LIFE HISTORY AND POPULATION DYNAMICS OF LAKE STURGEON, Acipenser fulvescens, IN THE MUSKEGON RIVER, MICHIGAN

by

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(Under the direction of Douglas L. Peterson)

ABSTRACT

The lake sturgeon was once abundant throughout Lake Michigan with an estimated 11 million fish prior to human exploitation. By the early 1900s, however, most populations had been decimated by severe over-fishing and habitat degradation. Despite recent interests in restoring the species in Lake Michigan, little is known about the current status of remnant populations. The primary objectives of this study were to estimate annual spawning stock abundance and to identify potential spawning habitat for lake sturgeon on the Muskegon River, Michigan. To capture adult lake sturgeon, I used large-mesh, bottom-set gill nets deployed at the mouth of the Muskegon River from mid-March through May, 2002-2005. Radio telemetry was used to monitor seasonal movements and to identify likely spawning habitats. Sampling for larval lake sturgeon was conducted in May of each year using D-frame drift nets anchored in the mainstream of the river channel. During the 4 years of the study, I expended more than 5000 gill-net hours and captured 59 individual adult lake sturgeon. Larval lake sturgeon were captured in 2 years, suggesting that at least some natural reproduction still occurs. Habitat analysis revealed that the lower Muskegon River likely contains extensive reaches of potential spawning habitat for lake sturgeon.

INDEX WORDS: Biology, population dynamics, habitat, lake sturgeon, life history, radio telemetry, migration, over-exploitation

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Over-Exploitation and Anthropogenic Factors Leading to Lake Sturgeon *Acipenser fulvescens* Declines on the Great Lakes

Introduction

The indigenous tribes of North America were the earliest “fishermen” in the Laurentian Great Lakes and were well established by 5000 B.P. (Tody 1974, Bogue 2000). Their methods for harvesting fish included spears, gaffs, weirs, and primitive hook and line devices (Bogue 2000). In the lower Great Lakes, the earliest gill nets were probably in use by 4500 B.P., becoming widespread in the northern Great Lakes by 2300-2200 B.C. During this period, the primary species targeted were northern pike (*Esox lucsius*), walleye (*Sander vitreum*), lake herring (*coregonus* spp.), lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and lake sturgeon (*Acipenser fulvescens*) (Bogue 2000). For native peoples, populations of these fishes became a predictable food source that greatly affected their seasonal movements and patterns of settlement. Anthropologist Charles E. Cleland suggested that these prehistoric fisheries played a major role in the development of many regional cultures and for many species the spawning season was the period of greatest susceptibility to early fishing gears because large numbers of adult fish could typically be found in shallow coastal or riverine waters (Bogue 2000). Although several species were regularly harvested during their annual spawning migrations, perhaps none was more vulnerable and more sought after than the lake sturgeon. Easily accessible in their spawning tributaries, lake sturgeon were highly prized for both the quantity and quality of the meat they provided (Bogue 2000, Saffron 2002). Yet native peoples seem to have never over-fished lake sturgeon populations as the harvest was limited to only what was needed for local consumption (Bogue 2000).

Prior to European settling in North America, the lake sturgeon was abundant throughout its range, particularly in the Great Lakes region (Houston 1987, Hay-Chmielewski and Whelan 1997, Slade and Auer 1997). Tody (1974) estimated the standing crop of lake sturgeon in the Great Lakes prior to 1830 to be in the tens of millions of pounds. Sturgeon were utilized to varying degrees by several Indian tribes (Holzkamm and Waisberg 2004). The large size of lake sturgeon meant that a single individual could provide the equivalent of food as many smaller fishes. The oily flesh was easily smoked and preserved, therefore could be consumed at a later time (Bogue 2000). Harkness and Dymond (1961) stated that the Jesuit Relations contain numerous references concerning the exploitation of lake sturgeon by North American indigenous peoples. In his 1761 writings, Père Francis Xavier Charlevoix describes methods by which the Indians captured sturgeon.

The earliest published accounts of Great Lakes ichthyofauna are associated with 17th Century European explorers and fur traders who witnessed the region at a time when the surrounding landscape was still largely pristine (Bogue 2000). In 1624, Gabriel Sagard, described the size and number of lake sturgeon harvested as bycatch in commercial fisheries targeting lake trout and whitefish on Lake Huron (Bogue 2000). These early commercial fisheries dealt the first major blow to lake sturgeon populations throughout the Great Lakes, although prior to 1860 the species was regarded as “nuisance bycatch” and most were either used as pig feed, fertilizer, or discarded (Harkness and Dymond 1961). At Amherstburg, Ontario, dead sturgeon were routinely stacked on local docks and once dry, used to fire the boilers of steamboats on the Detroit River (Harkness and Dymond 1961, Scott and Crossman 1973). While sturgeon flesh has always been held in high regard in Europe (particularly eastern Europe) and Russia, early North American settlers considered lake sturgeon a trash fish. The sharp scutes of the small sturgeon and the weight of the large ones often tore nets to pieces (Tody 1974). Prior to 1860, the prevailing view among settlers was that lake sturgeon flesh was fit only for “natives” and that their roe was poor quality and of no value (Wing 1890).

In the decades following 1860, the popularity, and hence, the value of lake sturgeon grew rapidly as European demand for caviar exceeded commercial production from Atlantic sturgeon (*Acipenser oxyrinchus*) fisheries operating on the Delaware and Hudson rivers. Recognizing this, two enterprising German immigrants, Siemon and John Schacht, established the first dedicated lake sturgeon processing facility in 1868 (Bogue 2000, Saffron 2002). Located in Sandusky, Ohio, the new plant found a lucrative market for almost every part of the fish; flesh was smoked or sold fresh, eggs were processed into fine caviar, and even the swim bladder was used to produce isinglass, paint additives, and other commercial products (Scott and Crossman 1973). By 1872, the Ohio plant was processing 10, 000-18, 000 lake sturgeon annually (Milner 1874). Even the skin of the fish was tanned and made into rough leather. Caviar produced at the plant was shipped to overseas markets, mostly in Germany, where culinary appreciation of caviar sustained high profitability (Bogue 2000, Saffron 2002).

Once new markets for lake sturgeon products had been established, targeted commercial fisheries grew exponentially. During his survey of the Great Lakes in 1871-72, James Milner, a young biologist from Kenosha, Wisconsin, reported a commercial catch of 14,000 individual lake sturgeons taken in 85 separate pound nets set in the Lake Erie waters near Sandusky, Ohio (Milner 1874). The weight of that catch was nearly a half million kg, but this mark was soon eclipsed by even larger catches from numerous other fisheries stretching from Toledo, Ohio, to Green Bay, Wisconsin (Auer 1999, Bogue 2000). At the height of the fishery, Lake Erie's productive shoals were the greatest fishing grounds for lake sturgeon with annual landings in excess of 3 million kg between 1885-1889 (Scott and Crossman 1973, Smith and Snell 1889, Hay-Chmielewski and Whelan 1997, Bogue 2000).

The creation of new markets for lake sturgeon products, however, was only partly responsible for the rapid growth of the fishery during the last half of the 19th Century. By 1890, several technological advances had dramatically increased the efficiency of the fishing fleet. Among these was the steam engine, which facilitated the construction of large fishing vessels that could reach more distant fishing grounds. With larger vessels came new power winches that could lift larger and stronger nets. Soon after these improvements, the introduction of ammonia refrigeration led to a further acceleration in the exploitation of Great Lakes sturgeon (Bogue 2000). Although formal catch records are incomplete, Tody (1974) reported that in 1880, lake sturgeon landings in Michigan amounted to 2, 000, 000 kg. The boom in commercial sturgeon fishing created by these technological advances, however, was short lived. By 1890, the total Michigan landings had fallen to 600, 000 kg and by 1895 the total annual Great Lakes catch had declined to only 1, 000 kg despite a steady increase in fishing effort (Baldwin et al. 1979).

Although declines of Great Lakes lake sturgeon populations were obvious by 1900, little effort was made to conserve stocks. Once new markets for lake sturgeon products had been established, commercial fisheries grew rapidly (Auer 1999, Auer 2004). By 1925, lake sturgeon had become the most valuable commercial species in the Great Lakes, but by this time many stocks had already collapsed (Tody 1974, Auer 1999). The basin-wide collapse of sturgeon stocks made for increasingly more stringent fishing regulations. The statistical agent for the 13th Biennial Report of the Michigan State Board of Fish Commissioners (1899) recommended that taking of small sturgeon be stopped and that the use of unbaited snag-lines be prohibited (Auer 1999).

By 1928, commercial harvest of lake sturgeon had been banned throughout the Great Lakes except for a limited fishery that has persisted in the Canadian waters of lakes St. Clair and Huron (Auer 1999). The U.S. ban on commercial fishing for lake sturgeon has remained in effect to the present, except for a limited re-opening of the fishery from 1950-1970 in the Michigan waters of Lake Michigan. The closure of the fishery was too little, too late; however, even these efforts were not completely effective in halting lake sturgeon declines as many fish were still harvested as incidental by-catch for many ensuing decades (Priegel and Wirth 1974, Baker 1980, Auer 1999).
In 1950, the commercial lake sturgeon fishery was reopened in Michigan waters of Lake Michigan, but close monitoring showed that stocks were in poor condition and the ban was re-imposed in 1970 (Auer 1999). Since 1994, the lake sturgeon has been listed as threatened by the Michigan Department of Natural Resources (MDNR) under the Michigan Endangered Species Act, and today, lake sturgeon are protected from commercial harvest in all U.S. waters of the Great Lakes (Auer 1999, Hay-Chmielewski and Whelan 1997, Auer 1999, Leonard et al. 2004).

The rapid boom and bust cycle of commercial lake sturgeon fisheries in the Great Lakes was typical of the many smaller inland fisheries operating in both the US and Canada (Harkness and Dymond 1961). On the Mississippi River for example, commercial landings declined from 113,046 kg in 1894 to 55,842 kg in 1899 - a decline of about 50% in only 5 years. By 1922, annual harvest had declined to only 3,178 kg; and by 1931, lake sturgeon had disappeared completely from the commercial catch (Carlander 1954). A similar scenario unfolded in Canada where most inland populations suffered similar declines during the first decade of the 20th century, although careful management and conservation have allowed a few limited fisheries to continue (D. Noakes, personal communication).

Habitat Degradation

Although over-fishing is likely the primary cause of lake sturgeon declines throughout North America, widespread construction of dams has been a major factor limiting recovery of most Great Lakes stocks (Auer 1996, 1999, 2004, Wilson and McKinley 2004). Impoundments on most spawning rivers have affected all life stages of lake sturgeon (LaHaye et al. 1992, Auer 1996, Chiasson et al. 1997, Cooke et al. 2002). Spawning success of migrating adults probably has been the most severely affected, as dams have blocked access to spawning grounds on virtually every major spawning tributary (Hay-Chmielewski and Whelan 1997, Smith and Baker 2005). While some stocks may exhibit reproductive success downstream of dams (Bruch 1999, Bruch and Binkoski 2002), there is no question that natural reproduction has been severely diminished by the loss of spawning habitat resulting from the numerous impoundments on spawning rivers (Auer 1996, Chiasson et al. 1997, Auer 1999, Noakes et al. 1999). In fact, the vast majority of historic lake sturgeon spawning habitat within the Great Lakes is now located in high-gradients areas of rivers now located at the bottom of deep reservoirs (Hay-Chmielewski and Whelan 1997).

Because lake sturgeon require swift water with coarse cobble or gravel substrates for spawning (Ferguson and Duckworth 1997, Peterson et al. 2003), any alteration or development of riverine habitats that affects the natural flow regime will likely have a negative impact on reproductive success. Unfortunately, the best locations for construction of a hydroelectric facility are the highest gradient reaches where maximum hydraulic head can be created. Construction of dams at these sites often eliminates access to the most important spawning sites for many lake sturgeon populations (Auer 2004).

While access to spawning sites may be less of a problem when impoundments are situated upstream of suitable spawning habitat, changes in flow and temperature regime caused by dam operation may severely impact spawning success (Auer 1996, Cooke et al. 2002, Jager et al. 2002). While specific cause-effect relationships are difficult to prove, several studies have shown that timing of spawning may be correlated with altered flow and temperature regimes resulting from hydroelectric operations (Auer 1996a, Pringle et al. 2000). These impacts may become especially severe, when hydroelectric facilities manipulate downstream flows to accommodate daily peaks in demand for electricity - a process frequently referred to as “peaking” (Auer 1996). In Wisconsin, for example, several researchers have noted that during periods of low demand, generation turbines may be shut down, resulting in a rapid reduction in flow that can actually cause dewatering and subsequent desiccation of developing embryos (Auer and Baker 1999, Bruch and Binkowski 2002). Conversely, periods of peak generation may trigger high water conditions that scour lake sturgeon embryos from spawning substrates (Duckworth et al. 1992). Ultimately, the ecological effects of hydroelectric peaking for spawning lake sturgeon are those of rapidly repeating drought and flood conditions.

Another major problem for lake sturgeon spawning in an impounded river is the loss of suitable spawning substrate that results from sediment starvation below a dam (Auer 1996, Auer 1999). Because dams physically block downstream transport of gravel and cobble bed materials required for successful spawning. These materials are not replenished once they are washed downstream during flooding (McKinley et al. 1998, Duckworth et al. 1992). Eventually, substrate in high gradient spawning areas becomes dominated by clean bedrock that is unsuitable for lake sturgeon spawning (Maser and Sedell 1994, McKinley et al. 1998).

Depending on the specific hydrological and geological conditions of the watershed, loss of suitable spawning habitat may become the most significant factor limiting the population recovery. Although studies of remnant lake sturgeon populations in the Great Lakes have only been attempted recently (Auer 1996, 1999, Auer and Baker 2002, Peterson et al. 2002), researchers have demonstrated that spawning in these remnant populations may be limited to a single site with only a few square meters of suitable substrate available for egg deposition (Peterson and Vecsei 2005). Dams further impact lake sturgeon by fragmenting populations into smaller, reproductively-isolated subpopulations (Anders et al. 2001, 2002, Jager et al. 2002, Secor et al. 2002). Although the impacts of population fragmentation have not been well studied, the associated loss of genetic variation may render such populations more susceptible to future environmental stressors (Ferguson and Duckworth 1997).

Other Threats

Despite loss of spawning habitat throughout the Great Lakes, lake sturgeon have been protected in all US waters since 1970 and recent studies have documented at least some successful reproduction in several tributaries (Auer and Baker 2002). These same studies, however, also show that most of these stocks are small with annual spawning migrations consisting of fewer than 100 adults (Auer and Baker 2002, Peterson et al. 2002). One possible explanation for this apparent contradiction may be the persistence of chronic anthropogenic factors unrelated to harvest. As the number of studies on Great Lakes sturgeon has increased in recent years, several researchers have documented a variety of human activities that result in disturbance or even mortality of both adult and juvenile lake sturgeon, particularly in spring, when adults and young-of-year can be found in shallow waters of their natal river systems. On the Detroit River, for example, Caswell et al. (2004) reported 5 adult sturgeon killed over a 2-year period by propeller strikes of large ships. While this may not be surprising considering the level of shipping activity in the Detroit River, a similar incident was documented in the Muskegon River in 2004, when local anglers recovered a freshly killed adult sturgeon in the swirling prop wash of a large freighter. Subsequent examination by fisheries biologists revealed that the fish was a 55-kg, age-28, female killed by a single laceration at the base of the skull that had nearly severed it from the body (Peterson and Vecsei 2004). Despite the somewhat anecdotal nature of these incidents, they suggest that mortality of adult lake sturgeon resulting from propeller strikes is yet another unquantified source of mortality affecting at least some Great Lakes populations.

Chemical contaminants are ever present throughout the Great Lakes watershed because of heavy industry. Although few North American researchers have examined the effects of chemical contamination on sturgeon physiology, Russian scientists have shown that chemical contaminants can have severe physiological effects in Caspian Sea sturgeons. These may include gonad re-absorption, pathological gametogenesis, and functional abnormalities in the liver, gills, spleen and kidneys (Altufiev et al. 1999). At present, information on contaminant exposure and uptake on lake sturgeon is limited; Doyon et al. (1998) described fin and craniofacial malformations linked to possible chemical contaminant effects.

Due to their life history characteristics of benthic feeding, late maturation, and long life span, lake sturgeon may be particularly susceptible to the bioaccumulation of persistent environmental contaminants (Ruelle and Keenlyne 1993). Within the Great Lakes, several chemical contaminants have been detected in the tissues of lake sturgeon including mercury, PCBs, DDT, and other organochlorine compounds (Hay-Chmielewski and Whelan 1997). While the population-level effects of these contaminants remain uncertain, they pose yet another challenge to lake sturgeon restoration.

Science of managing long lived, slow maturing fish populations

The lake sturgeon is a long-lived species characterized by slow growth and late maturity. While fecundity is high, recruitment can be infrequent or variable due to spawning periodicity and high mortality in young-of-year (Secor and Waldman 1999). The life history adaptations of lake sturgeon have made them particularly vulnerable to excessive mortality and stock collapse. Fisheries managers are aware of the unusual K-selected life history traits of lake sturgeon, having adaptations suited for: a) stable environments (biomass of population largely consisting of adults, delayed maturity, large adult size, extended spawning periodicity, altricial young, and rapid early growth; and b) unstable environments (complex age structure, high fecundity, and reproductively active for many years) (Van Eenennaam et al. 1996, Secor and Waldman 1999). Recovery is typically measured in decades (Boreman 1997, Bruch 1999) since age-at-mean replacement in sturgeon is up to 30 years (Secor and Waldman 1999). However, the lake sturgeon’s ability to produce up to 2 million eggs could help promote recovery rates if adequate spawning and nursery habitats are available (Secor and Waldman 1999). But lag time between strong year classes and their entry into the adult population requires 11 to 18 years (see chapter 3), depending on location and stock characteristics (Harkness and Dymond 1961)

Requirements for lake sturgeon management

With the exception of fisheries closures, there has been little done regarding lake sturgeon management until recently. State and federal agencies realized that to make sound management decisions and begin rehabilitation of remnant stocks, more data were necessary. Of particular importance was the need for in-river stock assessments. The lack of current and historic data for Michigan watersheds has limited the Michigan Department of Natural Resources' ability to manage depleted lake sturgeon stocks. Rivers are the spawning habitat for lake sturgeon and the nursery grounds for young-of-year, so river assessments are a first step to obtain data necessary for future rehabilitation attempts.

Limited information exists concerning the historic distribution and abundance of lake sturgeon in Michigan. A comprehensive review of records prepared by early surveyors would enable us to refine estimates of historic ranges overall and within watersheds. Old records and survey notes can also help identify historic lake sturgeon spawning areas. Existing spawning sites need to be identified and characterized. To protect critical life history stage habitats, more research should be focused on sub-adults, and young-of-year. Recently, studies on larval drift have been undertaken (Smith and King 2005) but these efforts were for an artificially landlocked population. While many rivers historically used by spawning lake sturgeon are dammed, there are few fishways intended for their use. It is also essential that lake sturgeon moving downstream from spawning, rearing, and feeding habitats be able to use fishways successfully.

The only U.S. state with a large, self-sustaining population of lake sturgeon is Wisconsin. The Lake Winnebago fishery has been regulated since 1903, with both the sturgeon population and harvest being carefully monitored since 1942 (Schneberger and Woodbury 1946, Priegel and Wirth 1978, Folz and Meyers 1985). Information obtained during the annual catch surveys were used to better understand lake sturgeon population dynamics (Bruch 1999).

Bruch (1999) summarized the regulatory and management actions taken in the Winnebago System and examined the current status of the population. The benefit of having historical population and harvest assessment is that the influence of regulatory, anthropogenic, or environmental factors on population dynamics can be better understood.

Unlike any other lake sturgeon fishery in the United States, Lake Winnebago has undergone an evolving, adaptive management-type program that has shown adaptability to address ever changing issues (Bruch 1999).

Study objectives

Lake sturgeon populations in the Lake Michigan watershed were estimated to number in the hundreds of thousands (Hay-Chmielewski and Whelan 1997). Since the mid-nineteenth century, over-exploitation and habitat loss have resulted in a substantial decline or collapse of stocks (Ferguson and Duckworth 1997, Auer 1999, Bogue 2000, Auer 2004). Today, these populations are approximately 1% of their historic size (Hay-Chmielewski and Whelan 1997). In response to this decline, the Michigan Department of Natural Resources listed lake sturgeon as a state threatened species (Section 36505 (1a), Part 324, Endangered Species Protection, of Act No. 451 of the Public Acts of 1994) (Hay-Chmielewski and Whelan 1997).

My work reviews the historical over-exploitation and loss of habitat that is believed largely responsible for the current state of lake sturgeon stocks in Lake Michigan. The objectives of my study were:

1. Establish life history and population dynamics data for lake sturgeon in the Muskegon River, Michigan; and
2. Quantify lake sturgeon spawning sites throughout the Muskegon River.

The results of my research will help the Michigan Department of Natural resources decide the course of action required to better manage the Muskegon lake sturgeon stock. My research could also help fisheries managers throughout the Great Lakes better understand the unique life history attributes and habitat requirements of long-lived species such as the lake sturgeon. Ultimately, my dissertation is a step towards the ultimate goal of the Michigan Department of Natural Resources, which is to conserve and rehabilitate self-sustaining populations of lake sturgeon to a level that will permit delisting as a threatened species.

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Chapter 2

Ecology and Biology of the Lake Sturgeon, *Acipenser fulvescens*

Abstract

The lake sturgeon is a large Acipenserid that was once common in most inland rivers and lakes of the U.S. and Canadian Midwest. World demand for caviar and sturgeon meat led to a dramatic rise in fishing and subsequent decline in lake sturgeon populations throughout much of its range. Along with overfishing, lake sturgeon populations have been negatively affected by habitat degradation and loss. Recruitment factors and early life history are poorly understood. Today, renewed interest in lake sturgeon restoration has led to numerous state and federally-funded research activities. Research has focused on identifying and assessing the size structure of remnant stocks, the availability of spawning habitat, and factors affecting reproductive success. Additional studies are needed to improve hatchery techniques, to better understand recruitment mechanisms, and how genetic diversity among and within meta-populations may affect long-term recovery of depleted populations.

Introduction

The lake sturgeon (*Acipenser fulvescens*) is a large, cartilaginous, benthic fish, endemic to larger mesotrophic and oligotrophic systems of the Central U.S., Laurentian Great Lakes, and the Hudson Bay drainages of Canada (Harness and Dymond 1961, Scott and Crossman 1973). Its life history, characterized by long life span, late age-at-maturity, and protracted spawning periodicity, is unique among North America's freshwater fishes (Harkness and Dymond 1961, Scott and Crossman 1973, Becker 1983). Although once abundant throughout its range, severe overfishing in the late 1800s and early 1900s decimated most populations (Auer 1999, 2004, Bogue 2000). Today, few healthy populations remain and many anthropogenic factors continue to hamper most conservation and restoration efforts (Noakes et al. 1999, Auer 2004, Wilson and McKinley 2004). Among these factors, hydroelectric dams that obstruct upstream access to historic spawning grounds and degrade critical downstream habitats by altering the flow regime are the most problematic (Auer 1996a, Wilson and McKinley 2004). Currently, the lake sturgeon is listed as extirpated, endangered, threatened, or of special concern in 12 U.S. states (Leonard et al. 2004, Holey and Trudeau 2005).

The unique appearance and life history of the lake sturgeon has generated considerable interest among many fisheries scientists (Jollie 1980, Findeis 1997). Since 1989, five separate international symposia have focused on the biology and management of lake sturgeons and other imperiled sturgeons. As many fisheries managers have become increasingly concerned with the conservation of endemic species in recent years, renewed interest in lake sturgeon has spurred several new research or restoration initiatives. Although these and many previous studies have improved our knowledge of lake sturgeon life history and population dynamics, the phylogeny of all sturgeon species, including that of lake sturgeon, remains unclear (Bemis et al. 1997, Findeis 1997, Birstein et al. 2002). In this paper, I describe several key taxonomic characters of lake sturgeon as they relate to sturgeon phylogeny. Furthermore, I synthesize existing studies of life history as well as current population status and management efforts.

Taxonomy and systematics

The oldest sturgeon fossils date to the Upper Cretaceous; however, the earliest members of the group probably evolved in the Lower Jurassic, approximately 200 million years ago (Bemis et al. 1997). Although sturgeon phylogeny remains somewhat uncertain, most taxonomists agree that Acipenseriformes is a monophyletic group, derived from the paleonisciform fishes (Bemis et al. 1997). In recent years however, ichthyologists have developed conflicting theories regarding phylogenetic relationships within the group, particularly within the *Acipenser* genus. For example, Birstein et al. (2002) questions the monophyly of the group and claims that current members of the genus do not share a single synapomorphic molecular character, which suggests multiple evolutionary lineages. Findeis (1997) proposed a similar argument and noted the absence of shared osteological characters within the genus. Regardless, investigators have noted an array of common morphological characters shared by all members of the genus including: 1) a disconnected gill membrane attached at the isthmus; 2) a small, downward-projecting, transverse mouth; 3) a long flattened stout that is either conical or narrow; 4) a set of four cylindrical or fimbriated barbells; a palatoquadratum connecting the symplecticum; 6) a stylohyale articulating with the posterior section of the symplecticum; 7) a linear arrangement of the palatoquadratum and the upper part of the maxillae; 8) and clustered basihyalia positioned along the median line of the rostrum (Antoniu-Murgoci 1936a,b, 1942).

Regardless of phylogenetic uncertainties, the Acipenseridae is comprised of 27 species distributed among four separate genera. The largest of these, *Acipenser*, contains 17 species, five of which are native to North America (Scott and Crossman 1973, Grande and Bemis 1996, Bemis and Kynard 1997, Findeis 1997). Among North American *Acipenser* species, only the lake sturgeon completes its lifecycle entirely within freshwater (Vladykov and Greeley. 1963, Auer 1996 b, Vecsei and Peterson 2004). As such, its evolutionary history and relationship among other members of the genus has been of particular interest.

Ontogenetic changes in lake sturgeon morphology have prompted many early investigators to suggest that *A. fulvescens* is actually composed of several discrete species (Harkness and Dymond 1961, Priegel and Wirth 1971). During the 19th and early 20th centuries, at least 17 different scientific names have been assigned to the various *Acipenser* populations of the Great Lakes, St. Lawrence, and Central U.S. (Scott and Crossman 1973). By the 1950s, ichthyologists had determined that these stocks all belonged to a single species. Following the rules of nomenclature, the oldest scientific designation, *Acipenser fulvescens* (Rafinesque 1817), has since been accepted as the valid scientific name (Harkness and Dymond 1961, Vladykov and Greeley 1963, Scott and Crossman 1973).

Morphology

General description

The physical appearance of lake sturgeon (Figure 2.1) is similar to most other *Acipenser* species; and like all other members of the genus, they are easily recognized by several primitive morphological features that distinguish them from other North American fishes. Perhaps the most noticeable of these is the scaleless body, which is protected instead by five lateral rows of bony plates or scutes. The heavy-set body is spindle shaped, the greatest body depth occurring slightly anterior to the midsection. The origin of the anal fin is located posterior to that of the dorsal, its tip rarely extending beyond the caudal fulcrate plate. Other morphological features that distinguish lake sturgeon from other North American freshwater fishes include a heavily armored skull, a spiral valve intestine, and a cellular swim bladder that retains some of the lung-like characteristics of early actinopterigeans (Harkness and Dymond 1961).

The lake sturgeon is generally similar to that of other acipenserids. The elongated body in cross-section is pentagonal in young juvenile specimens but becomes progressively more rounded with age (Scott and Crossman 1973). Dorsal, lateral, and ventral scute counts are typically 9-17, 29-42, and 7-12, respectively. Dorsal fin rays number 35-45; anal fin rays number 25-30

(Vladykov and Greeley 1963, Scott and Crossman 1973). The slightly upturned rostrum is disproportionately large in juveniles, often exceeding post-orbital distance <50 cm;however, this proportion is gradually reversed with age (Vladykov and Greeley 1963). The large, transverse mouth typically measures approximately 66-93 % of the interorbital width (Vladykov and Greeley 1963). The top lip is continuous, the bottom lip interrupted (Figure 2.2). Mouth shape and size in proportion to head width is most similar to that of shortnose sturgeon (*A. breviostrum*) (Vladykov and Greeley 1963, Hochleitner and Vecsei 2004). As in the elasmobranches, the sturgeon jaw is detached from the skull, allowing the mouth to project downward during feeding (Vecsei and Peterson 2004). Barbels are situated closer to the tip of snout than the origin of mouth - an important diagnostic character distinguishing the species from other Acipenserids. Gill rakers are short and typically number 25-40 (Vladykov and Greeley 1963). The thick-walled, gizzard-like stomach is connected to a spiral-valve intestine, a primitive alimentary arrangement shared by many Acipenserids, which is adapted to a diet of benthic crustaceans and molluscs (Harkness and Dymond 1961).

Body armoring is extensive on juveniles but becomes progressively reduced with age (Scott and Crossman 1973, Priegel and Wirth 1974, Vecsei and Peterson 2004). In juveniles less than 100 cm, the laterodorsal and lateroventral surfaces are protected by a layer of tightly-spaced denticles evenly distributed between the five principal rows of scutes. Sharp, apical hooks are particularly prominent on the scutes of juveniles, but these gradually disappear with age until the scutes themselves are almost completely resorbed later in adulthood (Figure 2.3). In contrast, most anadromous sturgeons retain ossified scutes that continue to grow throughout their entire lifecycle. Hence, the process of scute resorbtion in adult lake sturgeon probably illustrates an important trade-off in the functional morphology of body armoring within the genus.

The skull of all acipenserids, including the lake sturgeon, is heavily armored by a series of contiguous bony plates that are most apparent in juveniles and sub-adults (Figure 2.4). Variation and complexity in the ossification of the *Acipenser* skull roof has been noted by several researchers (e.g., Jollie 1980, Hilton and Bemis 1999); however, only the skull structure of shortnose sturgeon has been well studied (Hilton and Bemis 1999). Although the lake sturgeon skull is comparatively less variable, Jollie (1980) noted considerable intraspecific and ontogenetic variation. While the endocranial elements of Acipenseridae may be useful in understanding some phylogenetic relationships within the group, they are generally too complex and variable for use in species identification. Fortunately, the number and arrangement of dermal plates on the dorsum and ventrum of the posterior trunk are much more species-specific and less subject to individual or ontogenetic variation compared to the main rows of scutes (Harkness and Dymond 1961, Vecsei and Peterson 2004)

Although Vladykov and Greeley (1963) reported that predorsal plates may be used for taxonomic identification, the postdorsal and preanal plates are most commonly used for this purpose. In lake sturgeon the postdorsal plates are typically seen as 1-2 unpaired elements (Vladykov and Greeley 1963, Peterson et al. 2003); however, the second predorsal may appear as a paired element in some individuals. The relatively large preanal plates always occur in single file, and number 1-2 (Vecsei and Peterson 2004). These ossifications may be considered definitive in all cases except on very old individuals where they may be completely resorbed.

Body coloration of lake sturgeon is variable among stocks but is typically dark brown or dark gray dorsally with a similar, but slightly lighter coloration on the lateral surfaces. The ventrum is typically white or cream-colored. Some individuals have gray or black pigmentation on the underside of the head, particularly on the lips and barbels (Harkness and Dymond 1961). Adults may exhibit white or milky blotches or spots on the lateral body surfaces but this is rare. The dorsal and lateral scutes are typically the same color as the surrounding skin, although rare specimens may have slightly lighter lateral scutes or dark pigmentation on the lateral surfaces of the ventral scutes (Vladykov and Greeley 1963).

Although lake sturgeon exhibit considerable morphological ontogeny, the changes in color pattern from early juvenile to adulthood are among the most pronounced (Vladykov and Greeley 1963, Priegel and Wirth 1974, Peterson et al. 2003). In juveniles <30 cm, two large black saddles typically are present across the gray or brown dorsum and sides (Figure 2.5). Black speckling on the upper surfaces of the body also is common, often producing a ‘peppered’ appearance on the juveniles. Scutes and other dermal ossifications of juveniles are usually of the same color as the surrounding skin, but lateral scutes may sometimes be lighter (as in the adults). In 2-4 year old juveniles (>60 cm) the large saddle marks are lacking, but the black speckling may persist into early adulthood.

Distribution and legal status

The current distribution of *A. fulvescens* includes three major North American drainages: the Mississippi, the Laurentian Great Lakes, and the Hudson Bay (Priegel and Wirth 1971). The historic range of the species extended from the Canadian waters of Hudson Bay in Saskatchewan and Manitoba, east to the St. Lawrence River estuary. To the south, U.S. populations were found primarily in the Great Lakes and Mississippi River basins, with smaller isolated populations occurring further south in the larger rivers of the Tennessee and Ohio River drainages (Scott and Crossman 1973). Although found primarily in larger freshwater lakes and rivers, lake sturgeon are also native to the brackish waters of Hudson Bay and the St. Lawrence River estuaries (Figure 2.6) (Vladykov and Greeley 1963). Currently, lake sturgeon are not federally protected in either the US or Canada; however, the species was listed in 1975 under Appendix II of the Convention on International Trade of Endangered Species (CITES) (Leonard et al. 2004). Although this listing was temporarily suspended in 1983, it was reinstated in 1997. Within the US the species receives various levels of protection at the state level. Populations in Iowa, Indiana, Illinois, Ohio, Missouri, Pennsylvania, Tennessee, and Vermont are considered endangered while those in Nebraska, New York, and Michigan are listed as threatened (Johnson 1987, Auer 2004, Leonard et al. 2004). In Canada, lake sturgeon are listed as threatened in Alberta, Manitoba, New Brunswick, Newfoundland, Ontario, Quebec, and Saskatchewan (Freedman et al. 2001, TRAFFIC North America 2002). Despite the many anthropogenic factors that have decimated most populations, a few healthy populations still exist. The largest of these is probably that of the St. Lawrence River near Montreal where commercial fisheries in the 1980s and 1990s produced annual harvests of 15,000 – 30, 000 fish (Fortin et al. 1993). Recent studies by La Haye et al. (1992), however, suggest that this population is actually comprised of at least three distinct stocks. In US waters, the largest remaining population is in the Lake Winnebago System in central Wisconsin (Bruch 1999, Bruch and Binkowski 2002) where the species has been actively managed for the past 100 years. Recent studies by Thomas and Haas (2002) have shown that the largest remaining Great Lakes population is probably that of Lake St. Clair. All three of these populations support limited recreational fisheries, and some commercial fishing is permitted in both the St. Lawrence and the Canadian waters of Lake St. Clair.

Life history and ecology

The first comprehensive summary of lake sturgeon life history was provided by Harkness and Dymond (1961). More recently, studies of lake sturgeon biology and management have come from Wisconsin, where sizeable populations have been re-established through management, restoration of spawning habitat, and judicious stocking programs (Priegel and Wirth 1974, Thuemler 1988, Kempinger 1988, Larson 1988, Bruch 1999, Bruch and Binkowski 2002). Many of these management efforts have been aided by recent investigations of new propagation and habitat restoration techniques (Ceskleba et al. 1985, Conte et al. 1988).

Spawning periodicity and fecundity

Lake sturgeon life history is characterized by rapid growth during a protracted juvenile stage, with first spawning typically delayed until age 12-15 for males and 18-27 for females (Scott and Crossman 1973, Bruch 1999, Bruch et al. 2001). Physiological studies have shown that this delay in maturation results from an unusually disproportionate allocation of energy to somatic growth during the juvenile years (Beamish et al. 1996, LeBreton and Beamish 2004). This strategy could have the evolutionary disadvantage of delaying reproduction, but would yield a compensatory advantage by providing both the time and energy needed to maximize size-at-first spawning. Because natural mortality is largely size-dependent, this reproductive strategy is believed to limit mortality to the earliest life stages, thereby increasing potential life span (Duarte and Alcaraz 1989). As in other long-lived species, this strategy provides the adults with multiple reproductive opportunities spread over many years or even decades (Secor and Waldman 1999, Crouse 1999). In the absence of anthropogenic disturbance, this strategy presumably conveys the selective advantage of minimizing any loss of fitness resulting from year-class failures in any one year when spawning conditions are poor (Crouse 1999).

Large size at first spawning also provides the advantage of increased fecundity in lake sturgeon, which is among the highest of all freshwater species in North America (Harkness and Dymond 1961, Scott and Crossman 1973). Although the number of eggs produced on a per-weight basis is variable, fecundity generally increases as a function of size with a typical adult female producing 49,000-667,000 eggs in each spawning year (Harkness and Dymond 1961, Priegel and Wirth 1971). It has been suggested that lake sturgeon also rely on their high fecundity to help maximize reproductive output during years of favorable spawning conditions (Beamesderfer and Farr 1997).

Although a large female lake sturgeon may spawn more than a million eggs in a single spawning season, the species' reproductive rate is inherently low because of protracted spawning periodicity (Harkness and Dymond 1961). Typically, females spawn only once every 4-9 years, males every 1-3 years (Roussow 1957, Magnin 1966, Fortin et al. 1996). This low spawning frequency, coupled with a life span of up to 154 years (MacKay 1963), typically results in spawning migrations consisting 20 or more age classes in unexploited populations. Researchers have suggested that the complex age-structure of such populations helps buffer them against short-term environmental disturbances – an important key to their evolutionary success (Peterson et al. 2007). As demonstrated by Secor and Waldman (1999) and

Auer (1999), this inherent population resilience is quickly eroded when spawning adults are exposed to excessive harvest.

Spawning behavior

Lake sturgeon spawn during spring, usually from mid-April to early June; however, several researchers have noted that males typically arrive at the spawning grounds before females (Bruch and Binkowski (2002). On the Wolf and Fox rivers, Wisconsin, for example, Bruch and Binkowski (2002) observed males at several spawning sites 1-2 days before the females. Once females are present, spawning may begin as soon as water temperatures reach 10-15 °C (Harkness and Dymond 1961, Kempinger 1988, Auer 1996b, Smith and King 2005); however, specific temperatures that trigger spawning are variable and depend on the ovarian cycles of individual females (Webb et al. 2001).

Studies of courtship behavior in lake sturgeon are rare, but Priegel and Wirth (1971, 1974) and Bruch and Binkowski (2002) have noted that males often produce drumming sounds in the presence of gravid females. During spawning, 2-8 males typically crowd individual females on each flank, frequently pounding her with their caudal fins to stimulate egg release. These spawning bouts can be intense, but typically last only 1-2 minutes (Bruch and Binkowski 2002). The process is repeated several times with different males maneuvering into the group during each subsequent bout until the female is spent. Although this behavior leaves most fish in poor post-spawning condition, Bruch and Binkowski (2002) suggest that this polygamous mating system may help ensure the highest number of possible mates for both genders while minimizing the energy expended in finding suitable mates.

During spawning, females scatter their adhesive eggs widely over gravel or cobble substrates in water depths of 0.1 – 2 m (Priegel and Wirth 1974, Becker 1983, LaHaye et al. 1992, Auer and Baker 2002, Bruch and Binkowski 2002). Females usually complete spawning in 8-12 hrs, after which they leave the spawning area. Males may remain on the spawning site as long as a ripe female is present. Once all females have left a spawning site, males may move downstream until they find deeper water where they can await the arrival of additional ripe females (Vladykov and Greeley 1963, Bruch and Binkowski 2002).

Successful spawning in lake sturgeon largely depends on the suitability of both flow and temperature regimes, but optimal spawning conditions may vary substantially among populations (Cooke et al 2002, Jager et al. 2002). For most populations, optimal spawning habitat is found in the higher-gradient reaches of large rivers with current velocities of 0.5-1.3 m/sec and substrates of coarse gravel or cobble (Auer 1996a, McKineley et al. 1998), although a few populations are known to spawn on rocky, wave-washed lake shores (Harkness and Dymond 1961, Carlson 1995). Regardless of the specific spawning habitat selected, parental care is not provided, and spent adults typically migrate back downstream as soon as spawning has concluded (Harness and Dymond 1961, Kempinger 1988).

Early life stages:

Eggs

Immature lake sturgeon eggs are yellowish and attached to a fatty ovarian mass without a covering membrane (Detlaff et al. 1993, Bruch et al. 2001). The fully-developed embryos are olive-green, grey, or black and measure 2.6-3.5 mm (Bajkov 1930, Harkness and Dymond 1961, Priegel and Wirth 1974, Becker 1983). Hatching of lake sturgeon embryo typically occurs after 8-14 days (Kempinger 1988) with rate of embryonic development depending on water temperature (Kempinger 1988). Developmental studies by Wang et al. (1985) show that at 15 ^{o}C, gastrulation occurs at 37 hr, neurulation at 77.7 hr, and heart formation at 118 hours. Few studies have documented predation on lake sturgeon eggs; however, observations of Bruch and Binkowski (2002) suggest that male lake sturgeon may consume fertilized eggs while on the spawning grounds. Although directed studies are rare, lake sturgeon eggs are probably eaten by many fishes and invertebrates (Auer and Baker 2002). In the Muskegon River of western Michigan, for example, stomachs from several brown trout (*Salmo trutta*) harvested in the recreational fishery contained lake sturgeon eggs (personal observation).

Larvae

At hatching, the 9-11 mm yolk-sac larvae (or prolarvae) are poorly developed and many basic anatomical structures are barely discernable. The mouth is apparent only as an inward fold and the barbels as tiny stubs

(Kempinger 1988). At 17-18 mm, however, both structures are well developed and clearly discernable (Kempinger 1988, P. Vecsei personal observation). Other structures, including gills, fins, and lateral lines develop similarly late in the yolk-sac stage (Kempinger 1988). On live specimens less than 15 mm, the contrast between the transparent body and dark or olive-grey yolk sac is evident; however, dead or preserved specimens appear uniformly light grey (Vecsei and Peterson, personal observation). At 15 mm, the yolk-sac larvae develop dark pigmentation, which becomes most prominent along the lateral portion of the head and trunk. At this stage, a dark spiral valve and anal plug also become apparent (Wang et al. 1985).

Newly hatched larvae are pelagic, negatively phototactic, and move about actively in search of suitable hiding places within the interstitial spaces of the rocky substrates where they were spawned (Harkness and Dymond 1961; Wang et al. 1985; Kempinger 1988). Within 13-19 days after hatching, the 17-18-mm larvae emerge from the substrate at night and rapidly disperse downstream, often drifting with the current for several kilometers before settling on the river bottom (Kempinger 1988, LaHaye et al. 1992). Although the exact timing of this downstream dispersal is somewhat variable, a minimum water temperature of 16 ºC seems to trigger this behavior (Smith and King 2005).

The onset of exogenous feeding signals the transition from the prolarval to the larval stage. Kempinger (1988) noted that the anal plug is shed just prior to this transition when the larvae are about 22 mm. The postyolk-sac larva is easily identified by a prominent lateral band that extends the entire length of its body including the caudal fin. The trunk is pigmented in its entirety but is darkest along this mid-lateral band. The larval stage lasts for several weeks (depending on temperature) until the start of the juvenile stage at about 40 mm when all definitive fin structures are formed (Kempinger 1988).

Juveniles

In lake sturgeon, the transition from the larval to juvenile stage is marked by the formation of all definitive adult structures except for the gonads, which remain undifferentiated for several years (Priegel, G.R. and T.L. Wirth, 1974). The juvenile period is protracted and immature individuals may vary greatly in size and age. Like the adults, juveniles are thought to feed primarily on benthic invertebrates such as small crustacea, insect larvae, leeches, mollusks and isopods (Harkness 1923, Wallus 1990, Chiasson et al. 1997). Information on the movements and habitats of juvenile lake sturgeon is scant; however, available data suggest that yearlings may gather in large schools in shallow river mouths or adjacent bays during late summer and fall (Priegel and Wirth 1974, Becker 1983, Wallus et al. 1990). After their first year, juveniles are found in the same habitats as the adults (Priegel and Wirth 1974).

Adults

Age and growth

Adult lake sturgeon are among the largest of North American freshwater fishes. Adults males typically measure 100-185 cm and weigh 11-30 kg; adult females measure 130-215 cm and weigh 25-100 kg. Although larger individuals are currently rare, numerous specimens of 100 kg or more were reported from historical Great Lakes fisheries (Vladykov and Greeley 1963, Harkness and Dymond 1961). The largest documented specimen, taken from Lake Michigan in 1943, measured 241 cm and weighed 141 kg (Van Oosten 1956). Lake sturgeon, growth is variable, even within a population, and historical accounts suggest that average size tends to decrease in the southern part of the range (Stearns and Atkinson 1953).

Age estimation of most bony fishes is usually accomplished by counting inter-annual growth rings present on the scales or cross-sections of the otoliths; however, this method is not preferred by most sturgeon researchers. Although aging methodology is similar for sturgeons (Classen 1944, Currier 1951, Wilson 1987, Brennan and Cailliet 1991), the marginal pectoral fin ray is used instead because it is easier to collect and its removal is non-lethal (Roussow 1957, Rossiter et al. 1995). Typically, annuli appear as widely separated bands in early years but these become increasingly crowded near the outer margins of the fin ray cross-sections. Hence, age-determination in sturgeons becomes increasingly uncertain in older specimens (Keenlyne and Jenkins 1993). Rossiter et al. (1995) found that this method was easiest and most accurate for lake sturgeon up to age 15; and while age estimates of much older fish are frequently published, numerous studies have questioned their accuracy (Brennan and Callaiet 1991, Rien and Beamesderfer 1994).

Food Habits and Feeding

Lake sturgeons feed primarily on benthic invertebrates that they find using a combination of tactile, olfactory, chemosensory, and electrosensory receptors (Harkness and Dymond 1961, Binkowski and Doroshov 1985, Chiasson et al. 1997). The fish feed by sucking in prey items with rapid extension of the protractible mouth; the prey items are detected as the fish swims along the bottom with its barbels in contact with the substrate. (Priegel and Wirth 1974, Vecsei and Peterson 2004). Inedible materials, such as sand or silt, are sucked in with food items and expelled through the mouth or gills, while food items are retained and crushed against the ridges of cartilaginous palate before being swallowed (Harkness and Dymond 1961, Priegel and Wirth 1974). Although benthic macro-invertebrates are the most important prey consumed, the lake sturgeon diet varies considerably both spatially and temporally (Chiasson et al. 1997, Beamish et al. 1998). Prey items reported from lake sturgeon stomachs include leeches, snails, small clams, and small fishes, although when available, soft-bodied insect larvae may comprise up to 90% of the volume consumed (Harkness 1923, Bajkov 1930, Harkness and Dymond 1961, Priegel and Wirth 1974). Lake sturgeon forage actively throughout the year; however, feeding may slow during winter in northern portions of the range (Priegel and Wirth 1974).

Habits and movements

Lake sturgeon often migrate great distances in search of food, suitable spawning habitat, or simply to avoid seasonally unfavorable conditions (Auer 1996b, Bemis and Kynard 1997). Habitat selection however, depends on availability and specific requirements of each life stage. Young juveniles for example, often use deep (>2 m) pools within their natal streams for foraging and over-wintering, whereas adults typically inhabit shoreline or deeper water habitats of large lakes (Harkness and Dymond 1961, Brousseau 1987, Chiasson et al. 1997). Although adult lake sturgeon are rarely observed in non-spawning habitats, several studies suggest that they prefer depths < 9 m during cooler months but will readily move to much deeper water in summer (Harkness and Dymond 1961, Priegel and Wirth 1974). Other studies suggest that these deep-water habitats may also be used for over wintering (Bajkov 1930) or to avoid disturbance from intense boat traffic (Engel 1990).

Lake sturgeon can be found over a variety of substrate types, but prey abundance is possibly an important factor in determining habitat selection (Harkness and Dymond 1961). In shallow lakes such as Lake Winnebago, Wisconsin, where water depths are less than 7 m, lake sturgeons occupy all depths (Priegel and Wirth 1974, Lyons and Kempinger 1992). In deeper lakes such as Black Lake, Michigan, however, adult fish are typically found at depths of 6-12 m (Hay-Chmielewski 1987). Although seasonal habitat selection in these inland systems is probably more influenced by water temperature, corroborative studies are lacking.

Throughout their life cycle, lake sturgeon exhibit both random and non-random movements. Several studies have shown that most individuals move randomly within an established home range of 10 – 14 km; however, some individuals make longer unidirectional movements indicative of emigration (Harkness and Dymond 1961, Priegel and Wirth 1974, Larson 1988, Engel 1990). Early tagging studies in Wisconsin indicated that individuals with established home ranges rarely leave these areas except to spawn (Harkness and Dymond 1961, Priegel and Wirth 1974). Although lake sturgeon are known to migrate up to 200 km when returning to their natal streams, spawning-site fidelity has not been well studied and the environmental cues that trigger and guide these migrations are unknown. Although studies of imprinting in lake sturgeon have not been attempted, many biologists believe that juveniles are able to recognize their natal stream within only a few months after hatching (B. Kynard, personal communication)

Gerbilskiy (1957) and Bemis and Kynard (1997) characterized sturgeon spawning migrations as either a ‘one-step’ or ‘two-step’ pattern. Species exhibiting one-step migrations typically migrate in spring and spawn within a few days of reaching their natal spawning grounds. Those following the two-step migration pattern typically begin their migrations in fall, but overwinter in deep pools prior to spawning during the subsequent spring.

These two distinct migration patterns are not only exhibited by different sturgeon species, but also by different races or subpopulations (Bemis and Kynard 1997). Within the Great Lakes, one-step migrations are well documented for most lake sturgeon populations including the Manistee (Peterson et al. 2002), Muskegon (Peterson and Vecsei 2004) and the Sturgeon (Auer 1996b) rivers. In Wisconsin tributaries of Lake Michigan however, Bruch and Binkowski (2002) have found that both one-step and two-step migrations are typical of lake sturgeon populations spawning in the Fox and Wolf rivers. Regardless of which upstream migration pattern is used, adult lake sturgeon typically move rapidly downstream after spawning has concluded, eventually returning to a larger river or lake to replenish energy stores over the next several years before the next spawning cycle.

Other Mechanisms for Decline

Contaminants

Benthic feeding and long-lived fishes such as lake sturgeon are known to accumulate high toxin levels in their tissues (Hay-Chmielewski and Whelan 1997). Currently, nine chemicals are monitored by the Michigan Department of Community Health (Wood 1993). Mercury and polychlorinated biphenyls (PCBs) are the two substances most frequently found in high levels.

Dams

Hydroelectric dams and lamprey barriers prevent lake sturgeon from accessing spawning habitat in many river systems. Almost all of Michigan's larger rivers are impounded. This includes 90% of Great Lakes tributaries with a mean annual discharge greater than 1000 cfs (n=11), 69% of Great Lakes tributaries with a mean annual discharge between 150-302 cms (n=13), and 42% of Great Lakes tributaries with a mean annual discharge between 33-150 cms (n=33) (Hay-Chmielewski and Whelan 1997). For most of these systems, the first barrier is located on the lowest downstream high gradient. The remaining available un-impounded habitat in large rivers averages 42 river km per river with only 1.4 km of high gradient water (> 1.0 m/km) (Hay-Chmielewski and Whelan 1997).

Besides direct loss of habitat, barriers fragment existing habitat. This changes the dynamics of river systems resulting in further degradation of sturgeon habitat (Auer 1996a, McKinley et al. 1998). It also prevents use of optimal habitats for each life stage. Dams prevent transport of bed materials and woody debris necessary for maintaining a system in equilibrium. Loss of gravel and cobble leads to a direct loss in spawning habitat and frequently degradation of the bed to bare bedrock (Auer 1999, McKinley et al. 1998, Hay-Chmielewski and Whelan 1997).

Successful rehabilitation of lake sturgeon populations requires that upstream fishways be designed and installed at all barrier locations. Currently, there are no installed fishways that were expressly designed to pass lake sturgeon. On the Otter River, Lake Superior, adult lake sturgeon have been observed to pass a pool-weir fishway This structure has now been changed to a streaming flow system that allows lake sturgeon passage at different flow levels. Sub-adult lake sturgeon have been observed passing vertical slot fishways at South Bend, Indiana, None of the other 22 fishways in Michigan are properly sized or designed to pass lake sturgeon (Auer 1996b, Baker 2006).

Sea Lamprey

At present, sea lamprey (*Petromyzon marinus*) control consists of barriers, sterile male programs, and chemical treatments (Hay-Chmielewski and Whelan 1997). Spring sea lamprey spawning migrations overlap with lake sturgeon migrations. Barriers deigned to block lamprey upstream movement are a problem to rehabilitation and enhancement of lake sturgeon. The use of 3-trifluoromethyl-4-nitrophenol (TFM) can be toxic to young-of-year lake sturgeon (Johnson and Weisser 1993). Sea lampreys are more sensitive to TFM than lake sturgeon and concentrations of TFM have been determined that are fatal to sea lamprey but not to lake sturgeon. Johnson and Weisser (1993) found that sea lamprey mortality occurred between 1.8 and 1.9 mg/l TFM whereas for juvenile lake sturgeon, mortality occurred at TFM concentrations between 2.7-2.8 mg/l.

Recent changes in the federal sea lamprey treatment policy have led to timing of treatments to avoid spawning migrations and incubation times of lake sturgeon and to limit lampricide concentrations (Hay-Chmielewski and Whelan 1997). On the Muskegon River, and other Michigan streams where lake sturgeon spawn, application of TFM is used only after the lake sturgeon larval drift period (Hay-Chmielewski and Whelan 1997, O’Neil 1997).

Management approaches

Restoration of lake sturgeon populations to self-sustaining levels is a common goal shared by many contemporary state and provincial management agencies. Towards this end, the species receives varying levels of protection and, in some instances directed management, depending on the biological status of the various populations and local public support (Bruch 1999). Most traditional management approaches focus on regulations that prohibit or severely limit harvest (Johnson 1987). Such programs are based on the assumption that reductions in fishing mortality will result in higher numbers of spawners, higher recruitment of juveniles, and, ultimately, increased abundance of adult lake sturgeon. However, several authors suggest that this approach alone is inadequate to recover sturgeon stocks that have been severely depressed by overfishing (Secor and Waldman 1999, Secor et al. 2002). Lake sturgeon have low reproductive rates and spawning habitat for many populations has been either lost or degraded (Harkness and Dymond 1961, Priegel and Wirth 1975, Thuemler 1988). Hence, some management agencies have developed comprehensive restoration plans based on a combination of management practices. Although management or harvest regulations are typically included in these plans, habitat restoration, stocking, and public education are used increasingly to help expedite recovery.

Regardless of which management practices are chosen, successful lake sturgeon restoration requires a long-term approach because the protracted reproductive cycle of the species requires that many juvenile and adult year classes be established before a population can become self-sustaining (Noakes et al. 1999). Where populations have been extirpated, managers must first ensure that suitable habitat is still available and then develop innovative approaches to re-introduce and protect the stock as it is rebuilt over many years or even decades. Once established, populations must be carefully monitored and managed to prevent overharvest and habitat loss. Management regulations for recreational lake sturgeon fisheries in both Wisconsin and Michigan have included size limits, bag limits, harvest caps, and closed seasons (Priegel and Wirth 1974, 1978, Baker 1980, Larson 1988, Bruch 1999). Although these regulations may help stabilize extant populations, they have not yet proven to be effective at rebuilding depressed stocks (Becker 1983).

Lake sturgeon management is perhaps more complex than other North America sturgeons because the species' native range spans several different states, provinces, and international boundary waters between the US and Canada (Williamson 2003). In Canada, lake sturgeon are protected and managed by the provinces under the Federal Fisheries Act (Houston 1987). Alberta closed all commercial fisheries between 1940 and 1968 as did Manitoba in 1995 (Ferguson and Duckworth 1997). In Saskatchewan, a moratorium has been enforced since 1996; however, several small commercial fisheries still operate in the Ontario waters of lakes Huron, Nipigon, St. Clair, Namakan, Rainy, and the Seine River (Brousseau 1987).

From 1998-2000 the combined the quota from these fisheries totaled 11,553 kg. In Quebec, a commercial gill net season was restricted to the period of June 14 - October 31 to avoid harvest of ripe females. The annual catch quota since the mid-1990s has been approximately 150,000-200,000 kg with a total allowable catch of approximately 20,000-30,000 fish (Williamson 2003). Presently, commercial fisheries for lake sturgeon are prohibited in U.S. waters, where individual states maintain jurisdiction over their respective stocks. The largest annual recreational harvest is in Lake Winnebago, Wisconsin where approximately 1000 fish are taken annually in a limited-harvest spear fishery (Folz and Meyers 1985, Bruch 1999).

Restoration

The lake sturgeon is particularly vulnerable to overfishing because the success of its life history strategy depends on delayed maturation and infrequent spawning over a long life span, (Boreman 1997, Crouse 1999). Although most populations are currently protected, habitat loss and degraded water quality continue to threaten many remaining stocks (Auer 2004). In the Great Lakes for example, dams have been constructed on every known spawning tributary, fragmenting lake sturgeon habitat and interrupting spawning migrations (Auer 1996a, Peterson et al. 2007), which in turn can limit reproductive output and threaten population viability (Hay-Chmielewski and Whelan 1997). Effective sturgeon fishways have been constructed on some low-head impoundments and artificial spawning habitats have been successfully introduced in some rivers (Bruch 1998); however, the lack of effective fish passage systems around hydropower facilities (and other high-relief dams) continues to fragment habitat and degrade water quality on many river systems (Baxter 1977, Jager et al. 2001). Consequently, ongoing studies of fish passage structures specifically designed for lake sturgeon may hold the greatest promise for restoring populations where dams limit access to suitable spawning habitat.

Many remnant sturgeon populations have not recovered despite decades of legal protections, so the use of stocking to either reestablish or supplement existing stocks has become widespread. In recent years, lake sturgeons have been stocked as both fry and fingerlings in several states including Wisconsin, Missouri, Michigan, New York, Georgia, and Tennessee (Schram et al. 1999, Jackson et al. 2002, St. Pierre and Runstrom 2004, Smith and King 2005). Although recent studies have demonstrated the importance of using only native specimens in sturgeon stocking programs (Paragamin and Beamesderfer 2004, Secor et al. 2002), lack of suitable brood stock has prompted new interest in alternative stocking strategies. Among the most promising of these is an experimental method known as 'head start', in which naturally-spawned lake sturgeon larvae are captured from the wild and then transferred to a protective hatchery environment where they can be reared for several months before release back into their natal streams (D. Peterson, unpublished data). Because environmental conditions within the hatchery can be carefully controlled, first-year survival of the wild fry is typically much higher than in the wild. When used over many spawning seasons, this technique can dramatically amplify annual recruitment of *naturally* produced juveniles by *artificially* increasing critical-period survival. Unlike traditional stocking programs that typically rely on only a few wild adults to produce entire cohorts, the use of a head-start program can increase juvenile abundance while avoiding the potential problem of inbreeding depression. Although the new practice is not completely free of some artificial selection, the method may provide an important tool for restoration of depleted populations where at least some spawning still occurs. The first known use of the head-start method for lake sturgeon restoration occurred on the Black River, Michigan in 2001 (D. Peterson, unpublished data). Since the inception of this program, annual releases of “head-started” lake sturgeon fingerlings have helped restore lake sturgeon populations in the Black, Sturgeon, and Pigeon rivers of northern Michigan (D. Peterson, Pers.Comm.)

Research

The available literature on the biology and life history of lakes sturgeon seems comprehensive. However, the lake sturgeon has been extirpated from the southern portion of its range and is uncommon or rare in much of its remaining range (St. Pierre and Runstrom 2004). Numerous studies are currently underway to assess remaining populations as a first step toward restoration. While these studies will undoubtedly provide the scientific basis for future management, identification of limiting factors is currently the most critical research need (Hay-Chmielewski and Whelan 1997). Accordingly, investigations focusing on recruitment mechanisms and ecological links between habitat requirements and successful reproduction of lake sturgeon are of high priority. To ensure the success of current restoration efforts, additional studies are needed to address existing knowledge gaps regarding critical habitat requirements of the various life stages. This will be of particularly importance in regions where lake sturgeon populations are being reintroduced through stocking.

With baseline studies being completed by various government agencies and universities, immediate research needs should focus on improving hatchery techniques. Data obtained from studying the critical survival period of larvae could help fisheries managers better understand recruitment mechanisms. Recent studies on lake sturgeon genetic population structures (DeHaan et al. 2006) are providing data on how genetic diversity among and within meta-populations may affect long-term recovery of depleted populations.

Outlook

The outlook for lake sturgeon recovery range-wide is guardedly optimistic, thanks in part to renewed interest in the species, novel approaches to management, new opportunities to eliminate long-standing data gaps, and continued improvement in habitat restoration. Recent emphasis on maintaining biodiversity has prompted several new management initiatives to “bring back the natives”. This has been especially true for large, charismatic species and has contributed to the renewed interest in enhancing or restoring lake sturgeon populations range-wide. As a result, many state and federal agencies have initiated or are planning to initiate lake sturgeon restoration programs.

Novel approaches such as “sturgeon head start” and similar initiatives have increased recruitment success of naturally spawned lake sturgeon. In instances where natural reproduction is insufficient to support head start programs, stream-side rearing facilities are now being used to help ensure that juveniles produced for stocking are properly imprinted on their receiving waters prior to their release. Improved husbandry techniques such as converting hatchery-reared lake sturgeon to 100% commercial feed (Kornberg and Peterson 2005) also promises to help restoration efforts by increasing pre- and post-stocking growth and survival of such individuals.

The emerging application of conservation genetics techniques to fishery science also may improve artificial propagation programs. For example, mating protocols that manipulate parental crosses to maximize available genetic diversity have been developed and used for other species. The adoption of these approaches for artificial propagation of lake sturgeon will increase the effective population size in instances where brood stock is limited; and in turn, produce larger numbers of individuals for stocking than would have been available otherwise.

The increase in stocking programs to augment or re-establish lake sturgeon populations has provided new opportunities to study lake sturgeon in the wild. These new opportunities will provide data that were unavailable previously because lake sturgeon populations were limited in size or distribution. As a result, many known gaps in our knowledge about lake sturgeon biology, ecology, and life history could not be previously evaluated because of a scarcity of fish and the inability to study them in the wild. This limitation is being removed as an increasing number of populations are established throughout the species range.

Finally, as state and federal regulations intended to protect the environment are enacted and enforced, there has been a gradual improvement in lake sturgeon habitat quality and quantity. Though not yet available at historic levels, habitat improvement increases the probability of success of the aforementioned restoration activities. Further, as increasing numbers of lake sturgeon populations are enhanced or restored and then studied, our understanding of how lake sturgeon respond to habitat changes (positive and negative) should increase and allow for refinement of habitat mitigation and protection.

The recent interest in lake sturgeon has helped the species and its long-term prospects for survival. My guarded optimism for the survival of this species is not intended as an “all clear” regarding threats facing the species. Obviously, many threats still remain, and they will be diminished only by continued awareness of how anthropogenic activities affect lake sturgeon populations and continued efforts toward habitat preservation and restoration.

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Chapter 3

Lake Sturgeon of the Muskegon River: Population Dynamics

Abstract

The lake sturgeon was once abundant throughout Lake Michigan with an estimated 11 million fish prior to human exploitation. By the early 1900s, dams and over-fishing caused the extirpation or serious depletion of all lake sturgeon stocks within the Lake Michigan basin. Although anglers on the Muskegon River occasionally reported capturing lake sturgeon, little is known about the current status or trend of this population. The primary objectives of this study were to: 1) document the presence and estimate annual run size of adult lake sturgeon in the Muskegon River, 2) monitor upstream migration of adult lake sturgeon to identify high-use riverine habitats, 3) determine timing and duration of spawning migration and 4) to determine if lake sturgeon spawning habitat is adequate to support successful reproduction. Adult lake sturgeon were captured with large-mesh, bottom-set gill nets deployed at the mouth of the Muskegon River to intercept migrating adults as they entered the river from mid-March through May in 2002 -2005. Larval lake sturgeon were captured with an anchored D-frame drift nets set in the river from dusk until dawn during May 2003 and 2005. During the study, approximately 6000 gill-net hours captured 59 individual lake sturgeon that were pit tagged and released. Mark-recapture estimates of annual run size were not possible in some years, because of the low number of recaptures. Age analysis using cross-sections from pectoral fin ray samples showed that adults varied in age

from 11-33 years. Although larval lake sturgeon were not collected in 2002, I captured 11 larvae in 2003 and nine were caught in 2005. We were not able to successfully deploy larval nets in 2004 due to severe flooding. The results of our study document the existence of a small, naturally reproducing population of lake sturgeon in the Muskegon River, Michigan.

Introduction

Sturgeons are part of an ancient assemblage of fishes, with fossils of Acipenserids dating back to the Upper Cretaceous. Today, the family Acipenseridae contains four genera with a Holarctic distribution (Findeis 1997, Auer 1999). Sturgeons are unique in their morphology and behavior and are highly specialized for benthic habitats. Sturgeons represent a particular challenge to fisheries biologists because of their commercial value, unique life histories, and worldwide-endangered status (Bemis and Kynard 1997).

The lake sturgeon one of four members of the genus *Acipenser* that occur in North America. Their range extends from the St. Lawrence River in the east, to the Lower Hudson Bay in the north, west to the North Saskatchewan River in Alberta, and south to the Tennessee River in Alabama (Harkness and Dymond 1961, Scott and Crossman 1973).

Lake sturgeon are characterized by late maturation, low reproductive rate, low adult mortality, and large size (Priegel and Wirth 1974). Although these traits have proven to be successful evolutionary tactics for coping with variable environmental conditions, they render the species vulnerable to over-exploitation.

Lake sturgeon have evolved particular life history tactics that have enabled them to survive virtually unchanged since the Cretaceous. Delayed maturation, for example, allows lake sturgeon to reach a large size as energy is allocated to somatic development for the first 15-20 years (Dadswell 1979). In turn, rapid growth to a large size at maturity helps reduce predation mortality. In this way, natural mortality is limited to the early life stages, thereby increasing survival. By living longer, spawning opportunities are potentially increased, thus reducing the need for spawning in years when conditions are unfavorable (Dadswell 1979). The high fecundity of sturgeon, another advantage of their large size, improves spawning success during years of favorable spawning conditions (Beamesderfer and Farr 1997, Bemis and Kynard 1997).

Within the Great Lakes, lake sturgeon have endured more than a century of over-exploitation and habitat loss, and many stocks were extirpated by 1950. Prior to the current study, the Muskegon River, located in west-central region of Michigan’s Lower Peninsula, was believed to support a remnant population (see Hay-Chmielewski and Whelan 1997); however, the status of this population was unknown. Like many similar river systems in western Michigan, the Muskegon River has been dramatically affected by more than a century of urban and agricultural development throughout the watershed (Kilar 1990, O’Neil 1997). In particular, depletion of hardwood forests by industrial-scale logging in the late 1800s and early 1900s caused extensive habitat degradation (O'Neil 1997). During this period, virtually all virgin timber along the river was harvested (Kilar 1990). Downstream transport of large logs scoured channels and banks, destroying much of the existing spawning habitat. The widespread deforestation of the watershed caused extensive erosion, unstable flow patterns, and increased water temperatures, turbidity, and sedimentation.

Increased agricultural and urban development throughout the 1900s also had significant negative effects on the biological community of Muskegon River. Pollution and sedimentation from these sources peaked in the 1950s and 1960s, continuing unabated until the passage of the Clean Water Act in 1973 (O'Neil 1997). Today, water quality in the Muskegon River is considered good; however, many negative factors, including elevated water temperatures, increased sedimentation, bank erosion and loss of stream habitat that all affect spawning lake sturgeon persist (O'Neil 1997).

Degradation of spawning and juvenile rearing habitats was a major factor in the decline of Muskegon River lake sturgeon; however, the construction of numerous dams also blocked access to many high gradient reaches where historic spawning sites were located (O'Neil 1997). Although the lower-most dam located at Newaygo, Michigan, was removed in 1969, its construction in 1900 limited lake sturgeon access to the first 34 miles of the river for nearly 7 decades (O'Neil 1997). However, this reach of the river is dominated by low gradient habitats that are unsuitable for lake sturgeon spawning. Although the removal of this dam restored access to some high-quality spawning habitat further upstream, 32 other dams still exist in the Muskegon River watershed (O’Neil 1997).

In addition to the effects of habitat loss and degradation, exploitation may have been the most important factor in the decline of lake sturgeon in the Muskegon River and even throughout the rest of the Great Lakes. Beginning in the late 1800s, the commercial lake sturgeon fishery was virtually unregulated for several decades (Auer 1999). During this period, most Great Lakes populations were decimated, resulting in the complete extirpation from many watersheds (Auer 1999, 2004, Leonard et al. 2004). Although the fishery was closed in 1929, commercial harvest resumed along the eastern shore of Lake Michigan from 1950-1970 (Auer 1999). During this 20-year period, approximately 15,000 lbs of lake sturgeon were harvested from Lake Michigan (Baldwin et al. 2002). Although the population-level effects of this harvest are uncertain, stocks in most Lake Michigan tributaries were already severely depressed when this fishery was reopened.

In recent years, renewed interest in lake sturgeon has compelled the collaboration of management agencies throughout the Great Lakes to develop or initiate development of comprehensive plans for the preservation and rehabilitation of remaining stocks (Leonard et al. 2004) To provide information that would be needed in developing such plans for Lake Michigan, a basin-wide assessment of remaining lake sturgeon populations was initiated in 2001. The primary objectives of this assessment effort were to determine the status of remnant populations thought or known to persist and, subsequently, to determine the potential for future rehabilitation (Hay-Chmielewski and Whelan 1997).

While little is known about the historical abundance of lake sturgeon in specific tributaries of Lake Michigan, a major commercial sturgeon fishery was operating out of Muskegon by 1885 (Bogue 2000). My research team focused on Muskegon River as part of the greater basin-wide assessment program. The three primary objectives of my study was to: 1) estimate adult lake sturgeon spawning stock size in the Muskegon River; 2) locate and describe high-use habitats of spawning lake sturgeon in the lower river; and 3) determine if lake sturgeon spawning still occurs on the Muskegon and if so, whether viable larvae are produced.

Study Site

The Muskegon River drains a watershed of 6084 km^2 across 8 counties located in the north-central area of Lower Michigan (Figure 3.1). The River is 341 km in length, flowing southwesterly until reaching the eastern end of Muskegon Lake, which in turn, discharges into Lake Michigan via a 0.5 km shipping channel located at the western end of the lake.

There are currently four dams on the Muskegon River: Reedsburg, Rogers, Hardy and Croton Dam. Two dams (Newago and Big Rapids) once located on the mainstem Muskegon River have been removed. The removal of the Newaygo Dam in 1969 gave migratory fishes a further 30 km of free flowing river between Croton and Newago. In 1994, the Federal Energy Regulatory Commission (FERC) relicensed the hydroelectric dams on the Muskegon River for 40 years of operation (O'Neil 1997).

Today, the dam most affecting sturgeon movement and spawning location is Croton Dam. Constructed in 1907, this dam has limited lake sturgeon passage to the lower 72 km of the Muskegon River. Once completed, this hydroelectric dam functioned as a peaking facility until 1994 (O'Neil 1997), but has since been operated as "run of river" to mimic the natural flow regime (Rudy et al. 2003). A variety of fishes are found in the unimpounded reach between Croton and Newaygo, many of which require high gradient habitat that is most abundant in this part of the River. These species include river redhorse (*Moxostoma carinatum*), silver redhorse (*M. anisurum*), golden redhorse (*M. erythrurum*), shorthead redhorse (*M. macrolepidotum*) and rainbow trout (*Oncorhynchus mykiss*). Below Newaygo (rkm 54), the gradient is greatly reduced and substrates are comprised mostly of sand. The shoreline is largely undeveloped, although houses and roads have become increasingly abundant over the past two decades causing serious problems with stream bank erosion in some areas. (O'Neal 1997)

All sampling for adult lake sturgeon was conducted at the mouth of the Muskegon River at its confluence with Muskegon Lake. The 1618-ha lake had an average depth of 6-8 m and a bottom substrate consisting of silt, mud, and sand. The lake supports many game fishes including walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and largemouth bass (*Micropterus salmoides*). During spring and fall, large numbers of salmonids enter the lake during their upstream spawning migrations into the Muskegon River. Lake sturgeon also frequent the lake and river during early spring and are occasionally observed by steelhead anglers in April and May.

Methods

Estimation of Annual Run Size

Lake sturgeon were sampled daily (weather permitting) between mid-March and early June, 2002-2005. In 2002, gillnetting for adult lake sturgeon was conducted from March 21 through June 5. Adult lake sturgeon were captured using bottom-set gill nets, measuring 100 m X 2 m, set at the eastern end of Muskegon Lake near the mouth of the Muskegon River. Each net was constructed of monofilament webbing measuring either 20.3 cm, 25.4 cm, 30.5 cm, or 35.5 cm (stretch measure). Nets were deployed at dusk and retrieved at dawn. Typically, 7-12 nets were fished each night depending on weather conditions. As the nets were retrieved in the morning, captured sturgeon were immediately removed from the nets, weighed, measured, and inspected for passive integrated transponder PIT- tag pit tags. Unmarked individuals were marked with both a PIT tag and a serially numbered, colored t-bar anchor tag. PIT tags were injected under the 4th dorsal scute, between the skin and dorsal musculature, while t-bar tags were attached by piercing the cartilaginous integument located at the base of the dorsal fin. Sex and reproductive status of each fish was determined through visual examination of the gonads after a 2-cm incision was made in the midline of the belly, approximately 8-10 cm anterior to the vent. The incision was closed with a single stitch of an absorbable nylon 0.33 mm suture and sealed with quick-drying surgical glue. Prior to release, a 1-2 cm section of the marginal pectoral fin ray was collected for subsequent age estimation. Rays were collected as close to the base of the pectoral fin in order to get the best possible annuli reading for laboratory analysis.

Marked lake sturgeon captured in gill nets were counted as recaptures in the estimator only when they had been at large for at least 24 hrs, to help ensure random mixing of marked and unmarked individuals.

For comparative purposes between months and years, catch-per-unit-effort (CPUE) of lake sturgeon was calculated for each gill net mesh size and sampling week during each year of the study.

I then used Robust Design (Pollock 1982) to assess abundance and concurrently evaluate the relative effects of temperature and discharge on the capture and recapture probability and the effect of time since spawning on the probability that a sturgeon returned to the area. To allow the incorporation of individual covariates, , I used the Huggins formulation of the Robust Design within Program MARK (White and Burnham 1999, Huggins 1989).

For the robust design, the four “primary” sampling periods each corresponded to consecutive spawning seasons from 2002 to 2005 and the secondary periods consisted of individual net nights. The first primary period was 2002 with nine secondary periods. In 2003, (second primary period) there were eight net nights within the secondary period and in 2004, 14 nights and finally in 2005, 17 nights.

I then fit a total of 16 models that included: survival as constant; the return of formerly spawned fish (1-Gamma') as constant or as a function of time since last spawning; and capture probability as either equal to or different than recapture probability and both capture and recapture probabilities as a function of discharge in the Muskegon River (USGS gage number 04121970) and average water temperature during sampling. Because lake sturgeon are non-annual spawners, the emigration probability (gamma") was fixed at one for the first year following an individual's capture. All combinations of these parameters were fit and I evaluated the weight of evidence for each using the information theoretic approach outlined by Burnham and Anderson (1998). I based all inferences on the model with the greatest weight of evidence.

Age Estimation

Pectoral fin rays were air dried for at least one month prior to laboratory analysis. Once these samples were thoroughly dried, a low-speed, diamond-bladed saw was used to cut a 0.3-0.5-mm cross section from the anterior margin (closest to the integument) of each sample. Cross-sections were then mounted on a glass slide using clear, quick-drying glue and viewed under a 50X projection microscope. Ages of each individual lake sturgeon were assigned based on annuli counts by three independent readers. Only when everyone was in agreement was that fish's age considered final. When annuli counts among readers differed, then the average of the three counts was used in subsequent age-frequency analysis (after rounding to the nearest integer). Once age estimates for all adult lake sturgeon were completed, an age-frequency histogram and catch curve were constructed to depict the age structure and annual mortality rate for the adult population as described by Miranda and Bettoli (2007).

Radio Telemetry

Four adult lake sturgeon (one female, three males) captured in 2002, six (two females, eight males) captured in 2003, 10 (seven males and three female) captured in 2005 were radio-tagged (Advanced Telemetry Systems, Model F2080, Isanti MN, USA) to determine patterns of movement and habitat use during annual spawning migrations. The selection of individuals for radio-tag attachment was dependent on several logistical (weather conditions on day of capture) and biological considerations (individuals large enough to be mature); however, I attempted to select representative individuals from each sex. Radio tags were cylindrically-shaped, weighed 26 g, and were 57 mm long by 19 mm in diameter. All radio tags were mounted externally. A battery-powered, high-speed Dremel was used to drill a pair of 2-mm holes in the 3rd or 4th dorsal scutes. Stainless steel mounting wires were then threaded through these holes, carefully avoiding penetration of any soft tissue surrounding the dorsal musculature. Plastic retaining washers were then placed over the protruding ends of the attachment-wires until they lay flush against the opposite side of the dorsum. The wires were then crimped and cut within 1 cm of each retaining washer. Although each fish was held out of the water during this procedure, a continuous stream of fresh water was poured over the body, head, and gills throughout the duration of the procedure. Radio tag attachment was usually completed in less than two minutes. Once the tag was firmly in place, the sturgeon was returned to the water and allowed to recover by gently holding the fish upright until it exhibited strong swimming movements (usually about 3-5 minutes). The fish was then released by allowing it to swim away from its handler.

For several days following the release of each radio-tagged fish, telemetry tracking was conducted in Muskegon Lake to monitor the immediate post-capture movements of each individual. Once all radio-tagged lake sturgeon had entered the river, the position of each fish was monitored at least twice weekly by traversing the entire reach of the lower River, from Croton Dam to Muskegon Lake. Beginning at the Croton Dam boat launch, the telemetry team descended the river while monitoring frequencies of all radio-tagged lake sturgeon with a portable receiver and handheld loop antenna. Once located, the position of each fish was recorded using a handheld GPS. At the end of each field season, the collective movements of all radio-tagged fish were analyzed to identify high-use areas within the river. In both years of the study, radio-tracking of tagged fish was continued until all fish had either left the River or the transmitters had been shed (as indicated by a signal remaining stationary for several weeks).

Larval Sampling

During 2002, larval sturgeon sampling was conducted on eight nights from May 18-29, rkm 52 from the Bridge Street bridge in the town of Newaygo, Michigan. In 2003, a new site was chosen at rkm 60, immediately downstream of an active spawning site identified through radio telemetry during the first year of the study. During 2003, sampling for larval lake sturgeon was conducted at this site on 15 nights from May 12 through June 11. Specific dates of sampling during these periods were determined by weather conditions and abundance of larval lake sturgeon in the samples. During 2004, flows were too high to permit larval sampling, but in 2005, sampling was again conducted at rkm 60 on 13 nights from May 27 through June 23.

Because we were only interested in documenting the occurrence and timing of larval lake sturgeon emergence, the larval sampling methods we used were qualitative, rather than quantitative. All larval sampling was conducted using five D-frame drift nets each consisting of a stainless-steel "D-Frame" and a 2.8-m conical net constructed of 363-μm nylon mesh. The open-mesh to net-mouth ratio of these nets was 3.6:1. The nets were fished along a 40-m transect and held in place by a sturdy nylon rope stretched across the river and tied to trees on opposite banks. Nets were anchored to the substrate using two 5-kg cement blocks attached to the opposite corners of the D-frame. To maximize catches of larval lake sturgeon, the nets were not randomly distributed across the rope transect, but rather, they were grouped in areas immediately downstream of the suspected spawning site. Each net was randomly assigned to one of the five sampling locations on each night and nets were deployed sequentially at two minute intervals along the transect starting at the north river bank. During each sampling night, the nets were checked and reset hourly from 21:30 to 04:30. At each hourly interval, the contents from 3 of the nets were placed in white plastic tubs and sorted on shore under large portable lights. To expedite sample analyses during the field collections, contents of the 4th nets were preserved in a 10% formalin solution for subsequent analysis at the lab.

Larval fishes were identified to the lowest taxon possible and abundance of each taxon was recorded for each sampling event. Although larval lake sturgeon were distinguishable from other larval fishes due to their larger size, dark coloration, and rapid swimming movements, 20% of the collections from each night were randomly selected and preserved in 70% ethanol for laboratory corroboration of ID's. These samples were subsequently analyzed in the UGA Fisheries Research Laboratory for definitive identification and to ensure that larval lake sturgeon were not missed in the initial field examination. The first 10 larval lake sturgeon captured also were preserved for morphometric analyses. Larval lake sturgeon were measured to the nearest 0.05 mm and identified as pro-larvae (yolk-sac present) or larvae (yolk sac consumed) based on Wallus et al. (1990).

During the period of larval drift sampling, dissolved oxygen, pH and turbidity were measured using a water quality sensor (YSI 1600 QS Probe, Loveland CO, USA).

Habitat assessment

To estimate the availability of potential lake sturgeon spawning habitat in the lower Muskegon River, I conducted a micro-habitat assessment of the documented spawning site at rkm 60. Using quantitative data on velocity, depth, and substrate collected at this site, I then established a minimum “threshold” for identifying potential spawning habitat in the rest of the lower river (See Priegel and Wirth 1971, Baker 1980, Auer 1996, Bruch et al. 2001, Bruch and Binkowski 2002). This threshold was based on lake sturgeon spawning criteria described in previously published findings. Although other habitat characteristics also may be important in habitat selection of spawning lake sturgeon, these 3 characteristics (substrate, velocity and depth) are believed to be the most important (Bruch and Binkowski. 2002, Manny and Kennedy 2002, Caswell et al. 2004, Smith and Baker 2005).

Micro-habitat assessment of the lake sturgeon spawning site at rkm 60 included fine-scale measurements of substrate, velocity, and depth. To describe depth and velocity at this site, I first established a straight-line transect across the river at 3 randomly-selected locations, perpendicular to the flow. The first of these crossed the spawning pool at a point where I observed several adult fish holding in the current in the days immediately prior to spawning. The second transect was taken across the site where we observed lake sturgeon eggs deposited on the substrate while the third was positioned a few meters upstream of this site, at the head of the spawning pool. Velocity (taken approximately 5 cm off bottom) and depth measures were recorded at 1-m intervals along each transect. To evaluate substrate within the spawning pool, I first established a zig-zag transect through the spawning pool as described by (Bain and Stevenson 1999). Using the Bain and Stevenson (1999) category ranking, substrate diameters were then determined using a meter stick to measure the width of the nearest rock observed at each 100 cm along the transect.

Macro-level habitat assessments were conducted at intervals throughout the lower Muskegon River. The starting point for these assessments was established directly downstream of Croton Dam at rkm 73.7. Moving downstream, I established 1000-m sampling zones at intervals of 1 km from rkm 73.7 (Croton Dam) to rkm 66. From rkm 66-54 I reduced the sampling interval to 500 m because this was the highest gradient reach of the river and likely contained the most potential spawning habitat (Scott and Crossman 1973, Auer and Baker 2002, Bruch and Binkowski 2002). From rkm 54-48, I assessed habitat at each 2-rkm, and from rkm 48-0 at every 6 km, because the low gradient in these reaches was unlikely to support lake sturgeon spawning habitat. At each habitat sampling interval, I first established a rectangular 9-point grid survey consisting of 3 rope-transects, each containing 3 distinct survey points. At each of these nine points, I measured water depth using the velocity meter pole. Current velocity at 5-10 cm off bottom, along each transect (+ 0.03 m/s) were recorded using a digital water-velocity meter (FP101 Global Water Instruments Inc., Gold River CA, USA). I also estimated relative abundance of boulder, cobble, gravel, pebble, and sand through visual examination of the substrate contained within a 1-m quadrate deployed on the river bottom at each transect point (See Bain and Stevenson 1999).

Results

Robust Design: The time factor and water temperature

The results from fitting several models examining the differences in capture and recapture probabilities and effects of time since initial capture on probability that a lake sturgeon stays away once it has emigrated (Gamma') are shown in Table 3.2. The best approximating model (lowest AIC, highest weight) indicated that the best model included immigration modeled as a function of time since last spawning event and capture probability as a function of average water temperature during sampling. Parameter estimates from this model indicated that the probability of a sturgeon returning to the spawning area was positively related to time since last spawning (Table 3.3). Sturgeon capture probabilities were negatively related to average water temperature. I estimate that sturgeon were 1.36 time less likely to be captured for each 1 ^{o}C increase in water temperatures.

Spawning Stock Size

Parameter estimates from Robust design showed that between 2002-2005, the spawning run of lake sturgeon in the Muskegon River ranged from 18-33 individuals (Table 3.4).

Age structure

During the 4 yrs of this study, length and weight, were obtained for 43 of the 45 adult lake sturgeon captured. Of these, seven were confirmed female, two were suspected female, and 36 were confirmed male. Because of inclement weather, three fish were released before fin ray sampling or sex determination could be performed. Based on relative girth, we suspected that 2 of these individuals were female. The largest lake sturgeon captured measured 189 cm and weighed 57-kg (suspected female).

Pectoral fin ray samples collected from 39 individuals were used to construct an age-frequency histogram (Figure 3.2) and catch curve (Figure 3.3) of the adult population. Analyses of fin ray samples revealed that the oldest fish captured, was a 52-kg male estimated to be age-32. The youngest verified spawning adult was a 5-yr-old male weighing only 8.6 kg.

Seasonal Habitat Use

Radio tracking was conducted on 27 separate occasions in 2002 from April 14 to May 2. During this period, we followed 3 of the 4 radio-tagged fish from their capture site on Muskegon Lake, into the Muskegon River

(Appendix I). The tag on the 4th fish appeared to have failed. Although the fish were never found together during their upstream migration, all 3 individuals entered the River between April 15-24. Water temperatures at the mouth of the Muskegon River during this period were 13-14^{o} C. Once in the river, the fish tended to move upstream through a series of punctuated movements – often residing in a location for several days before moving upstream several kilometers in one night. For the first 3 weeks after entering the river, daily movements appeared random. On May 8 however, all three of the radio-tagged individuals converged at a single site locate at rkm 60, known locally as the “Boathouse Pool”. Water temperature at this time was 12^{o} C. Although we tried to observe the fish at this suspected spawning site, high water and poor visibility precluded visual verification of spawning activity. Two days after the fish had converged at Boathouse Pool, the female (#7-8-4) left the pool and moved rapidly downriver until exiting the system. The 2 males also moved downriver after May 10; however, they remained in the Muskegon system until May 19, after which time they too, presumably returned to lake Michigan.

In 2003, radio tracking was conducted for 26 days beginning on April 15 and concluding on May 14. Prior to this period, we had attached radio tags to six individual lake sturgeon; four males and two females. Unfortunately, the transmitters on two of these individuals (one male, one female) were shed during recapture events in the lake. The four remaining radio-tagged individuals entered the Muskegon River between April 15-20.

Water temperatures at the mouth of the Muskegon during this period were 7.0-7.2° C. Of the four fish that entered the river with transmitters, only two (one male, one female) retained their transmitters long enough for us to track their movements throughout the spawning season. Of the other 2 remaining individuals, the female reached the Boathouse Pool on April 30, whereas the male did not arrive until May 8. Water temperatures at this time were 10.8-11.2°C.

In 2004, radio-telemetry was not attempted; however, in 2005, we attached radio tags to 10 adult lake sturgeon captured from March 23 to April 10 (three females and seven males). From March 30 to June 7, we tracked these individuals on 49 separate occasions. Of the 10 fish we tagged, two individuals remained in the lake for the entire season; however, the other eight entered the river between March 31 and April 16. Water temperature at the river mouth during this period was 9.5° C. Of the eight fish that entered the river, only two (both males) retained their transmitters long enough for us to follow their movements to the suspected spawning site at Boathouse Pool. The first of these individuals arrived at there on May 12, the other on June 2. Water temperatures in the river during this period varied from 15.0-18.3° C.

Verification of spawning success

From April through May 2003, the water was clear enough to observe spawning behavior of several adult lake sturgeon at the Boathouse Pool (rkm 60) in the lower Muskegon River. From May 25-27, we observed five to seven adult lake sturgeon displaying pre-spawning behavior and actual spawning at a water temperature of 13.9° C. Although we observed the fish for several hours during the day, courtship did not become apparent until dusk and, presumably, most spawning occurred at night. Within Boathouse Pool, courtship and spawning appeared to be restricted to a single 6-m^2 site located in the main channel of the River. Depth of this site was 1.7-2.0 m and mean current velocity just above the substrate at spawning was 0.70 m/sec. Examination of substrate during subsequent habitat analysis showed that small cobble and gravel were the dominant substrate types although a few boulders and some sand were present as well (Table 3.5).

From May 27-June 9, 2002, we sampled a total of 82.5 hrs on 13 different nights and captured a total of 11 larval lake sturgeon. Water temperatures during this period were 13.5 - 16.0° C. Peak larval drift (73% of captured larvae) occurred between June 6-9 at water temperatures 14-16.0° C. As anticipated, the highest CPUE was obtained from the drift-net located directly downstream of the area where we had observed the fish spawning. At the time of sampling, the wetted width of the stream along our larval sampling transect was 64.5 m with water depths of 0.55-1.83 m. Current velocities along the sampling transect were 0.61 to 0.88 m/sec and mean discharge during larval sampling (May 12-June 11) was 32.23 m/sec. Dissolved oxygen was typically 95-100% saturation with a pH of 8.0-8.4. Turbidity during the larval sampling period was 1.2 to 4.4 NTU.

Although we began sampling larval drift shortly after sunset and continued until the following dawn, all larval lake sturgeon were captured from 21:30 – 04:30, and most (82 %) were captured between 22:00 and 24:00 hours. Interestingly, we captured both prolarvae (n=3) and larvae (n=8) in our drift-net samples. The prolarvae ranged in size from 15-18 mm total length (TL) and were easily identified by their prominent yolk-sacs. Larvae did not have yolk sacs and were also much larger (20-21.5 mm TL) than the prolarvae.

In 2004, water flow was too high to sample for larval lake sturgeon; however, in 2005, we returned to rkm 60 and resumed larval sampling efforts. From May 27-June 12 of 2005, we sampled a total of 310 net hours on 13 different nights and captured a total of 16 larval lake sturgeon. Water temperatures during this period were 15 - 22.4° C. Peak larval drift (when most larval lake sturgeon were captured) occurred between June 6-9 at water temperatures 14-16.0° C.

Habitat analysis

Micro habitat assessment of the rkm-60 spawning site was conducted on June 10, 2005 – approximately 2 weeks after spawning had concluded. At this time, mean wetted width along the 3 transects was 64.5 m. Mean current velocity at this site was 0.63 m/s with a range of 0.59 – 0.95 m/s along the three transects. Mean water depth was 1.41 m with a range of 0.41 – 3.0 m. Substrate analysis revealed that 57.7% of benthic particles were either gravel or larger material such as cobble (Table 3.5). In comparing 40 other sites on the lower river, we found that 5 sites had mean velocities $\geq$ 0.63 m/s, 16 sites had a mean depth of at least 1.41 m, and 16 sites had substrates comprised of at least 57.7% gravel (or larger). However, none of these sites met or exceeded habitat measures in all 3 categories (Table 3.6), although habitat measures at several sites were within 10% of those at rkm-60.

Discussion

Adult Run Size

The migratory behavior of lake sturgeon populations makes them particularly well suited for spawning stock size or abundance estimation using a two-sample population model. In most Great Lakes populations, migrating adults pass through the mouth of their natal rivers twice during each spawning run; once during upstream migration (marking phase) and once during their return to Lake Michigan after spawning (recapture phase). In previous studies of lake sturgeon on the Manistee River (Peterson et al. 2002), this migratory cycle was used to establish two distinct capture periods separated by several days of upriver spawning when marked and unmarked fish were allowed to mix randomly. In the Muskegon River however, few fish were captured during their downstream migration (only one fish in 2003 of the study). Consequently, we had to restrict our mark-recapture sampling to the pre-migratory or “staging” phase of the run in Muskegon Lake. Unfortunately, transmitters on several of these individuals were pulled out and lost as the fish struggled in the nets. While we could have implanted internal transmitters to alleviate this problem, I believed that the surgical procedures required for internal implantation were too invasive for use on ripening lake sturgeon – especially for females. Ultimately, transmitter loss during recapture events did not affect the outcome of our study and the recapture data obtained was critical in calculating meaningful estimates of annual run size.

From the initial model analysis and the subsequent highest AIC weight, there is evidence that capture and recapture probabilities are different (the latter being much lower). This indicates that the Schnabel method is inappropriate since they assume equal probability of capture and recapture. Despite the advantages of the robust design in estimating run size, the low recapture rates I encountered in this study were problematic – especially in the last 2 years of the study. Although marked fish may have been able to avoid recapture (trap shyness), this seems unlikely given the low water clarity of Muskegon Lake and the fact that we sampled only at night. Although some marked fish could have left the study area, we did not observe such behavior in the radio-tagged fish; all of which continued mill about at the Muskegon River-mouth after their release.

Discharge may not have been an important cue for upstream migration. Interestingly, the relationship between temperature and capture/recapture probability was negative. That is, as temperature increased, capture and recapture probability decreased. The results of the analysis were consistent with my hypothesis that temperature and temperature is an important cue in determining when lake sturgeon move up river. I also tested time interval since initial capture on the probability of a recapture. Not surprisingly, that relationship was positive: as the number of years since the initial capture increased, the greater the probability of recapturing an individual lake sturgeon (Table 3.2).

The Muskegon population is probably much reduced. However, the presence of spawning adults in every year of the study and the successful production of larval sturgeon in 2003 and 2005 demonstrate that the population is still reproductively viable. Furthermore, larval sampling and habitat data show that suitable spawning habitat is still accessible and that viable larvae are produced in at least some years.

The age-frequency histogram of the adult population shows that over half of the adults captured in this study were males < age-15. Because male lake sturgeon mature 3-5 years earlier than females, these data suggest that numbers of spawning females should increase sharply in the near future. The data also suggest that males begin entering the spawning population at about 11 years while females don't begin to mature until reaching approximately 17 years of age. Priegel and Wirth (1971) noted females mature at approximately 24-26 years while males usually matured at 14-16 years. Based on my age data, the Muskegon River stock consists of primarily first time spawning males and females with a few repeat spawners from both sexes.

Sex ratio data on entire populations of lake sturgeon has rarely been assessed, however, Bruch (1999) estimated the Lake Winnebago stock to consist of 43841 adult males (26,867 to 87,682 95% CI) and 7,850 adult females (4,194 to 24,979 95% CI).

Population Age Structure

Although lake sturgeon are known to live for more than 100 years (Harkness and Diamond 1961) the oldest lake sturgeon captured in our study (age-33), was born in the spring of 1970. Interestingly, the last commercial fishery for lake sturgeon on Lake Michigan was closed in that same year (Auer 1999, Bogue 2000). In our study, the absence of adult lake sturgeon older than age-33 suggests that the resumption of commercial fishing in Lake Michigan from 1950-1970 probably caused further a depletion of the Muskegon River population. Although water quality within the Muskegon watershed has improved markedly over the past three decades, the 1970 closure of the sturgeon fishery probably prevented the extirpation of the Muskegon River stock. Healthy lake sturgeon populations typically have many more age classes than what is present in the Muskegon River stock (Harkness and Dymond 1961). Bruch (1999) found the mean age of adult Lake Winnebago spawning stock was 21 years for males with individuals ranging from 12 to 44 years of age and a mean of 29 years for females with individuals ranging from 20 to 59 years. Furthermore, the Lake Winnebago lake sturgeon have been subjected to an intense, but well managed and monitored spear fishery. The range of age classes may be even greater in stocks that are unexploited. Earlier investigators found females in excess of 80 years of age (Bruch 1999).

There are fewer old Muskegon lake sturgeon since large, old individuals were subjected to the increased risk of natural mortality and a longer fishing period. Under current commercial closure of lake sturgeon harvest, the fishing period consists primarily of sturgeon captured as by-catch in the commercial fishery and poaching. However, any decline in the recruitment of lake sturgeon would translate into an underestimate of the age of mortality. Also, the catch curve assumes equal mortality rates among age classes and that they are equally vulnerable to the fishery. For this reason, data from 4 years was used and ages of fish corrected to fit for 2002 (Figure 3.3) (Pauly 1979). A basic requirement prior to generating a catch curve is that the sample should not be biased against size of certain age groups. I used a variety of mesh sizes and captured both young adults and older individuals that are likely repeat spawners.

Seasonal Habitat Use and Spawning Migrations

Despite some variation in migration timing, some general movement patterns were discernable. Upon entering Muskegon Lake, for example, lake sturgeon appeared to congregate near the river mouth at depths of 5-15 m until temperatures reached 8-11º C, at which time they usually entered the river and began moving upstream. Once there, most fish exhibited a pattern of punctuated upriver movement - typically holding for several days in deep pools followed by rapid movements upriver of 2-3 km per day. This pattern was typical of most individuals, but only during periods of stable weather. The onset of cold fronts appeared to interrupt upstream migration as most fish remained stationary in deep pools during these periods.

Perhaps the most striking and important behavior observed in this study, occurred on May 8-9 in 2002, when fish #7-2-4 and fish #8-1-4 (both ripe males) converged at a large graveled run located at rkm 60. Within 24 hours of the males' arrival at this site, fish #7-8-4 (a large gravid female) moved approximately 300 m downstream, to join the two males at this site. The movements of these fish were notable because their convergence occurred within a 24-hr period following several weeks of inactivity and because the males moved upstream while the female moved downstream. Hence, the convergence of these radio tagged fish was not simply a result of males following ripe females, as is typical of many other spawning fishes. Instead, the direction and timing of the behaviors observed in this study seemed to be initiated by some unknown biological or environmental cue. How this behavior was synchronized remains unknown although it could have been a mere coincidence. Regardless, this observation was critical in our discovery of the spawning site at rkm 60.

In all years that we conducted radio-telemetry, adult fish reached the spawning grounds in the 2nd week of May. While this too may have been coincidental, weather conditions and seasonal warming trends were markedly different in each year, which suggests that several environmental cues (e.g., temp, photoperiod, discharge) work synergistically to influence and possibly, synchronize, the timing of upstream migration. Based on telemetry data, personal observation, and the collection of larval lake sturgeon in 2003, we believe that lake sturgeon spawning occurred in each year as soon as water temperatures had warmed to 12-15 ºC. While timing of downstream migration of post-spawn adults varied, females appeared to leave the rive immediately after spawning, while males typically lingered for at least 7-10 days, often holding in the deeper pools for several days before moving further downstream. Our failure to capture adult lake sturgeon after spawning, despite extensive sampling efforts, suggests that post-spawn adults returned to Lake Michigan quickly once they left the Muskegon River.

Reproduction and spawning habitat

Several previous studies suggest that the predominance of gravel, cobble, or larger substrates are of paramount importance in determining spawning site selection by adult lake sturgeon (Priegel and Wirth 1971, Scott and Crossman 1974, Bruch and Binkowski 2002). Although my visual observations suggested that suitable spawning habitat was abundant in the lower Muskegon River, quantitative habitat assessment of the known lake sturgeon spawning site at rkm 60 revealed that this site was characterized by a unique combination of substrate, depth, and current velocity. While I was able to identify several sites on the lower Muskegon with substrates similar to those at rkm 60, either depth or current velocity at those sites was comparatively inadequate. Hence, when all three of these habitat characteristics were used to establish minimum criteria for identifying potential spawning habitat, I found that other sites on the lower Muskegon did not meet or exceeded this standard. However, given the small size of the current spawning population the assumed lack of competition for spawning sites may allow most (if not all) adults to spawn at the single best available spawning site. This area is approximately 12.2 rkm upstream from the removed dam at Newago. Based on depth, current velocity, and substrate – all of which are known to be important to spawning lake sturgeon (Bruch and Binkowski 2002, Auer 1996, Baker 1980), - that site is probably the one at rkm 60. Although somewhat speculative, this theory would also explain how so few adults (as evident from our annual run estimates) are able to coordinate their spawning activities at a single time and place in the lower 73 rkm of the Muskegon River. More importantly however, these findings may suggest that other sites, especially those with suitable substrate and at least one of the other two habitat criteria may be used by spawning lake sturgeon as the population recovers and competition for spawning sites increases. The fact that we captured larvae at different developmental stages gives credence to this possibility. In fact, previous studies of lake sturgeon spawning habitat in Wisconsin rivers (Priegel and Wirth 1971, Bruch and Binkowski 2002) suggest that adults often select spawning sites with current velocities as low as 0.5 m/s and depths of only 0.5 m. By substituting these criteria for those obtained from the micro-habitat assessment at rkm 60, I found that 12 of the other 40 sites sampled (30%) on the lower Muskegon may provide suitable spawning habitat for adult lake sturgeon (Table 3.7). Based on the proportion of these suitable sites in each of the four river reaches sampled, I estimated that the lower Muskegon may actually contain more than 11 rkm of suitable spawning habitat.

The minimum criteria for current velocity ($\geq$0.5 m/s) was established from published values lake sturgeon spawning habitat in Wisconsin (Priegel and Wirth 1971). The minimum criteria for substrate (>58% gravel or larger particles) was established from substrate measurements at the known spawning site (rkm 60) on the Muskegon River.

Although more detailed habitat analyses are needed to confirm and further refine this estimate, these findings suggest that the lake sturgeon population of the Muskegon River may be an excellent choice for future restoration efforts because the abundance of potential spawning habitat greatly increases the likelihood that this remnant stock could someday recover to self sustaining levels.

Conclusion

The results of this study show that the Muskegon River still supports a small, but naturally reproducing population of lake sturgeon and that riverine spawning habitat is probably sufficient to support a restored population (Table 3.6). I have documented evidence of lake sturgeon reproduction in 2003 and again in 2005. Because of the current scarcity of adult spawners however, the Muskegon population may require many years to fully recover. Ultimately, recovery of this population may depend, not only on protection of the remaining individuals, but also on our ability to protect spawning fish and their habitats from further human disturbance. If active restoration of lake sturgeon is attempted on the Muskegon River, concurrent studies will be needed to monitor the population's response, and to evaluate success or failure as a guide for other restoration programs. To determine whether current closures on exploitation are enough to help this population increase, the Muskegon Lake sturgeon should at least be monitored for several years. Based on the population trend, further restoration plans could then be implemented.

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Chapter 4

Synthesis

Lake sturgeon were once an ecologically and economically important species throughout the Great Lakes (Scott and Crossman 1973, Tody 1974, Slade and Auer 1997). Although quantitative studies of historic abundance are lacking, some authors estimate that the historic population in Lake Michigan may have exceeded 11 million individuals (Baldwin et al. 1979, Lyons and Kempinger 1992). As discussed in my summary of historic fishing practices and failed fisheries management strategies presented in Chapters 1 & 2, the severity and duration of historic lake sturgeon declines throughout the Great Lakes has been well established (Smith and Snell 1889, Tody 1974, Bogue 2000). Unfortunately, population declines that began in the 19th Century have been difficult to reverse because of the species' slow intrinsic population growth rate and the chronic degradation of sturgeon habitats throughout the region (Auer 1996). Log drives and pulp and paper mill industries were well developed on most Michigan rivers by the early 1900s and many of prime lake sturgeon spawning tributaries were severely altered by unsustainable logging practices. Pulp effluents also destroyed nursery sites, critical for early life stages (Brousseau and Goodchild 1989). As a result, the Michigan Department of Natural Resources has listed the species as threatened throughout the state (Section 36505 (1a), Part 324, Endangered Species Protection (Hay-Chmielewski and Whelan 1997).

Because lake sturgeon are long lived, spawning runs are typically comprised of hundreds or even thousands of adults from year classed that have accumulated over many decades. My results from the Muskegon River, however, showed that the annual spawning run was <50 individuals (Table 3.4). Furthermore, the age-structure of the adult population was comprised primarily of young males, many of which were likely first-time spawners. In fact, the oldest fish captured – age 32, was less than one-fourth of the maximum known age for the species. Within the context of lake sturgeon life history discussed in Chapter 2, my data suggest that the Muskegon is probably near extirpation. Still, the disproportionate number of young males age 9-12, suggest that many young females may soon recruit to the spawning population, given that females typically mature 3-5 years later than males.

Although the causes of the Muskegon lake sturgeon population decline are unclear, they probably include chronic overfishing, and several of the habitat disturbances outlined in Chapter 2. During my 4 field seasons on the Muskegon, I collected data and observations that documented many anthropogenic disturbances, including altered flow regime, degraded water quality, and physical disturbance by boats and anglers. Despite these many problems, however, my data do provide some hope for recovering the population. Not only did my larval collections demonstrate that adults are still able to spawn below the Dam at rkm 73, but also, that viable larvae are produced – at least in some years. Furthermore, my survey of potential spawning habitat suggests that while sturgeon were only observed spawning in one location, other spawning sites may be used in the future if/when the population increases. Further studies are needed to quantify larval production and to better understand the linkages between habitat and survival of early life stages.

Until recently, lake sturgeon management strategies within the Great Lakes have failed to appreciate the unique nature of lake sturgeon population dynamics. Consequently, initial attempts to manage lake sturgeon stocks failed to stop the rangewide collapse of most stocks (Harkness and Dymond 1961, Ferguson and Duckworth 1997, Auer 2004). Although recent restoration efforts have provided new hope that some populations can be restored, implementation of effect restoration programs have been hindered by a general lack of life history information (Smith and King 2005). Unfortunately, the life history characteristics that have made them an evolutionary success have continued to hamper recovery efforts today (Crouse 1999, Secor and Waldman 1999). For example, the results of my study suggest that the annual spawning runs are currently so small, that recovery of the adult population will likely require many decades of protection of both the fish and critical spawning habitats. Nonetheless, the habitat data I collected in 2006 suggest that the Muskegon River still has enough high quality spawning habitat to support significant population growth. As such, future restoration of the Muskegon population may be possible.

Despite the final closure of the lake sturgeon fishery in 1970, current commercial fishing practices on the Great Lakes may continue to threaten to the Muskegon River population. Fortunately, juvenile sturgeons are relatively resilient to when captured in most types of commercial fishing gear - at least when gear soak times are less than 24 hours (Secor and Waldman 1999). As current restoration efforts for lake sturgeon begin to yield positive results, recovering populations must remain protected from both legal harvest and from incidental by-catch in other commercial fisheries. Recently, gill nets have been banned in several Great Lakes commercial fisheries in favor of entrapment gear that is much less destructive to most non-target species including lake sturgeon (Rob Elliot-USFWS, Pers. Comm.).

Although habitat destruction and overfishing have devastated most Great Lakes populations of lake sturgeon, recent restoration efforts have been hampered by a lack of information regarding current distribution and habitat availability (Lyons and Kempinger 1992, Auer 2004). The results of my studies show that while the Muskegon River population has suffered a similar decline, the River still supports a small but reproductively viable population – making it one of the last remaining stocks within the Lake Michigan Basin (Holey et al. 2000, Peterson et al. 2002, Peterson and Vecsei 2004, DeHaan et al. 2006). My study has also provided new methods for future lake sturgeon assessments on other Great Lake tributaries, as well as baseline data on current status of the Muskegon population. The result of my study have also provide new information regarding sex ratio, age structure, and the temporal and spatial variations in seasonal migration and spawning.

Given that the primary goal of rehabilitation is to re-establish self-sustaining populations (Hay-Chmielewski and G. Whelan 1997), a logical first step must be to complete a comprehensive inventory of current stocks and habitat availability. In this study, I used Robust Design population estimates, to show that there is a lack of evidence that discharge effected capture and recapture probabilities. However, the analyses did find evidence that time away and water temperature was related to capture/recapture probabilities suggesting that the lake sturgeon spawning cycle may be particularly sensitive to seasonal changes in temperature. Although these estimates are the first of their kind for the Muskegon River population, future studies are needed to evaluate long-term population trends and recruitment mechanisms. The results of these future studies should provide the basis of specific management plans for restoration of the Muskegon River population (Hay-Chmielewski and Whealan 1997, Bruch 1999, Bruch and Binkowski. 2002).

In Chapter 3, I present a quantitative habitat assessment of the lower (free- flowing) reach of the Muskegon River. The single spawning site documented in this study, was characterized by a unique combination of substrate, depth, and current velocities. Although I also identified several other potential spawning sites with similar substrates in this reach, other parameters were not within the range of those where lake sturgeon spawning was observed. Nonetheless, several of these other sites were similar enough that they may provide suitable spawning habitat as the population recovers. Several previous investigations (Priegel and Wirth 1974, Bruch and Binkowski

2002, LaHaye et al. 1992) have shown that spawning lake sturgeon prefer sites with a depth of 0.5 m, current velocities of 0.5 m/s, and cobble substrates. Although lake sturgeon spawning was observed at only 1 specific site on the Muskegon River, my habitat assessment revealed several other sites with similar ranges of these habitat variables.

As lake sturgeon rehabilitation programs are considered, the genetic structure of extant sub populations is receiving increased attention. Species with high dispersal rates often exhibit low levels of interpopulation variance in allele or haplotype frequency (Stabile et al. 1996). Species such as sturgeons, however, possess strong natal homing tendencies (Auer 1996, Lyons and Kempinger 1992, Auer 1996, DeHaan et al. 2006) and, consequently, would be expected to show increased levels of spatial structure. Tag returns from previous studies of sturgeon movements indicate that lake sturgeon exhibit natal philopatry (Auer 1999, Gunderman and Elliott 2004). Likewise, genetic studies shown that most extant lake sturgeon populations exhibit inherently low levels of genetic diversity and low levels of spatial genetic structure (Ferguson et al. 1993). Ferguson and Duckworth (1997) found only two mtDNA haplotypes in a survey of several lake sturgeon populations and assumed genetic diversity to be low. However, lake sturgeon have a broad, yet fragmented, range throughout the Great Lakes (Holey et al. 2000) and typically, would exhibit some level of spatial genetic structuring (DeHaan et al. 2006). The results from Ferguson and Duckworth (1997), however, lacked the genetic resolution to identify specific local populations of individual fish from a specific drainage. To identify management units, more hypervariable markers were required (DeHaan et al. 2006). DeHaan et al. (2006) observed a high diversity of haplotypes in 11 lake sturgeon populations in Lake Superior and Lake Michigan when a more variable region of the mtDNA genome was sequenced. They concluded that genetic diversity was high despite the small size of remnant stocks investigated. Data on the degrees of differentiation within lake sturgeon populations could give valuable insight into the amount of genetic variation among distinct stocks (Leary and Brooke 1990, Lyons and Kempinger 1992).

Agencies should consider a population's genetic structure into any basin-wide lake sturgeon management plan. The origin of all sturgeons caught in the Great Lakes could be traced to their natal river system. Such measures may prove important for effective management of distinct remnant stocks (Welsh and McClain 2004). Fisheries managers should try to preserve the genetic diversity and long-term health of rehabilitated sturgeon populations by using only brood stock originating from the system being rehabilitated (Auer 1996, DeHaan et al. 2006). Genetic diversity of hatchery-reared fish must be paramount in any future stock enhancement efforts to prevent target populations from risks of genetic drift and/or inbreeding depression. While these problems have not yet been detected in any North American sturgeon species, their deleterious effects on reproductive output have been well documented in small populations of several other vertebrates (Kapuscinski and Miller 2007).

Previous studies of lake sturgeon have focused on adult movements and habitat use (Fortin et al. 1993, McKinley et al. 1998, Auer 1999, Peterson et al. 2002). Long-term tagging studies have shown that adult lake sturgeon migrate from lakes or large rivers to spawning sites in upstream tributaries (Bemis and Kynard 1997, Smith and Baker 2005). These migrations are thought to increase likelihood of successful reproduction by depositing eggs in habitats favorable for incubation and survival of the vulnerable early life stages (Legett 1977, Auer 1996, Bemis and Kynard 1997). Previous studies also have shown that adults select distinct habitats throughout the year (Fortin et al. 1993, Rusak and Mosindy 1997, Knights et al. 2002), depending on specific needs at each stage of the life cycle. During the course of my radio telemetry tracking of adult lake sturgeon in the Muskegon system (Chapter 3), I have documented the annual movement of adults from Lake Michigan into Muskegon Lake and their subsequent upstream migration to the spawning grounds at rkm 60. Within the River, I found several discrete sites that were used repeatedly by migrating adults, during and after spawning. These results not only demonstrate a high degree of site fidelity among adult lake sturgeon, but more importantly, they emphasize the importance of protecting these specific habitats types within the lower river.

Prior to upstream migration, lake sturgeon were located in the deep waters in the vicinity of the river mouth. Water temperature has been previously cited as the dominant factor in triggering upstream movement of spawning lake sturgeon (Scott and Crossman 1973, Rusak and Mosindy

1997). In the Muskegon River, adult lake sturgeon began entering spawning tributaries as water temperatures reached 5-8 °C. Thereafter, the rate of upstream migration was positively correlated with river temperature. When temperatures declined during extended cold fronts, adults remained stationary in deep pools which appeared to serve as resting or staging areas. After spawning adults left the river within a few days; a behavior commonly observed by other lake sturgeon researchers (Harkness and Dymond 1961, Lyons and Kempinger 1992, O'Neil 1997, Auer 1999, Peteson et al. 2007). In the Muskegon River, as in many Great Lakes tributaries, my studies of adult lake sturgeon movements showed that spawning migrations are typically comprised of a series of gradual transitions from riverine to lacustrine habitats.

Although the results of my study show that the Muskegon River still contains considerable lake sturgeon spawning habitat, the effects of Croton Dam at rkm 73 are difficult to assess. Like most dams built in the early 1900s, Croton Dam was operated as a hydroelectric 'peaking' facility until 1994. This caused significant fluctuations in hourly discharge throughout the day. During the relicensing process in the 1980s and 1990s, new instream flow requirements were implemented and Croton Dam began operating as 'run of river'. The resulting changes in flow regime probably helped improve conditions for lake sturgeon spawning, and ultimately, young-of-year survival. Although the age frequency histogram presented in Chapter 3 would seem to support this assertion, is still threatened by a precariously small spawning stock and by the physical barrier of Croton Dam that has blocked access much of high gradient spawning habitats once available to this population.

Although a few examples of impounded lake sturgeon populations can be found in both Wisconsin and Michigan (Priegel and Wirth 1974, Priegel and Wirth 1978, Folz and Meyers 1985, Smith and Baker 2005), habitat fragmentation is probably the single most serious impediment to restoration of most remnant stocks(Auer 1999, Auer 2004, Peterson et al. 2006). Unfortunately, nearly all the Great Lakes watersheds are chronically affected by human developments. Over the last 100 years, flows in most spawning tributaries have been drastically altered by a variety of industries. Too often, fish habitats considered vital to species restoration, have been defined on a site-specific basis. Because of their complex life history, lake sturgeon require access to a variety of broadly distributed habitats (Beamesderfer and Farr 1997). Consequently, sturgeon habitats identified for protection must be defined in terms of watersheds and natural flow regimes (Beamesderfer and Rien 1993, Carlson et al. 1985).

Ultimately, lake sturgeon populations of the Great Lakes may become a positive example of how effective protections offered by state endangered species legislation can provide the first steps toward restoration. Because of their long-distance migrations, lake sturgeon almost always will fall under the management responsibility of several state, federal, tribal, and international jurisdictions. To date, the recently implemented management plans in Michigan and Wisconsin have precluded the need for listing lake sturgeon under the federal Endangered Species Act (Welsh and McClain 2004). Public involvement and support also have been critical for in these efforts. With an increased public awareness concerning the current threatened state of most lake sturgeon stocks, compliance with the regulatory framework is more likely.

In recent years, many state agencies throughout the Great Lakes have worked together to develop an integrated lake sturgeon management strategy (Welsh and McClain 2004). In some areas, tribal efforts have helped acquire additional data to facilitate better management of local lake sturgeon populations. In fact, tribal governments in Wisconsin, Minnesota, and Ontario are currently engaged in lake sturgeon management programs aimed at re-establishing sustainable fisheries (Holzkamm and Waisberg 2004). Although lake sturgeon have not been listed under the ESA, the possibility of federal listing has probably acted as a “wake-up call” for many state agencies to better manage their local populations and to improve state endangered species protections (Walsh and McClain 2004).

Whether remnant lake sturgeon populations can be saved without wide-scale habitat restoration remains to be seen; however, recent efforts to establish a coordinated research and management program within the Great Lakes have provided some reason for optimism. In the Muskegon River, lake sturgeon access to historic spawning sites above Croton Dam has been lost, but the results of my study show that high-quality spawning habitats are still available downstream. Furthermore, a recent assessment of lake sturgeon rivers within the Great Lakes region ranked the Muskegon as “highly suitable” based on the quality and diversity of habitats still available (Lyons and Kempinger 1992). Not only has my habitat evaluation confirmed these assertions, but it also has provided the first documentation of an active spawning site within the lower reach of River. Although the mark-recapture estimates presented in Chapter 3 suggest the annual spawning run may be precariously small (<50 adults/yr), the availability of high-quality spawning habitat below the dam suggests that the population could be rehabilitated. The future success of management efforts, however, will inevitably depend on effective protection of these critical riverine spawning habitats.

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Tables

Table 3.1. Catch-per-unit-effort (CPUE) of lake sturgeon in different mesh sizes of 100-m gill nets set at the mouth of the Muskegon River. Calculations of CPUE were limited to the interval of sturgeon captures during spring 2002-2005.

2002			
Mesh Size (cm)	**Effort (hr)**	**Captures**	**CPUE (fish/hr)**
20	200	1	0.00500
25	330	6	0.01818
32	240	7	0.02917
36	90	0	0.00000
2003			
20	360	1	0.00278
25	770	8	0.01039
32	350	3	0.00857
36	220	7	0.03182
2004			
20	179	0	0.00000
25	199	6	0.03016
32	227	2	0.00888
36	130	1	0.00769
2005			
20	153	0	0.00000
25	632.5	2	0.00316
32	536	6	0.01124
36	396	9	0.02273
Totals for All Years			
20	892	2	0.00224
25	1931.5	22	0.01139
32	1353	18	0.01330
36	1672	17	0.01017

Table 3.2. Model selection summary for Huggins Robust Design models relating lake sturgeon abundance in the Muskegon River to variations in immigration (1-gamma') and capture probability.

Model	-2LogL	K	AICc	ΔAICc	wi
Survival(.), Immigration (time since), Capture(temperature)	364.15	5	375.28	0.00	0.39
Survival(.), Immigration(.), Capture(temperature)	368.60	4	377.34	2.05	0.14
Survival(.), Immigration (time since), Capture(temperature, discharge)	364.01	6	377.63	2.34	0.12
Survival(.), Immigration (time since), Capture(recapture, temperature)	364.15	6	377.77	2.48	0.11
Survival(.), Immigration(.), Capture(temperature, discharge)	368.44	5	379.57	4.28	0.05
Survival(.), Immigration(.), Capture(recapture, temperature)	368.60	5	379.73	4.44	0.04
Survival(.), Immigration (time since), Capture(recapture, temperature, discharge)	364.01	7	380.20	4.92	0.03
Survival(.), Immigration (time since), Capture(recapture)	369.70	5	380.83	5.54	0.02
Survival(.), Immigration (time since), Capture(recapture, discharge)	367.44	6	381.05	5.77	0.02
Survival(.), Immigration (.), Capture(recapture, temperature, discharge)	368.42	6	382.04	6.75	0.01
Survival(.), Immigration (.), Capture(recapture)	374.07	4	382.81	7.53	0.01
Survival(.), Immigration (.), Capture(recapture, discharge)	371.84	5	382.97	7.69	0.01
Survival(.), Immigration (time since), Capture(discharge)	373.14	5	384.27	8.99	0.00
Survival(.), Immigration (.), Capture(discharge)	377.65	4	386.39	11.10	0.00
Survival(.), Immigration (time since), Capture(.)	378.59	4	387.33	12.04	0.00
Survival(.), Immigration (), Capture(.)	383.06	3	389.50	14.21	0.00

Table 3.3. Parameter estimates for the best Huggins robust design model relating lake sturgeon abundance in the Muskegon River to immigration (1-gamma') and capture probability. Emigration probability (gamma") was fixed at 1. All parameter estimates are on the logit scale.

Parameter	Estimate	Standard error	95% confidence interval	
			Lower	Upper
Survival				
Intercept	1.491	1.144	-0.388	4.045
1 - Immigration				
Intercept	-0.300	1.384	-2.994	2.515
Time since spawning	-0.778	0.122	-1.035	-0.555
Capture probability				
Intercept	-2.226	0.396	-3.002	-1.450
Average water temperature during sampling	-0.304	0.087	-0.475	-0.133

Table 3.4. Robust Design Population Estimate for Muskegon Lake sturgeon from 2002-2005

Year	Estimate	Standard error	95% confidence interval	
			Lower	Upper
2002	31	8.97	20	58
2003	23	7.13	15	45
2004	19	6.28	12	39
2005	34	9.36	23	62

Table 3.5. Substrate composition of known lake sturgeon spawning site at rkm 60 of the Muskegon River, 2006.

Transect	Substrate Composition (%)				
	Sand	Pebble	Gravel	Cobble	Boulder
1	30	30.0	23.3	16.7	0
2	20	23.3	26.7	16.7	13.3
3	10	13.3	60.0	3.3	13.3
Mean	20	22.2	36.6	12.2	8.9

Note: The minimum criteria for current velocity ($\geq$0.5 m/s) was established from published values lake sturgeon spawning habitat in Wisconsin (Priegel and Wirth 1971, Bruch 2001). The minimum criteria for substrate (>58% gravel or larger particles) was established from substrate measurements at the known spawning site (rkm 60) on the Muskegon River

Table 3.6. Abundance of potential spawning habitat for adult lake sturgeon on the Lower Muskegon River.

Reach (rkm)	Sample Sites	# Sites Meeting Min Criteria for Substrate	# Sites Meeting Min Criteria for Velocity	# Sites Meeting Both Min Criteria	RKM of Potential Spawning Habitat
73.7–66.0	8	3	2	1	0.96
66.0–60.8	11	8	9	7	3.31
60.8–54.0	11	4	7	3	1.86
54.0–0.0	11	1	4	1	4.91
Totals:					10.04

Figures

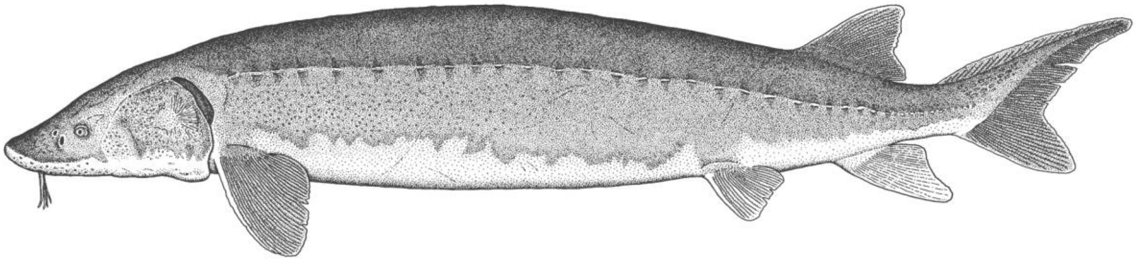

Figure 2.1. Basic morphology of the adult lake sturgeon.

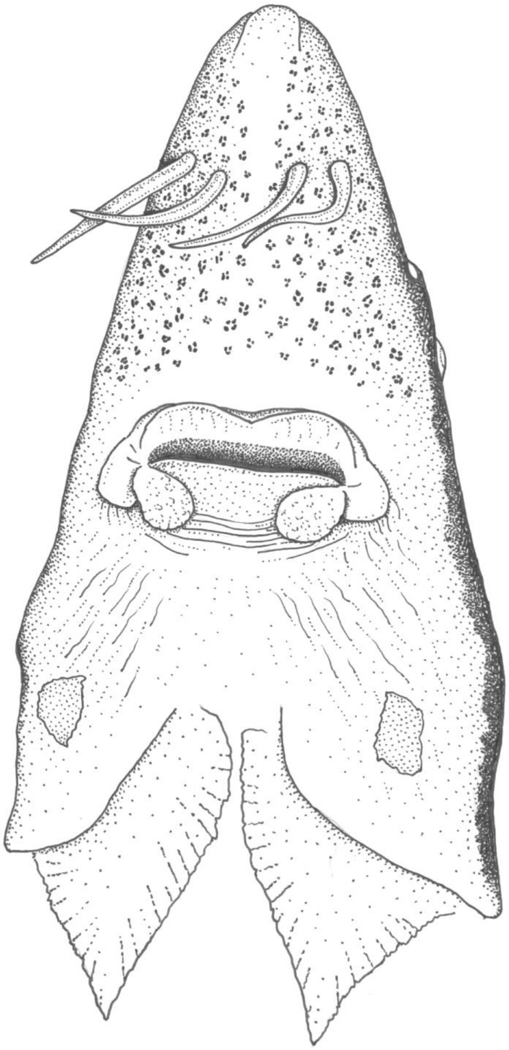

Figure 2.2. Ventral view of lake sturgeon head, showing distribution of sensory pits and relative position of barbells and mouth.

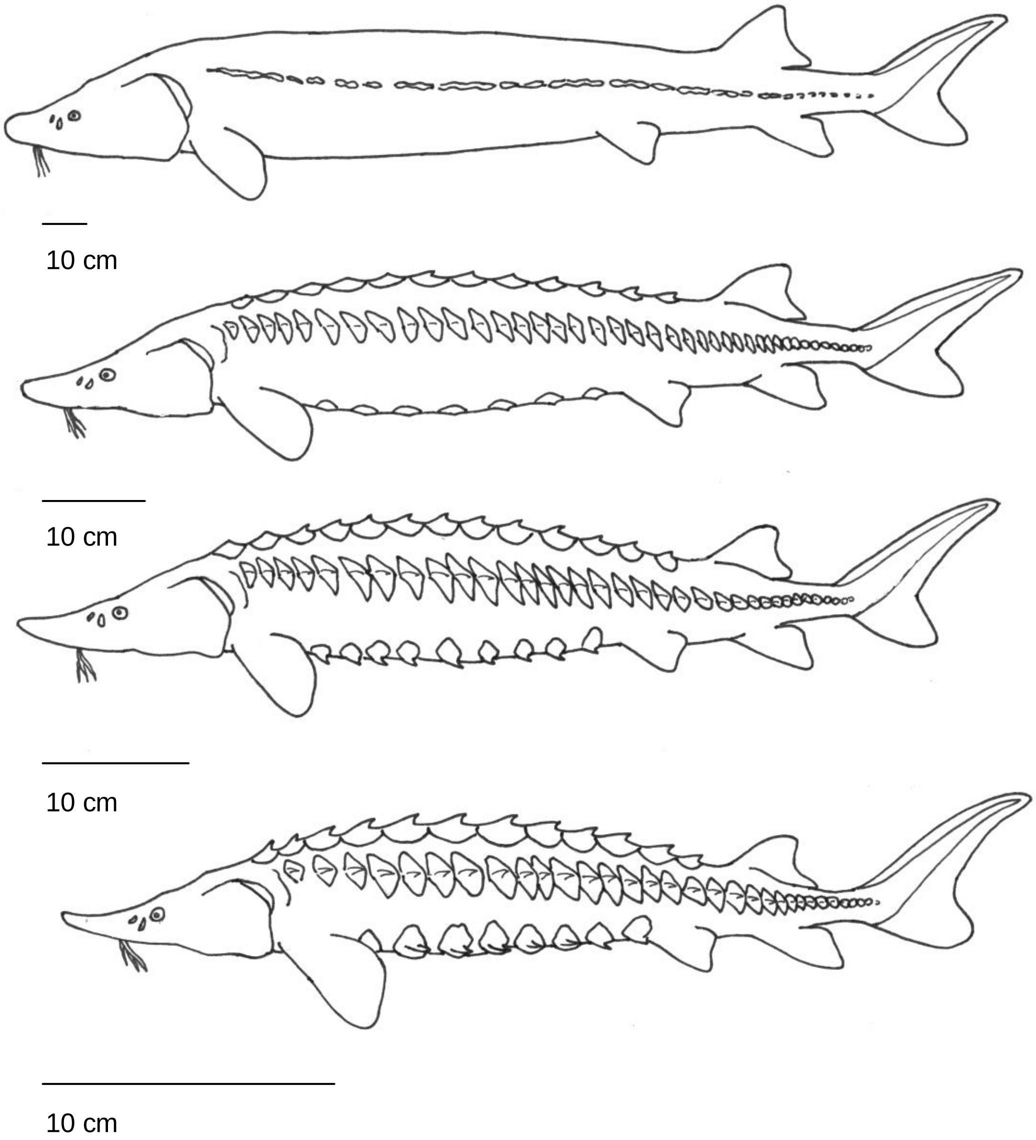

Figure 2.3. Ontogenetic changes is body armoring of lake sturgeon from early juvenile stage (bottom) through late adulthood (top).

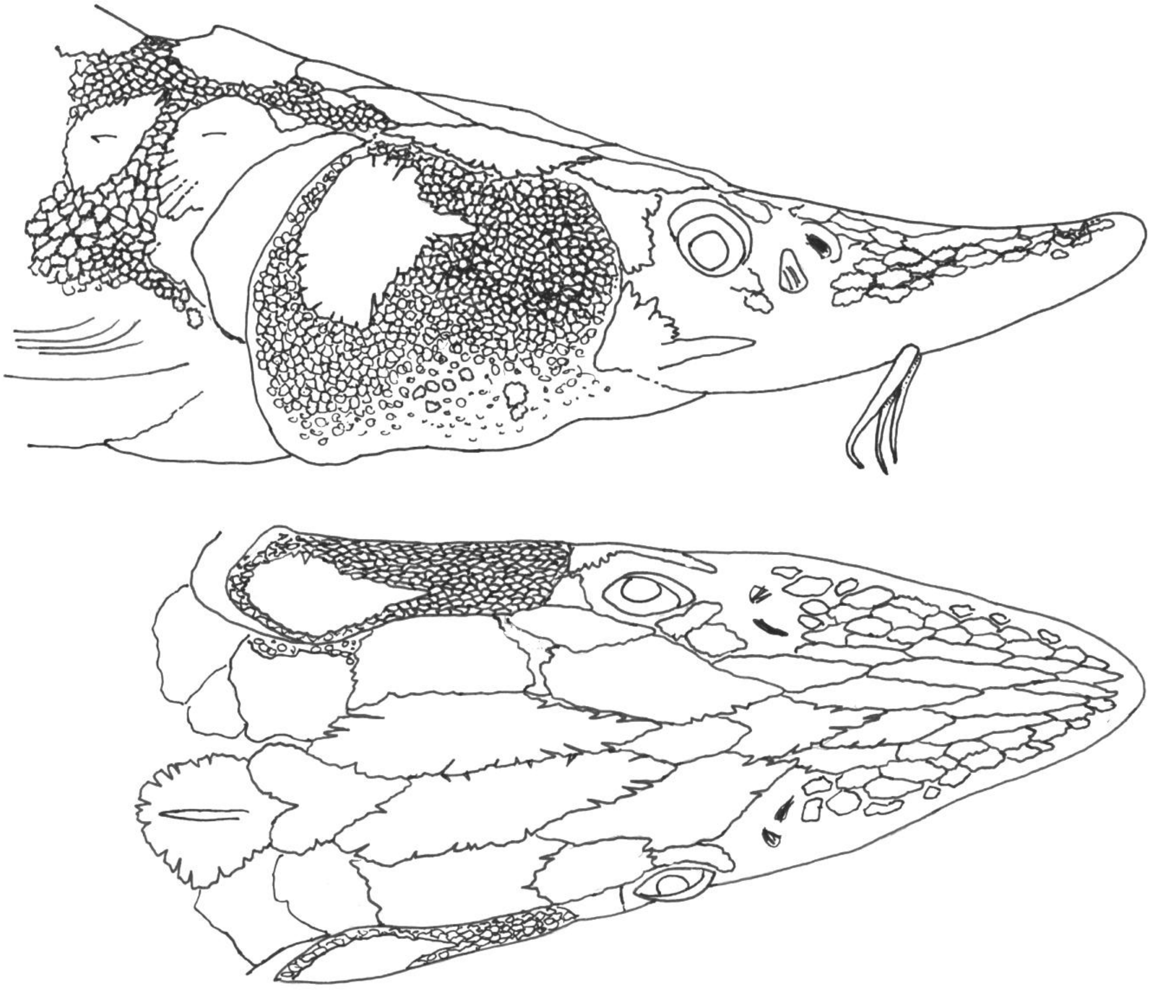

Figure 2.4. Armoring of the lake sturgeon skull.

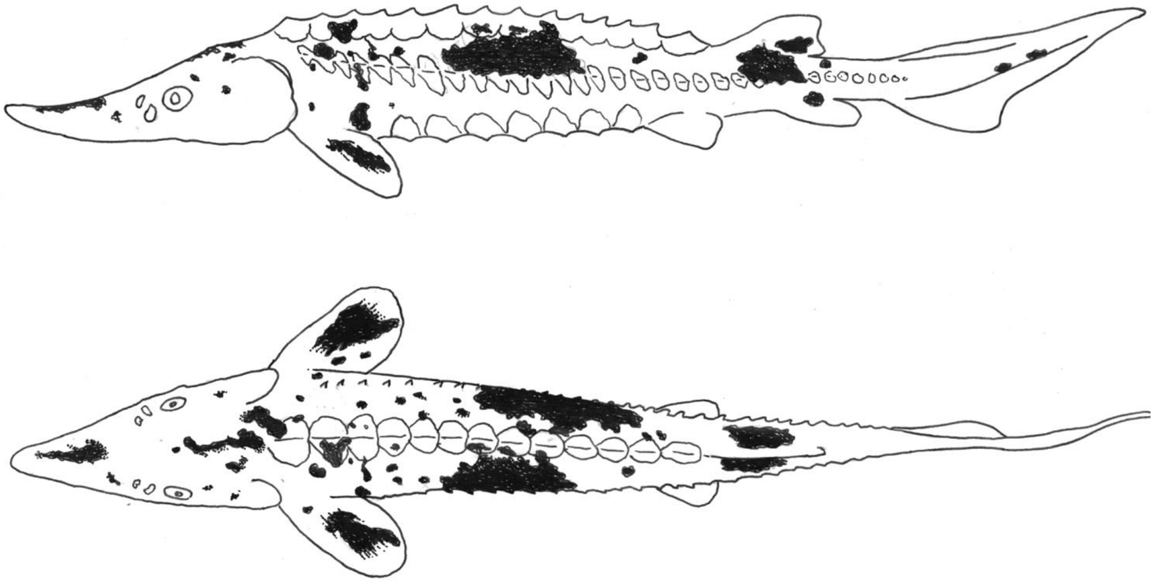

Figure 2.5. Basic morphology and coloration of juvenile lake sturgeon (<30 cm).

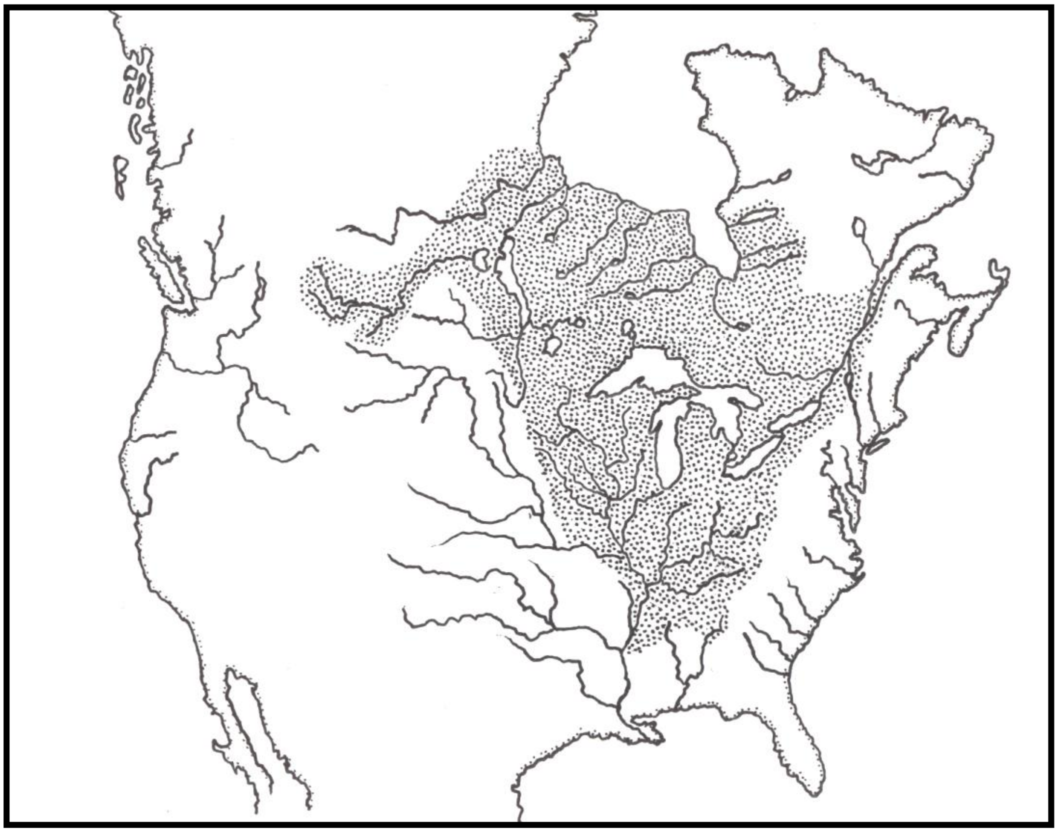

Figure 2.6. Historic distribution of lake sturgeon in North America (adapted from Scott and Crossman 1973, and CITES 2000).

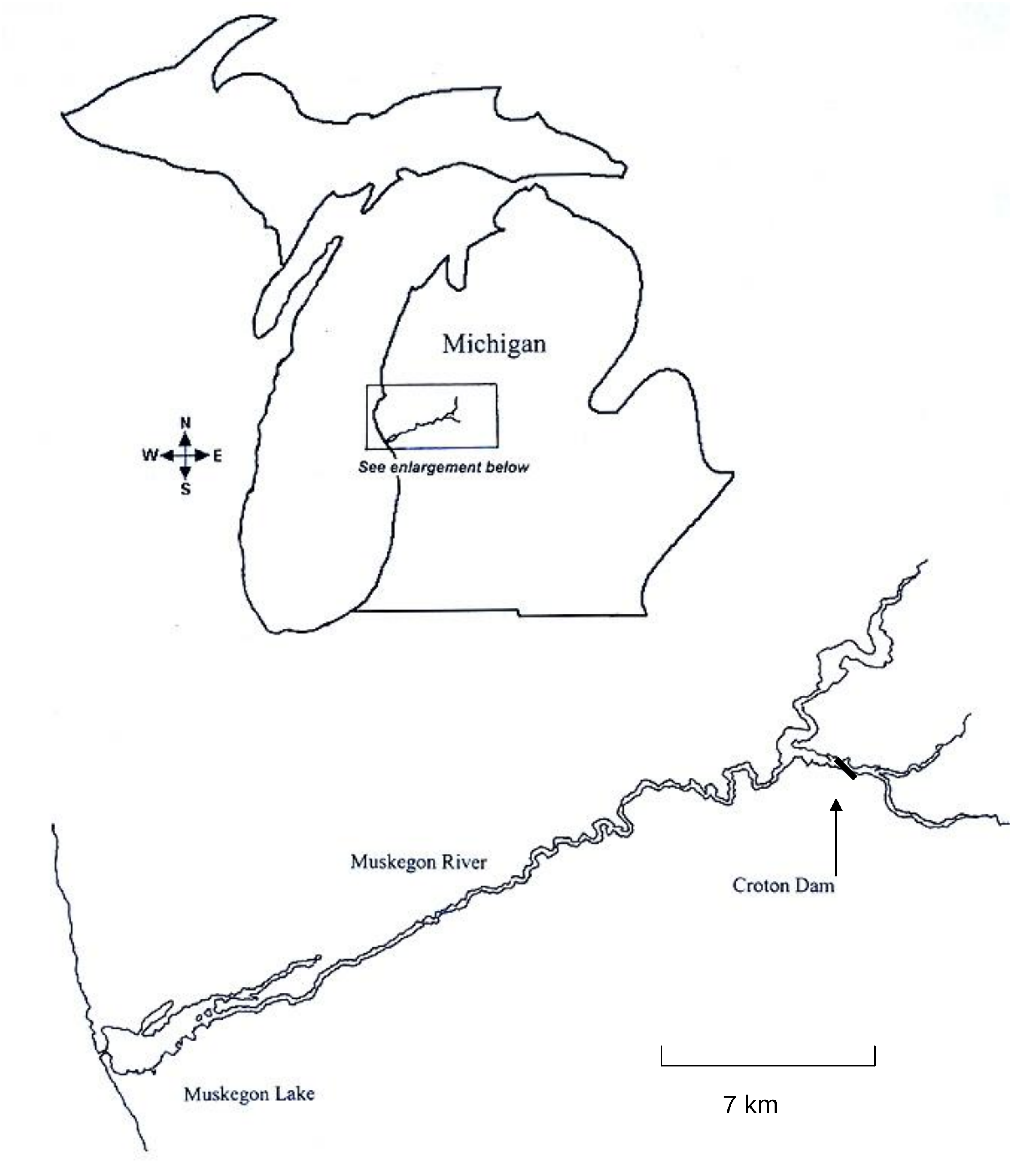

Figure 3.1. Lake sturgeon study site on the Muskegon River, Michigan.

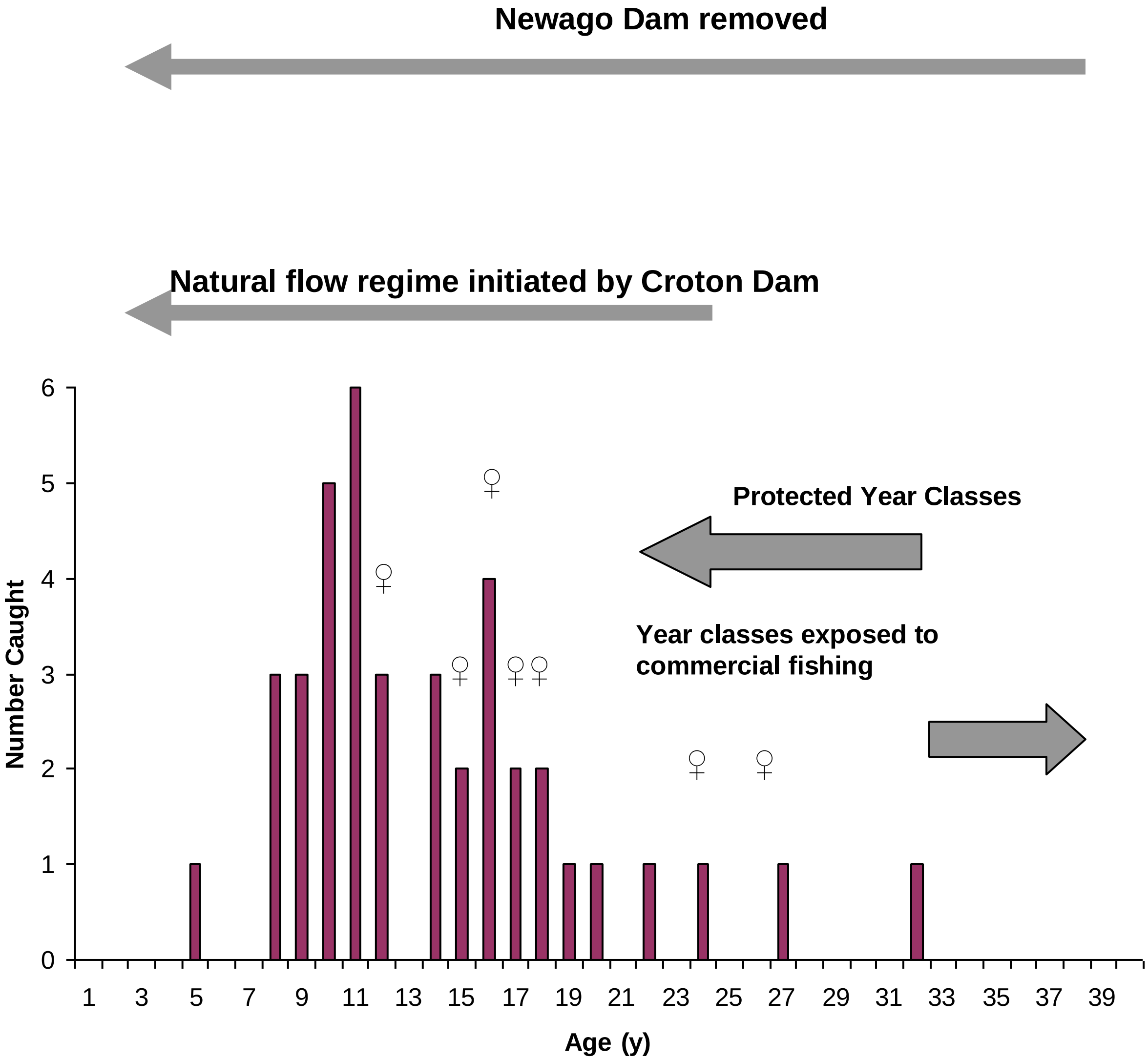

Figure 3.2. Age-frequency distribution of adult lake sturgeon captured at the mouth of the Muskegon River, 2002-2003. Arrows illustrate protected and exploited year classes of lake sturgeon based on the closure of the last commercial fishery in Lake Michigan in 1970, Newago Dam removal and start of natural flow regime by Croton Dam

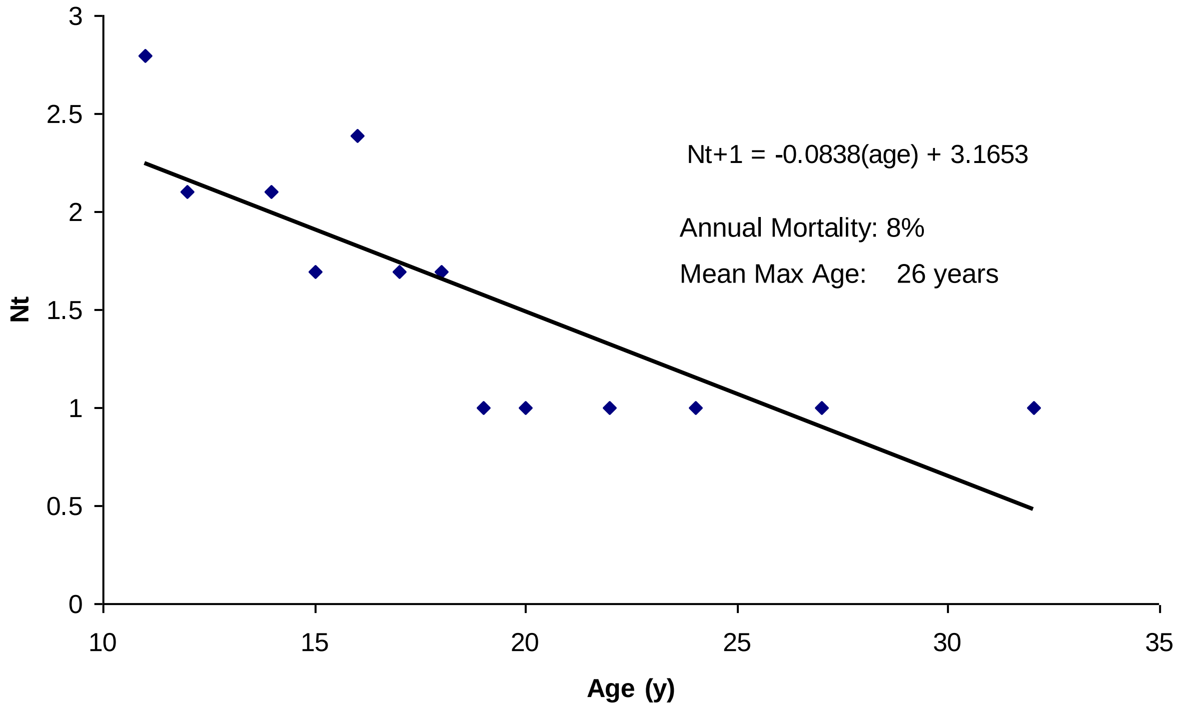

Figure 3.3. Catch curve of adult lake sturgeon captured in the Muskegon River, 2002-2005. Note: ages of all fish captured from 2003-2005, were adjusted to represent their estimated age in 2002 (e.g., an age-12 fish in 2003 is depicted here as age-11 in 2002).

Appendix I

Catch data and biological statistics of radio-tagged lake sturgeon captured in the Muskegon River, 2002-2005.

Fish ID	Date of Capture	Sex	1st Contact in River	Temp (°C)	River Contacts	1st Contact at Spawning Site	Temp (°C)
				2002			
8-1-4	Mar 21	♂	April 15	14.0	10	May 8	12.0
7-8-4	Mar 27	♀	April 16	13.2	9	May 8	12.0
7-2-4	Apr 5	♂	April 24	13.5	9	May 8	12.0
7-6-4	Apr 14	?	*	*	*	*	*
				2003			
8-5-4	Mar 28	♂	Apr 15	7.0	18	***	***
7-4-4	Mar 28	♂	Apr 15	7.0	19	May 9	11.1
8-3-4	Mar 31	♀	**				
6-9-5	Apr 1	♂	Apr 15	7.0	5	***[1]	***
8-7-1	Apr 2	♂	**				
6-7-4	Apr 7	♀	Apr 20	7.2	7	Apr 30	10.8
				2005			
3-7-2	Mar 23	♂	Apr 9	9.5	14	Jun 02	18.3
4-1-2	Mar 24	♀	Mar 31	9.4	11	Lost contact	
8-9-2	Mar 29	♀	Apr 9	9.5		Stayed lower	
2-9-1	Mar 24	♂	Apr 9	9.5	11	May 9	
4-5-1	Apr 1	♂	Never ran				
6-1-1	Apr 2	♂	Apr 11	9.2			
2-7-2	Apr 4	♀	Apr 16	5.8	17	Left river	

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[1] On April 25, the fish was snagged by an angler and fought for approximately 45 minutes. Upon retrieving his line, the angler found that his hook had actually snagged the transmitter which was apparently pulled from the fish during the ensuing fight.

Fish ID	Date of Capture	Sex	1st Contact in River	Temp (^{o}C)	River Contacts	1st Contact at Spawning Site	Temp (^{o}C)
5-0-2	Apr 4	♂	Apr 9	7.0	29	May 12	15.0
3-5-2	Mar 27	♂	Apr 16	9.2	16	Too slow	
2-5-2	Apr 10	♂	Never ran				