in emergency closures of Atlantic sturgeon fisheries (Anon., 1996a, b). Later, an amendment of the A. oxyrinchus fishery management plan (Atlantic States Marine Fisheries Commission) imposed a long-term ban on A. oxyrinchus harvest. The amendment stated that "The 1990 fishery management plan simply did not contain conservation measures sufficient to protect the portion of the [A. oxyrinchus] population and individual spawning stocks remaining at the time" (Anon., 1998). The key objective of the amended plan is to establish 20 protected yearclasses of females in each spawning stock, and it was estimated that 40 years would be required to attain this objective. The actions of the Commission were made largely in response to the effect of fishing on Hudson River A. oxyrinchus, since this was the only population being harvested in a targeted fishery during the 1990s. The Commission's decision ended a century of marginal sturgeon fisheries, with one brief period of peak harvest that appears to have halted the recovery of the Hudson River sturgeon population.

THE HABITAT

The Hudson River

A. oxyrinchus is limited to the tidal portion of the Hudson River, between New York and the Troy Dam (figure 1). Limburg, Levin and Brandt (1989) describe the Hudson River and its estuary in detail, and selected data from their work are provided here to define the available river and estuary habitat of A. oxyrinchus. The average width of the river is 1 280 m (range 260 to 5 520 m), maximum depth is 35 m, and tidal flow (5670-8500 m³/s) far exceeds river discharge (mean 623 m³/s). Average water temperature is 12.3 °C, and nutrient levels are high due to sewage inputs from the New York City metropolitan area and several other significant urban areas. The salt front commonly reaches river km 100 in the summer and early autumn, and during periods of high river discharge the salt front can be as far downriver as km 32. The river channel was formed by glacial scouring, so much of the shoreline is rock and channel depths are greater than would result from typical fluvial processes.

Life cycle of Hudson River A. oxyrinchus

Hudson River A. oxyrinchus are amphidromous (diadromous fish that move between fresh and sea water for reasons beyond reproduction; McDowall, 1992), because spawning and early development occurs in the freshwater portion of the Hudson River, whereas adult and large juvenile sturgeon occupy marine waters, and some of these fish will annually occupy low salinity sites in the Hudson River and other coastal rivers in summer. After spawning in freshwater habitat, adults may go to the sea or remain in the lower river until early autumn, when they move to marine waters. Larvae are believed to remain in the freshwater portion of the river and gradually move downstream during the summer and autumn (Dovel and Berggren, 1983). This

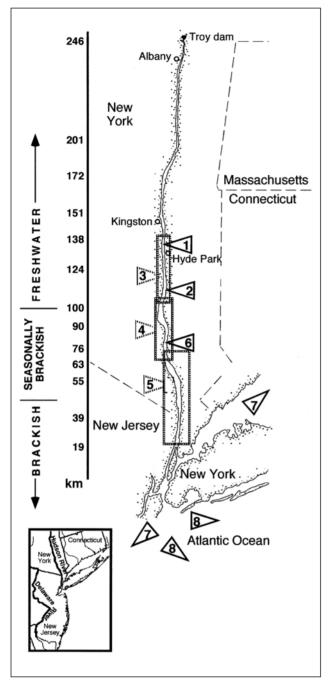


Figure 1. Map of the tidal portion of the Hudson River, showing *A. oxyrinchus* habitats. Numbers in the symbols correspond to the numbered habitats described in table II, and reviewed sequentially in the text

movement may be governed by the development of salinity tolerance in young *A. oxyrinchus*, as suggested by studies of salinity tolerance in other sturgeon species (McEnroe and Cech, 1987). Juvenile *A. oxyrinchus* grow rapidly in the Hudson River, exceeding 70 cm total length (63 cm fork length) by 3 years of age (Stevenson, 1997). Juvenile sturgeon

of this size and age begin migrating to marine waters (Bain, 1997), and Dovel and Berggren (1983) concluded that all or most age 6 or younger sturgeon are marine migrants. These marine migrant juveniles have been observed to move back into coastal river systems during summer (Smith, 1985; Keiffer and Kynard, 1993), and one location in the Hudson River supports marine migrant juveniles (> 63 cm fork length; > 70 cm total length), adults, and fish that had spawned earlier in the same year (figure 1). Male and female Hudson River A. oxyrinchus reach maturity at 117 and 173 cm fork length (133 and 197 cm total length) and ages 12 and 14, respectively (Van Eenennaam et al., 1996; Van Eenennaam and Doroshov, 1998). Using optical and chemical analyses of fin rays and otoliths, Stevenson (1997) estimated that females spawn once every four years, whereas males are thought to spawn every year (Vladykov and Greeley, 1963).

Distribution of the population

Hudson River A. oxyrinchus are genetically distinct from other populations associated with rivers along the US Atlantic coast (Waldman et al., 1996). Waldman, Hart and Virgin (1996) used data from mitochondrial DNA restriction fragment length polymorphism analysis to estimate the relative contributions of different populations of Atlantic sturgeon to the New York Bight fishery in 1993 and 1994. The New York Bight includes coastal waters of New Jersey and New York (figure 1), and this region is in the middle of the A. oxyrinchus range. The results of Waldman, Hart and Wirgin (1996) indicate clearly that the sturgeon fishery in the New York Bight is supported overwhelmingly by individuals from the Hudson River population. Dovel and Berggren (1983) tagged A. oxyrinchus in the Hudson River, and recovery of tags indicated that the Hudson River sturgeon range extends from about just north of Cape Cod (Massachusetts) to Cape Hatteras (North Carolina). In the 1800s, sturgeon in this region included substantial numbers of fish from spawning populations in the Delaware River and the rivers of Chesapeake Bay. The nearly complete dominance of Hudson River A. oxyrinchus in the recent New York Bight fishery suggests that the other populations are now negligible. On a regional scale, the habitat of Hudson River A. oxyrinchus includes marine waters, estuaries, and rivers from Massachusetts to North Carolina, and in this region the Hudson sturgeon dominated the fishery catch.

Spawning habitat

Hudson River A. oxyrinchus were documented as using two spawning sites during our field studies from 1993 through 1998. The major spawning site was located in Hyde Park, New York at river km 134 (table II). This site has been known since the 1880s, when it was a major fishing location. The spawning habitat is along one side of the river (figure 1), among rock islands with irregular bedrock and substrate of silt and clay. The location is freshwater year round, with water depths ranging from 12-24 m. Mature male fish were captured in this habitat from late May through the end of June, with spawning occurring mostly in June. During 1994 and 1995, many fish were captured at the time of spawning (water temperatures 14-24 °C) with gill nets, and mostly male sturgeon were tagged with sonic transmitters.

Sonic-tagged male sturgeon revealed a second spawning site located at river km 112 (figure 1). Again, the site was located along one side of the river, in water 21-27 m deep with clay, silt, and sand substrate. The habitat was in freshwater, and used for spawning in mid-July at water temperatures around 26 °C (table II). Gill nets set at the time the habitat was occupied by sonic-tagged fish revealed ripe males and females, confirming the site as an active spawning location. No other spawning sites were indicated by sonic-tagged fish in 1994 and 1995, suggesting that these sites were the only ones being used by the Hudson River population.

Larval rearing habitat

Eggs of Atlantic sturgeon are adhesive, and the larvae remain on the bottom in deep channel habitats. Atlantic sturgeon larvae are about 7 mm total length at hatching, and in hatcheries they reach 19.9 mm total length in 20 days (Smith, Dingley and Marchette, 1980). We estimate water temperatures in habitats used for spawning would have been 19-28 °C, from observations of other life stages (table II). The transition from the larval stage to juveniles appears to occur at about 30 mm total length, based on Hudson River specimens (Bath *et al.*, 1981). *A. oxyrinchus* larvae have been recorded in the Hudson River from river km 60 through 148 (Dovel and Berggren, 1983), a range including some brackish waters (figure 1). However, larval sturgeon have limited salt tolerance, so larval habitat must be well upstream from the salt front (Van Eenennaam *et al.*, 1996). No further information is available on this stage of the *A. oxyrinchus* life cycle. Therefore, we presume that the preferred habitat for larval *A. oxyrinchus* is near the spawning habitat, with larvae extending downstream as they grow and attain the ability to endure brackish water (table II).

Early juvenile rearing habitat

Juvenile A. oxyrinchus less than 70 cm total length (63 cm fork length) and 6 years of age occupy summer rearing and overwintering habitats in the Hudson River. The summer growing season habitat was well described by dispersed gill-net sampling in the entire tidal river during 1995 and 1996 (Haley, 1999). From April through October, early juvenile A. oxyrinchus were primarily found between river km 68 and 107 at water temperatures 24-28 °C (figure 1). This is the highland gorge and wide estuary sections (Coch, 1986) of the Hudson River, where the transition from freshwater to brackish water is found. Juvenile sturgeon were most often captured in salinities ranging from 0-5 ppt (table II). Water depths associated with most captures ranged from 10-25 m, and the substrates were primarily silt and sand.

Early juvenile wintering habitat

The winter habitat of *A. oxyrinchus* has been defined by Dovel and Berggren (1983) from trawl and gill-net sampling between 1975 through 1978. When water temperature in the river reaches 9 °C, most juveniles that have not migrated to the sea congregate in a deep-water habitat between river km 19 and 74 (figure 1). Water temperatures during winter could reach 0 °C in this portion of the Hudson River. Salinity in this region ranges from 3-18 ppt, and water depths in the channel commonly range (navigation maps) from 20-40 m (table II).

Table II. Review of the life stages and habitats of Hudson River A. oxyrinchus from field data and observations from 1993
through 1998 and some past studies. Map code numbers refer to locations identified in figure 1. ⁽¹⁾ : Inferred from water tem-
perature at spawning sites and the expected hatching period

Map code	Life stage	Time period	Locations (river km of notes)	Water temperature (C)	Salinity (ppt)	Water depth (m)	Bottom material	Source of information
1	Spawning	Late May and June	134	14-24	0	12-24	Rock clay silt	64 gill-net sets from late May through mid-August. 59 adult fish recorded from late May through the end of June. Historic site
2	Spawning	Mid-July	112	26	0	21-27	Clay sand silt	Site was identified from sonic telemetry of adult fish that congregated in mid-July. Two gill nets captured 6 adult fish, including a spawning female
3	Larvae	June to August	Vicinity of spawning	19-28(1)	0	-	Clay silt	Little is known about larval habitat We assume that the habitat is close to the spawning sites
4	Early juvenile	April- October	68-107	24-28	0-5	10-25	Silt sand	166 gill-net sets captured 48 juvenile fish from June through early October. The habitat values reported are for the locations used by most (means \pm 1 one standard deviation) fish
5	Early juvenile	October- March	19-74	0-9	3-18	20-40	Clay sand silt	Dovel and Berggren (1983) describe the movement of non- migratory juveniles to the lower estuary from net and trawl sampling
6	Late juvenile and adult	June- September	78	20-26	0-6	16-35	Clay silt	Site was identified from sonic telemetry of 33 adult fish that congregated in mid-July. 80 gill-net sets recorded 171 fish that were largely marine migrant juveniles and adults, including post-spawner
7	Late juvenile and adult	May- October	Coastal waters and distant rivers	Unknown	Marine to brackish	30-40 at two coastal sites	Mud at two coastal sites	Hudson Atlantic sturgeon have been recorded at several very specific locations in coastal marine waters and in the brackish water portion of rivers from New Englan through the Chesapeake Bay. River sites are expected to be like habita 6 (above) in the Hudson River. Tw coastal sturgeon concentrations were sampled by trawling in Long Island Sound. 60 Atlantic sturgeon were captured by trawling in July, including tagged Hudson rish. No fish were at the sites in the late autumn
8	Late juvenile and adult	October- May	Marine waters	Unknown	Marine	Un- known	Un- known	We presume Atlantic sturgeon move to deeper and coastal waters further offshore during the winter. There is reliable data that adult and juvenile sturgeon are not found in brackish estuary sites (habitat 6) or shallow coastal sites (habitat 7) used in the summer. Offshore trawling b the US National Marine Fisheries Service has recorded Atlantic sturgeon in marine waters in winter

The river-bottom sediment maps of Coch (1986) show that most juvenile sturgeon habitats have clay, sand, and silt substrates.

Late juvenile and adult summer habitat

Marine migrant juvenile *A. oxyrinchus* are older than 6 years of age and longer than 70 cm. These fish use marine habitats during the winter, and rivers, estuaries, and coastal marine habitats in the summer. We believe that adults display the same migratory behavior as marine migrant juveniles, because our sampling of river and coastal concentrations of large sturgeon (>70 cm total length) recorded a mix of adults and juveniles. Accounts of concentrations of *A. oxyrinchus* larger than about 150 cm have been reported from other rivers, but the literature shows no thorough characterization of the size and life-stage composition of sturgeon in these habitats.

One of the summer brackish water habitats we have studied is in the Hudson River at river km 78 near Garrison, New York (figure 1). Here, the Hudson River is very narrow and deep. Sonictagged spawning sturgeon revealed this location when they congregated after spawning. Gill nets set at the location captured late juveniles, adults, and post-spawn tagged adult fish in 1994 and 1995, from June through the end of September. The habitat ranged from 0-6 ppt salinity, depending on river discharge, but the fish remained in the same habitat despite salinity variations. Water temperature varied from 20-26 °C, and water depth ranged from 16-35 m. The substrate in this habitat is clay and silt, with the shoreline composed mainly of rock.

Late juvenile and adult *A. oxyrinchus* from the Hudson River are also known to occupy similar habitats in other rivers. Dovel and Berggren's (1983) map of tagged Hudson sturgeon captures shows many fish in rivers of Chesapeake Bay and the Delaware River. There are also some accounts of concentrations of late juvenile and adult *A. oxyrinchus* in coastal marine waters during the summer. We inventoried two such habitats in Long Island Sound off the Connecticut coast in the summer and autumn of 1996. Sixty from 70-200 cm fork length were captured by trawling in mid-July, and one fish was tagged in the Hudson River. The habitat was 30-40 m deep with mud substrate.

Sampling in the autumn failed to capture sturgeon, so we assume that they left this habitat for their wintering areas.

Late juvenile and adult wintering habitat

No known habitats of marine migrant juvenile and adult Hudson River sturgeon support fish in the winter. Autumn captures of sturgeon leaving coastal areas and estuaries have been reported by fishermen in Chesapeake Bay, marine fishermen from New York and New Jersey, and some scientific investigations (e.g. Kieffer and Kynard, 1993). Winter trawling by the US National Marine Fisheries Service has recorded *A. oxyrinchus* in offshore marine waters, but this information has not been further investigated for its value in identifying winter habitats.

LESSONS FOR RESTORATION

Our review of the fishery and habitats of Hudson River A. oxyrinchus reflects the species's complex life history and the ineffective management of the population to date. Three fundamental lessons for sturgeon restoration emerge: basic life-history knowledge is essential, fishery management is difficult, and effective population monitoring will be needed. The Hudson River A. oxyrinchus recovered from severe overexploitation in the late 1800s and approximately reached a management goal, signalling successful restoration. This restoration was extinguished by rapid overexploitation, because management agencies and researchers were too late in understanding the situation. Future sturgeon restorations can avoid the thwarted success of the Hudson River population by implementing measures to address biology, management, and monitoring from the start.

The life cycle of *A. oxyrinchus* is complex, and a major Hudson River sturgeon research effort, involving many university and agency scientists, showed how difficult it can be to understand this species's complex behaviour and habitat use. Intensive research using expensive and labour-intensive techniques, such as telemetry and large-scale tagging, were needed to identify some key migratory behaviours and habitats. While one spawning site has been well known in the Hudson River for more than 100 years, the discovery of a

second site was a surprise, or a rediscovery of a forgotten location. The summer and early autumn congregation behaviour of marine migrant juveniles and adults in the rivers and coastal waters escaped past investigators, even though evidence for this behaviour can now be seen in past research results and reported observations. Fishery biologists know the critical importance of the details of life stages and growth rates, and this information was available, and enhanced in recent research. However, knowledge of movements and habitats were equally important for managing the Hudson A. oxyrinchus. The susceptibility of migrating juveniles to near coastal fisheries was not realised, because no one understood that immature fish have annual migrations in and out of the Hudson River and other estuarine systems. The nearly complete dominance of the coastal fishery by Hudson River sturgeon was not appreciated, so the concentrated harvest of one population was not clear.

Despite unprecedented research by many scientists in the 1990s, some key information remains unknown, such as male repeat spawning, sex ratio at spawning, precise winter habitats, larval biology, complementarity of adult migrations with large juveniles, and age or size on first marine outmigration. Present understanding of the marine movements of the Hudson River population are based mainly on recaptures of juveniles from one period of relative abundance in the late 1970s and early 1980s. This information is important, because long movements of adults and large juveniles can lead to exploitation in distant waters not linked to a restoration effort. Another complication of long movements and the annual use of distant rivers is the misunderstanding that the presence of sturgeon in a river or estuary indicates a local population. We now believe that the only reliable information indicating a population is the capture or confirmed records of numerous small (<70 cm total length) juveniles or adults in spawning condition. Our first lesson is that A. oxyrinchus conservation efforts need to place high value on understanding basic species biology. The Hudson River case shows that managers need to take a long look at what habitats are used by a population; be on the lookout for intrusions by disturbance or fishing in habitats with sturgeon concentrations; recognise that distant fisheries can impose significant harvest on a recovering population; and consider seriously the evidence for a river population when using historical observations.

A second lesson from the Hudson River is that fishery management proved more difficult than managers anticipated. We believe great caution and a protective philosophy should be fundamental to management planning. For Hudson A. oxyrinchus, regulations to control total weight harvested failed to protect the population. The actual harvest varied greatly in response to specific regulations, and it exceeded the intended levels. Second, fishery management was too slow, because over-intensive harvest of the recovering population occurred faster and with a major effect before fishery managers could react. The population was already greatly diminished by the time full knowledge of the situation became known through field studies. Finally, much of the harvest of the Hudson population occurred outside of the immediate river and estuary; for example, along the coast of New Jersey, where past harvests would have been attributable to other river populations. Overall, effective sturgeon population restoration will require very secure control of harvest over a large area, complete certainty in management objectives, and regulations that fully and directly protect juveniles (a high minimum size or strict gear specifications).

Our third lesson is mainly a consequence of the other two: population monitoring needs to be a central component of a restoration programme. In Waldman and Wirgin's (1998) review of options for restoration of North American A. oxyrinchus, they recommend that population-specific information is necessary to determine management measures. For the Hudson River A. oxyrinchus, managers might have been able to recognise that the population had recovered in time to protect it, if some monitoring had been underway. Also, population information at the start of the recovery could have signalled vulnerability and overharvest before overexploitation collapsed the population. In cases such as the European Atlantic sturgeon A. sturio, some populations have been extinct for so long that little or no retrospective information is available on population biology, habitats, and fishery harvest. For such cases, monitoring of the population under restoration will be needed to learn about the biology of and threats to the population as the restoration programme progresses. Information on the Hudson River A. oxyrinchus population used in concert with monitoring results regarding A. *sturio* populations can guide managers on potentially important sources of mortality, likely population range, life history properties, and probable key habitats. Our experiences show that knowledge of the species biology and fishery is critical, and for restoring *A. sturio* this knowledge will most likely come by learning while restoring; that is, monitoring from the start.

In future restoration efforts, managers should be aware that restoration will be attempted with many unknowns and potential impediments. Clearly successful population restoration will likely require many decades, so a long-term perspective must be built into programme planning. Comparative biological information for Hudson River *A. oxyrinchus* can serve to guide initial plans. The North American fishery experiences illustrate some threats to watch out for, and to avoid. Finally, close monitoring of restoration populations will be needed to recognise successes, failures, and threats as they emerge.

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