MODELING THE POPULATION DYNAMICS AND SUSTAINABILITY OF LAKE STURGEON IN THE WINNEBAGO SYSTEM, WISCONSIN

by

Ronald M. Bruch

A Dissertation Submitted in

Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

In Biological Sciences

At

The University of Wisconsin-Milwaukee

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Major Professor Dr. Michael J. Hansen — Date

Graduate School Approval — Date

ABSTRACT

MODELING THE POPULATION DYNAMICS AND SUSTAINABILITY OF LAKE STURGEON IN THE WINNEBAGO SYSTEM, WISCONSIN

by

Ronald M. Bruch

The University of Wisconsin-Milwaukee, 2008
Under the Supervision of Dr. John Janssen and Dr. Michael J. Hansen

The sustainability of exploited animal populations is increasingly a concern as species extinction rates accelerate due to the impact of human activities on the environment. Sturgeon are a group of large-sized, long-lived and late-maturing periodic-strategist anadromous and freshwater fishes that over the last 100 years suffered excessive harvesting of adults primarily for their prized caviar, and consequently, are now seriously threatened throughout their holarctic range. To achieve recovery and effective management of sturgeon, their population dynamics must be clearly understood.

I used 60 years of data, bomb radiocarbon dating, and a series of fisheries models including a statistical catch at age analysis of lake sturgeon (*Acipenser fulvescens*) from the Winnebago System in east central Wisconsin, USA, to validate age estimates, define age and growth, weight-length relationships, size and age at maturity, fecundity, eggs per recruit, recruitment, mortality rates, abundance and yield per recruit. Age estimates of pectoral fin spines underestimated true age after age 14 defined by the power function *True Age = Estimated Age^1.054796*. Frontal cross sections of the otoliths accurately estimated true age.

Growth of Winnebago lake sturgeon occurs in two growth stanzas with an inflexion point at 96 cm (total length), age 12, with dimorphic separation of length at age occurring between males and females at 131 cm, age 25. Weight-length relationships were also best defined in two growth stanzas with an inflexion point at 71 cm, and by sex and stage of sexual maturity.

The population of lake sturgeon of the Winnebago System exhibits a protracted maturation period with males reaching 50% maturity at 120 cm, age 20, and females at 139 cm, age 27. Mean fecundity was 445703 (12767 eggs/kg body weight) with weight the best predictor of fecundity. Mean recruitment during 1955-2007 was estimated at 9002 yearlings each year, although stock-recruitment exhibited a Ricker-style inverse relationship. Instantaneous natural mortality was estimated at 0.055, and total annual mortality at 8.8% during 1977-2007. Abundance of lake sturgeon increased fourfold during 1954-2007 in the Winnebago System, an intrinsic rate of increase of 0.049, likely reaching carrying capacity in the 1990s due to long-term management policies beginning in 1874, and increased non-point pollution during the 1960s–1980s.

Long term simulation modeling predicted Winnebago lake sturgeon maintain population robustness at or below an annual exploitation rate of 4.7%, but significantly decline at higher exploitation levels, and go extinct at 20% exploitation.

Dec 11 2008

Major Professor Dr. John Janssen — Date

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Major Professor Dr. Michael J. Hansen — Date

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Introduction

The sustainability of exploited animal populations is increasingly a concern as species extinction rates accelerate due to the impact of human activities on the environment. Extinction rates are estimated to be 100 - 1000 times the geological background rate of fossil records and predicted to increase another 10-fold in the foreseeable future (Pimm et al. 1995). Since 1996, the total number of animal species worldwide threatened with extinction has increased from 5,205 to 7,266 including one of four mammals, one of eight birds, one of three amphibians, one of two tortoises and freshwater turtles, one of five sharks, rays and chimeras, and potentially higher rates in some areas for freshwater fishes (Baillie et al. 2004).

Concern about the sustainability and extinction of animals has its foundation primarily in human need and use. When a species of animal ceases to exist, human beneficial uses of the species also cease. Other concerns are grounded on the paradigm that all living species have some place and role in their respective ecosystem that ensures an ecological balance is sustained and that in turn is beneficial to humans and life overall. The argument used for this level of species protection goes beyond uses for human consumption and emphasizes protection of biodiversity. In the end, we are generally able to justify protection, or at least the recognition of some intrinsic value, of nearly any living organism on the planet. Not all humans share this attitude of natural resource stewardship though and subsequently animal extinction rates continue to increase.

Extinction risk of vertebrate animals is best understood in relation to their importance as human food (IUCN 2004). The distribution of rare and threatened vertebrates shows that extinction risk of individual species is caused by a complex array of factors that

may be species-specific, but typically include overexploitation and habitat loss (Grenyer, et al. 2006). Overexploitation is a serious threat to fish, mammals, and birds. Degradation and fragmentation of habitat through human transformation of terrestrial and aquatic ecosystems is the predominant threat to extinction and impacts 86% of threatened birds, 86% of threatened mammals and 88% of threatened amphibians. Pollution and invasive species, including pathogens and parasites, are also serious man-caused threats to a wide variety of vertebrate animals (IUCN 2004).

Life history characteristics of vertebrates also play a role in their risk of extinction from human activities. The larger, slow growing and late maturing animals are more prone to extinction due to human activities, especially over-harvest and habitat degradation and fragmentation (Musick 1999, IUCN 2004). Animals that are short-lived, small-sized and early-maturing have been classified as r-strategists, whereas animals that are long-lived, large-sized and late-maturating are K-strategists (*r*, the intrinsic rate of population increase, and *K,* the carrying capacity of a species in a particular population; Pianka 1970). Winemiller and Rose (1992) suggested an expanded model to group 216 North American freshwater and marine fish species into three life history strategy endpoints along a trilateral continuum: 1) opportunistic strategists – small, early-maturing short- lived species; 2) periodic strategists – large, late-maturing, relatively fecund, long-lived species; and, 3) equilibrium strategists – intermediate-size species that often exhibit parental care and produce fewer but larger offspring. Under both of these models, K-selected animals, and periodic strategists would be considered to be at the greatest risk of extinction due to anthropogenic factors.

Although recovery of periodic strategists is problematic because of their intrinsic life history characteristics, both opportunistic and periodic strategists experiencing increased risk of extinction can respond positively to management designed to reduce or eliminate the risk and stabilize individual populations of a species. Of all threatened bird species, 24% have benefited from active management actions including species specific measures, habitat protection and changes in national or regional policies. The status of some species has improved to the point where they have been removed from the IUCN red list, such as the Hawaiian goose, short-tailed albatross, and Chinese crested ibis (IUCN 2004).

Keys to successful management, in addition to having adequate financial resources and government support, are an understanding of life history characteristics and population dynamics of the species in question, habitat protection and restoration, captive breeding and reintroduction, effective law enforcement, and public involvement. While these basic management tools comprise a relatively short list, they encompass the components necessary for holistic and long term successful management, sustenance and beneficial uses of animal populations. Habitat protection and restoration includes understanding a species' habitat requirements, inventories of critical habitats, legal protections, enhancement and restoration activities, and monitoring. Captive breeding includes understanding a species' reproductive biology, and genetically sound and practical breeding and stocking plans. Promulgating effective laws and implementing meaningful law enforcement is critical for protection of species through harvest controls and protection of habitat. Public involvement in species management programs is vital to ensuring the political support necessary to not only secure adequate and stable program funding, but also to ensure long-term program viability. Success of a program designed to minimize the extinction risk of a threatened

species may be measured in decades or longer, especially for periodic strategists, which poses a challenge to resource managers for sustaining interest, momentum and funding for such long-term animal restoration and management programs.

Information is perhaps one of the most important and powerful tools. With this tool properly engaged, decisions can be made, political support can be garnered and sustained, and funding can be secured for population and habitat research and management activities. When a resource is intrinsically limited, or becomes limited, resource management actions become more important and decisions leading to the development and implementation of those actions need to be based on the best possible information about the resource. Long-term sustainability of a resource depends upon the quality and proper application of this information.

An information tool increasingly utilized by resource managers over the last two decades to better understand an animal and its sustainability is population modeling, typically a statistical model used to examine the dynamics of an animal's population and the risk of its extinction in response to exploitation or changes to its habitat. Through complete understanding of a species' life history, habitat requirements, population dynamics, and the population's long-term viability, is crucial to effective species' restoration, management and sustainability.

In management of marine and freshwater fisheries, population models have been used for decades to explore fish stock dynamics and assist with management decision making (Ricker 1975, Everhart and Youngs 1981, Hilborn and Walters 1992, Haddon 2001). Models commonly used in fisheries include population growth, surplus production, stock-recruitment, yield, body size and growth, and mortality.

Population growth models estimate one of the most important population parameters, the rate of population increase, the difference between births and deaths that reflects the ability of a population to sustain itself in the face of demographic and environmental stochasticity (Lande 1993). Animal populations may also have to contend with the carrying capacity of their environment that ultimately limits population growth through density-dependent reductions in population growth rate. The density dependent model follows a logistic curve with carrying capacity at the asymptotic population level and maximum population growth occurring at the inflection point or ½ the carrying capacity. Carrying capacity is not likely to be an immediate concern of threatened populations at low densities where the rate of population increase becomes the primary factor affecting recovery. Marine animals including sharks, groupers, and sea turtles with low rates of intrinsic population increase (r) and relative growth (K – von Bertalanffy growth coefficient), were found to be the species most vulnerable to excessive harvest, facing very long recovery times when overexploited if proper protections were not put in place until after stock reduction or collapse (Musick 1999) . Musick (1999) suggested that population indices such as intrinsic rate of increase and growth rate could be used to identify the species at highest risk of extinction from anthropogenic factors.

Surplus production models also produce a logistic curve, but instead describe maximum biomass production at the inflection point or at ½ the asymptotic population biomass. The stock is considered an undifferentiated biomass, and recruitment, growth and mortality are all pooled into a single production relationship. This is especially useful for management of fisheries in tropical waters where fish age is often difficult to estimate. The model typically is used to assess the response of a stock's productivity to different levels of

fishing effort. Surplus production models were quite popular 2 - 3 decades ago in fisheries management, and are still used today for some opportunistic-strategist species such as yellowfin tuna in the eastern Pacific where the model has been successful in predicting the relationship between catch and effort (Tomlinson 2001). Surplus production models have been inadequate for management of long-lived, periodic-strategist species with slow growth and low intrinsic rates of population increase, such as some sharks, because of the long lag between surplus production and stock density (Musick 1999). Surplus production models have also fallen out of favor because of the overoptimistic harvest forecasts often predicted by the model due to violations of the assumption of a fish stock at equilibrium, and the difficulty of effectively sampling sufficient contrast in effort and harvest data (Haddon 2001).

Yield per recruit models are currently popular, especially for evaluating the potential impact of size limits on recreational fisheries (Hilborn and Walters 1992). The model utilizes parameters from the von Bertalanffy (1938) (vB) growth model to estimate the fishing mortality rate and age at which a particular fish species would produce the greatest yield (reliability of the model is therefore subject to reliability of age estimates used in the original vB model). Application of yield models in management of threatened species would be limited to management of stocks that are still robust enough to support a fishery, and for developing potential minimum harvest size or age and acceptable fishing mortality rates for recovered stocks.

The von Bertalanffy (vB) growth model is often used to provide a key stock parameter that can be used to make a preliminary assessment of a species extinction risk. A low vB growth rate (k) can be used along with a low intrinsic rate of population increase to

flag a species' vulnerability to overharvest and its potential, in the face of a poorly regulated or unregulated fishery, to be listed as endangered on the IUCN Red List. The vB model also provides estimates of average asymptotic size (L_∞) length at infinity and time to fertilization (t_0), key attributes of the species' life history and risk to anthropogenic forces.

Mortality models utilizing age estimates are among the most functional models for both recreational and commercial fisheries management, especially for fisheries from temperate waters (Hilborn and Walters 1992). Mortality models for periodic-strategist long lived, late maturing and slow growing species are often difficult to develop due to the long term, often decades worth of data needed to develop the model. If available, age and size data, along with fisheries effort data can be used to estimate numerous population parameters, including population density, growth, mortality, recruitment, and catchability. For example, Linton (2002) used an age-structured model to estimate abundance, recruitment, mortality, gear selectivity, catchability and harvest of lake trout in Lake Superior. During 1980-2001, he found that recruitment of wild lake trout was erratic whereas recruitment of stocked lake trout diminished until stocking was discontinued in 1996, and he predicted that overall abundance of wild lake trout would increase and stocked lake trout would decrease if historic survival and recruitment trends continued. Similarly, Wilberg et al (2005) used an age-structured model to show that extreme fishing mortality rates contributed to the rapid decline of the yellow perch population in southwestern Lake Michigan during 1986-1997, ultimately resulting in the closure of commercial fishery and severe restrictions on the recreational fishery.

Despite their usefulness, age-structured models, and the von Bertalanffy growth model, are particularly sensitive to errors in estimation of ages of sampled fish. Age-

estimation error can render model outputs un-interpretable and useless, and is often the result of the use of non-validated age structures or inadequate equipment and techniques (Campana 2001). Therefore age estimates must be derived from structures that have been validated to ensure that age data will allow model parameters to be used with confidence in management decision making.

A family of qualitative and quantitative models, known as Population Viability Analysis (PVA), can be used to predict a population's sustainability and to integrate and assess a wide range of information about an animal population such as birth, death, immigration and emigration rates, and how environmental and ecological factors affect these rates through time. Estimates of the individual rates of birth and death are the results of mathematical exercises using population data and population dynamics models. Immigration and emigration rates can be derived from population dynamics models, from field telemetry data, or from an accurate knowledge of the population's specific habitat requirements and life history. While PVA models can be completely qualitative or analytically comprehensive, and still provide estimates of population trends and extinction risks (Ruggiero, et al. 1994), some researchers have called for a more rigid and focused definition of PVA that is restricted only to a formal quantitative model (Reed et al. 2002). The PVA can be used to examine the risk of extinction of an animal population and provide insight into factors that contribute greatest to the risk.

PVA modeling can be useful for examining alternative strategies for recovery plans for species threatened by human activities. For example, Nieland (2006) used PVA modeling to assess extinction risk of lake trout in Lake Superior and quantified acceptable commercial and recreational fishing mortality rates that minimized the risk of extinction in

the face of sea lamprey mortality. Similarly, Hart et al. (2004) used a PVA simulation model to estimate the extinction risk for threeridge mussels (*Amblema plicata*) in the Mississippi River, another relatively slow growth animal, under pressure from zebra mussel (*Dreissena polymorpha*) competition and commercial harvest. As with other slow growth periodic-strategist animals such as sea turtles (Crouse 1999) and some sharks (Musick 1999), Hart et al (2004) predicted that excessive removal of adult threeridge mussels would have the most serious impact on the stability of its population. In the face of zebra mussel competition, even if annual commercial removals were kept at 5%, the threeridge mussel population was predicted to decline by 50% in only 40 years (Hart et. al 2004).

Sturgeon are a group of large-sized, long-lived and late-maturing periodic-strategist marine and freshwater fishes that over the last 100 years suffered excessive removals of adults primarily for their caviar, and consequently, are now seriously threatened throughout their holarctic range. Of the 26 recognized species of sturgeon and related paddlefish of the order Acipenseriformes, 24 are listed as threatened to critically endangered, and several subpopulations listed as extinct (Birstein 1993; IUCN-SSG, 2006). The most critical regions for sturgeons are the Caspian and Black Seas, but nearly all sturgeon species and populations worldwide have been negatively impacted by anthropogenic factors, primarily overharvest, loss and fragmentation of spawning and nursery habitat due to the building of dams, and their intrinsic periodic-strategist life history. The extinction of this unique taxon of ancient ray-finned fishes would be a significant loss of biodiversity and resources for fisheries, aquaculture, science and education.

Because sturgeon species throughout the family's range have experienced reductions or losses of populations due to overexploitation and habitat loss, many efforts and strategies

have been employed to understand sturgeon life history and population dynamics, and to restore suppressed stocks and sustain viable stocks (Rosenthal 2002, 2006). While population simulation modeling or PVA can be used to predict a sturgeon population's sustainability and assess extinction risk of alternative management approaches, sufficient long term population data on sturgeon are often not available to allow estimation of model parameters with confidence.

The population and harvest of lake sturgeon, *Acipenser fulvescens* Rafinesque, in the Lake Winnebago System in east-central Wisconsin, consistently monitored since the early 1940's (Schneberger and Woodbury 1946; Probst and Cooper 1954; Priegel and Wirth 1975, 1978; Folz and Meyers 1985; Bruch 1999), provides a unique long-term time-series of data that can be used to develop population models. This lake sturgeon population has been actively managed since the late 1800s and is likely the largest current population of the species within its native North American range that has supported a recreational spear fishery each winter since 1932. Previous studies have focused primarily on estimating population density, age and size composition, harvest, mortality and exploitation rates. Harvest was estimated through creel surveys during 1941-1954 (except for 3 years during WWII). Harvest and effort were enumerated during 1955–2007 through mandatory registration of all harvested fish, and through aerial counts of spearing shanties. Catch at age data have been collected for harvests during 1954-1969, 1976, 1981, 1991, and 1993-2007. Sex and maturity stage data on harvested fish have been collected in1954 and during 1991-2007. Sex and total length data have been collected and tagging studies have been conducted on lake sturgeon captured in the upper Fox and Wolf Rivers and their tributaries during spawning runs out of Lake Winnebago during 1954-1963 and 1975-2007. Total

length and CPE data were collected and tagging studies were conducted on lake sturgeon captured in fyke and trap nets on Lake Winnebago and the three small lakes upstream (the Upriver Lakes) during 1951-1964, and on lake sturgeon captured in trawls used on Lake Winnebago for freshwater drum (*Applodinotus grunniens*) removal operations during 1971-1990. Data collected over the years were used primarily to increase understanding of the population dynamics in the Winnebago system and to adjust regulations to manage harvest through the 1950s, and to limit annual exploitation to 5% or less after the 1950s (Priegel and Wirth, 1975).

Harvest of lake sturgeon in the System seems to be under relatively good control, and the adult population has increased (Bruch 1999), but other changes in the aquatic ecosystem of the System, including non-point pollution controls and subsequent changes in the littoral habitat with improvements to water clarity since the early 1990s, and appearance and proliferation of zebra mussels during 1998-2007, may impact the lake sturgeon population and the fishery. Environmental stochasticity, along with expectations of spearers for a sustained sturgeon spear fishery, demands an accurate understanding of the sustainability, recruitment, mortality, growth and yield of the lake sturgeon population in the Winnebago System to ensure effective management of the fishery.

The diverse and rich long-term data base on lake sturgeon populations and fishery in the Winnebago System provides an opportunity to model the dynamics and sustainability of the population. Such modeling can expand insight into past relationships between the sturgeon population and fishery, and how the fishery can be effectively managed in the future. Given the limited availability of long-term sturgeon population data from other areas of the world, results from modeling the lake sturgeon population and fishery in the

Winnebago System will not only provide insight into the dynamics and future management of the System's lake sturgeon population, but also insight into the dynamics of other populations of lake sturgeon and other sturgeon species throughout their holarctic ranges. Such insights can be used to develop effective sturgeon management and recovery plans, and help guide population and life history research efforts for other threatened sturgeon populations.

My general hypothesis is that the lake sturgeon population and fishery in the Winnebago System can be sustained at robust levels by limiting annual exploitation to 5% or less. The goals of the Winnebago lake sturgeon management program are to maintain an average adult lake sturgeon density of 10,000 females and 20,000 males (comprised of a full range of age classes and fish of both sexes within 95% of asymptotic size), and to sustain an annual minimum spear harvest of 1000 fish (comprised of an average of approximately 18% juvenile females, 36% adult females and 46% males, or no more than 5% of harvestable stock). Examining the long-term dynamics of the lake sturgeon population in the Winnebago System in the context of harvest management policies enacted since the late 1800s will allow a thorough review of the feasibility of current management goals and harvest management strategies. Developing a forecasting simulation model will test my general hypothesis of sustaining a robust population through a 5% exploitation limit.

Objectives

My first objective was to validate age estimates for lake sturgeon in the Winnebago System. The most valuable information that can be collected on fish is age (Hilborn and Walters 1992). Fish age provides the basis for the most important management decisions on fisheries such as growth and mortality rates used for development

of virtual population analysis and statistical catch-at-age models. Accurate age estimation is especially important for periodic-strategist long-lived and highly-vulnerable species such as sturgeon.

Using under-estimated age data for making harvest management decisions can lead to overexploitation of the stock. For walleye pollock (*Theragra chalcogramma*) in the Bering Sea, where age estimates were derived from otoliths, dorsal and pectoral fin rays and scales, systematic underestimates of age resulted in substantial bias in parameter estimates for mortality, growth and yield models that would lead to over-fishing if the estimated optimal fishing mortality rate was utilized in the pollock management program (Lai and Gunderson 1987). Similarly, age estimation errors for cod (*Gadus morhua*) in the eastern Baltic lead to overly optimistic Total Allowable Catch estimates Revees (2003). For red snappers (*Lutjanus erythropterus, L. malabaricus, and L. sebae*) of the Great Barrier Reef, underestimation of age caused serious overestimates of natural mortality of the periodic-strategist snappers that would lead to serious over-fishing if these natural mortality estimates were applied to the red snapper management program (Newman et al. 2000).

Techniques currently used to estimate age of sturgeons using pectoral fin rays cross sections and other boney structures (primarily otoliths) were developed in the first half of the 20th Century beginning in Russia and Europe and later in North America. Validation of true age over the full range of ages of any sturgeon species has not yet been accomplished, and sturgeon harvest management programs relying on age data collected from non-validated age estimation structures run the risk of establishing inadequate and possibly dangerous harvest targets.

Examining structures of known age fish is the best method for validating age estimates and the Winnebago System lake sturgeon database contained a substantial number of known-age fish available for a validation study. The next best age validation method, used on fish born prior to 1970, is a relatively new technique assaying the concentration of Radiocarbon ^{14}C (a carbon isotope placed in the atmosphere by atomic bomb testing beginning in 1958) in the core of calcified tissue, in this case fish otoliths. Validated ages of lake sturgeon can be used to evaluate of the effect of age estimation errors on estimates of population model parameters. Determining the accuracy of growth marks on lake sturgeon pectoral fin ray and otolith sections would be an important contribution to the knowledge of lake sturgeon life history, and would profoundly impact all sturgeon management programs. Validation of sturgeon age estimation would allow more accurate estimates of critical population parameters such as mortality and growth rates, and yield, to be developed and implemented in sturgeon harvest, management, and recovery programs across the world.

My second objective was to model the population dynamics of lake sturgeon in the Winnebago System, and evaluate the impact of past harvest management strategies, environmental changes, and public involvement on those dynamics. As periodic-strategists, sturgeon are particularly sensitive to overexploitation, like other long-lived animals with low intrinsic rates of population increase, causing population growth, as well as recovery to be a very slow process (Musick 1999). Modeling the dynamics of the Winnebago lake sturgeon population over a 60-year period would provide insight into the long-term trends in their age and growth, size and age at maturity, weight-length relationships, relative condition, fecundity, eggs per recruit, recruitment, mortality, abundance, intrinsic rate of population

growth, and yield per recruit. Such insight could be used to correlate relationships between the population dynamics on Winnebago lake sturgeon and harvest management strategies, broad environmental changes, and public involvement over the last 125 years; and increase the understanding of the dynamics of other sturgeon populations, and the effectiveness of harvest management on population sustainability.

My third objective was to determine how various levels of exploitation would potentially affect the sustainability of the Winnebago System lake sturgeon population. Fisheries are dynamic and therefore cannot be managed as a static system (Hilborn and Walters 1992). Management strategies must be evaluated for their potential impact on long-term sustainability of fish populations in light of uncertainty imposed by stochastic environmental variation. Sturgeon species must be managed carefully because of their high vulnerability to overexploitation and slow intrinsic rate of increase, so future management options must be thoroughly evaluated before implementation. Age-structured models can be used to simulate future dynamics of population abundance and thereby allow examination of extinction risk as a criterion for evaluating sustainability of a sturgeon population in the face of varying exploitation rates, and demographic and environmental stochasticity. When evaluating sustainability of the population, the model must be tailored to specifics of the population and fishery, including catchability, selectivity, fishing mortality, natural mortality, recruitment, and stock size. Simulation modeling results would provide insight into harvest rates that may be sustained without risk of overexploitation. Such insight can be used to improve management of the lake sturgeon population in the Winnebago System, and to develop harvest management strategies for other lake sturgeon fisheries.

Study Area

The Winnebago System is a large, eutrophic riverine-lake system in east central Wisconsin (Figure 1). Lake Winnebago and the three Upriver Lakes (Butte des Morts, Winneconne and Poygan), collectively known as the Winnebago Pool Lakes, comprise 668 km^2 of surface water, situated at the lower end of a 15,540 km^2 watershed through which flow the Wolf and upper Fox River Systems. The Winnebago Pool Lakes were formed by a moraine deposited at the north end by Two Rivers-Younger Dryas ice advance 13.5 to 11.0 thousand years ago (Smith 1997). The lower 200 km of the Wolf River, along with its major tributaries, and 60 km of the upper Fox River contain spawning and nursery grounds for the Winnebago System sturgeon population. Lake Winnebago has a maximum depth of 6.4 m and a mean depth of 4.7 m. The Upriver Lakes are also relatively shallow with a maximum depth of 5.4 m and a mean depth of 1.8 m. The Winnebago Pool Lakes have a methyl orange alkalinity of 119-124 mg/L, a pH of 7.7-8.5., and are characterized by large, open pelagic areas with a soft sediment base, seasonal poor water clarity due to nonpoint pollution, and re-suspension of sediments from wave action and algal blooms (Wisconsin DNR 1989).

In addition to lake sturgeon, the fish community in the Winnebago System includes 76 species, with freshwater drum (*Applodinotus grunniens*), walleye (S*ander vitreus*), sauger (*Sander canadense*), yellow perch (*Perca flavescens*), white bass (*Morone chrysops*), trout perch (*Percopsis omiscomaycus*), gizzard shad (*Dorsoma cepedianum*), and emerald shiner (*Notropis atherinoides*) the most dominant (Becker 1964, Priegel 1967a).

The Winnebago System was invaded by zebra mussels (*Dreissena polymorpha*) in 1998, which spread throughout the lakes and reached extremely high abundance in 2002,

but have since declined to a more stable lower relative abundance. Zebra mussels are preyed upon heavily by freshwater drum, carp (*Cyprinus carpio*), and to a lesser extent by several other fish species including lake sturgeon (Stelzer et al, 2008; R.M. Bruch, Wisconsin Department of Natural Resources (WI DNR), Oshkosh, unpublished data).

The role of lake sturgeon in the Winnebago System ecosystem is primarily as a benthivore that consumes the rich benthic invertebrate fauna inhabiting the vast soft sediment areas of the lake system. Diet studies over the years have shown that Chironomid larvae have traditionally been the primary prey of lake sturgeon inhabiting Lake Winnebago (Schneberger and Woodbury 1946; Probst and Cooper 1954, Priegel and Wirth 1977). Since the early 1990s, a significant portion of carbon assimilated by lake sturgeon in Lake Winnebago has been coming from fish, specifically gizzard that, following a surge in abundance beginning in the late 1980s, have suffered massive die-offs each winter that make them easily available to scavenging lake sturgeon (Stelzer et al. 2008). Lake sturgeon use a wide array of habitats in the Winnebago System including spawning and nursery areas in at least six rivers that are tributary to the Winnebago System, juvenile rearing areas in the rivers and the Upriver Lakes, and sub-adult and adult rearing areas in Lake Winnebago (Schneberger and Woodbury 1946; Probst and Cooper 1954; Priegel and Wirth 1977; Folz and Meyers 1985; Bruch 1999; Bruch et al. 2001; Bruch and Binkowski 2002).

The Winnebago system lies within 120 km of 2 million people and is heavily used by recreational boaters and anglers (Wisconsin DNR 1989). Economic surveys indicate that the winter sturgeon spear fishery is worth $3-million annually to the local economy while the year-round sport fishery for other species is worth over $300-million annually to the local economy (Personal communication, K. Kamke WI DNR, Oshkosh). Winnebago lake

sturgeon are an important cultural species for the Native American Menominee Tribe, with its reservation along the Wolf River 216 km upstream of Lake Winnebago, and for residents of the Winnebago region who participate in the winter spear fishery or view sturgeon during the spawning season.

The lake sturgeon stock in the Winnebago System is a Great Lakes population (Holey et. al 2000), and while not subject to immigration from other Great Lakes stocks due to dams on the lower Fox River below Lake Winnebago, emigration of Winnebago sturgeon contributes genetic material or individuals to other Great Lakes stocks. Tag returns indicate that up to 80% of the lake sturgeon spawning below the DePere Dam on the lower Fox River 60-km downstream of Lake Winnebago are emigrants from the Winnebago System to Green Bay (WI DNR, unpublished data). Tag returns have also shown that Winnebago System sturgeon have emigrated to Lakes Michigan, Huron and Erie where they were recaptured in commercial and recreational fisheries.

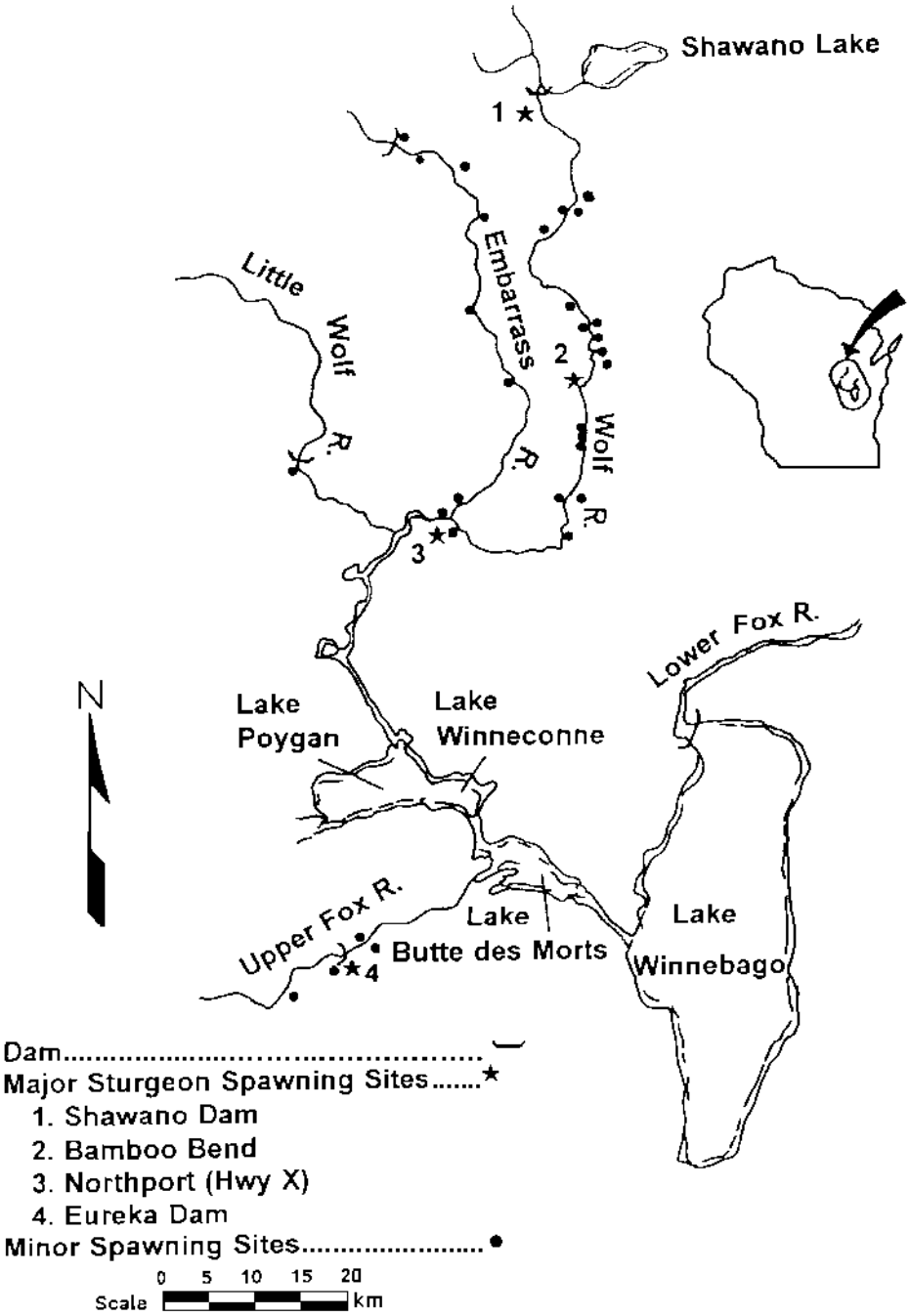

FIGURE 1.—Map and location of the Winnebago System, Wisconsin

CHAPTER 1

Age Validation of Lake Sturgeon

Using Bomb Radiocarbon and Known Age Fish

Introduction

Although critical to effective use of fish age data, validation of the accuracy of growth increments counted on a boney structure used to estimate age (e.g. scales, fin rays or otoliths) has often been neglected by fisheries biologists (Beamish and McFarlane 1983; Campana 2001). For example, of 372 papers on fish age estimation that were published between 1983 and 2001, only 15% actually validated the age of their respective species of fish (Campana 2001).

The best method for validating accuracy of fish age estimates is to use known-age fish that are individually marked at a point in their life when their true age is known, or when their true age can be reasonably approximated, and then captured later in life for age estimation (Campana 2001). Bomb radiocarbon dating generally provides the best method for validating the age of long-lived fish. A sharp increase in atmospheric ^{14}C in the late 1950s from nuclear testing led to increased ^{14}C levels in organisms living at that time. Otolith cores of fish hatched before 1958 contain very low amounts of ^{14}C, whereas otolith cores from fish hatched between 1958 and 1968 contain increasingly elevated levels that can be used to validate methods of age estimation (Campana 2001).

Sturgeon comprise a group of large-sized, long-lived, and late-maturing anadromous and freshwater fishes that are now seriously threatened throughout their holarctic range due

to overharvest, and loss and fragmentation of spawning and nursery habitat due to the building of dams and pollution (WSCS 2005). Of 26 recognized species of sturgeon and related paddlefish of the order Acipenseriformes, 24 are listed as threatened to critically endangered, and several populations are listed as extinct (Birstein 1993; IUCN 2008). Accurate age data are critical for the development of population models that will contribute to effective long-term management of sturgeon stocks.

Various structures from sturgeon have been used to estimate age, including bones from the pectoral girdle, scutes, caudal fulcra, otoliths, and the leading spine of the pectoral fin (Kler 1916; D'Ancona 1923; Harkness 1923; Holzmayer 1924; Probatov 1929; Schneberger and Woodbury 1944; Cuerrier 1951; the first 1–2 rays of the pectoral fin of all acipenserids are sheathed in dermal bone and are considered a fin spine, Findeis 1997). The first attempts to estimate age of sturgeon were with bones from the pectoral girdle (cleithrum and claviculum), but were relatively unsuccessful due to problems with bone resorption (Soldatov 1915; Kler 1916). Kler (1916) concluded that pectoral fin spine cross sections showed great potential for estimating age of four sturgeon species, Russian sturgeon (*Acipenser gueldenstaedtii*), stellate sturgeon (*A. stellatus*), sterlet (*A. ruthenus*), and beluga (*Huso huso*), but suggested that the age be verified using at least one additional bone. Pectoral fin spine sections of sterlet raised in captivity at seasonal temperatures for 1-10 years had the same number of growth increments on the sections as the number of years of growth (Holzmayer 1924). Harkness (1923) used whole sagittal otoliths to estimate the age of lake sturgeon (*Acipenser fulvescens*) from Lake Winnipeg, Manitoba, Canada, but did not validate the estimated ages. Growth increments on pectoral fin spine sections of European sturgeon from the Guadalquivir River in Spain

were distinct out to age 8 or 9, but became narrower and less distinct at older ages (Classen 1949). Average length at age from back-calculation of growth increments on fin spine sections corresponded well to measured lengths at estimated age (Cuerrier 1951), but would be regarded today as age corroboration, not age validation (Campana 2001).

Previous work attempting to validate ages of various sturgeon species estimated from their boney structures has shown a consistent pattern among species where ages estimated from pectoral fin spines are accurate for younger fish, but begin to lose their accuracy as the fish gets older. For example, the number of pectoral fin spine growth increments outside the OTC band equaled the number of years between OTC injection and recapture for ten lake sturgeon 4–18 years old from the Moose River in northern Ontario, Canada (Rossiter et al. 1995). Pectoral fin spine age estimates of older white sturgeon *Acipenser transmontanus* from the Columbia River, Washington, USA were unreliable (Rien and Beamesderfer 1994). Similarly, pectoral fin spine age estimates of older shovelnose sturgeon *Scaphirhynchus platorynchus* and pallid sturgeon *Scaphirhynchus albus* from the Missouri River system, Missouri and South Dakota, USA were also unreliable (Hurley et al. 2004; Whiteman et al. 2004).

My primary objective was to determine if age can be estimated accurately from lake sturgeon pectoral fin spines and otoliths. Here, I report the first application of radiocarbon as a dated marker for any sturgeon species. My secondary objective was to compare growth increment formation on pectoral fin spines and otoliths of juvenile lake sturgeon younger than age 14.

Methods

Study area.—The Winnebago System is a large, shallow, eutrophic riverine-lake system in east central Wisconsin. Lake Winnebago and the three Upriver Lakes (Butte des Morts, Winneconne and Poygan), collectively known as the Winnebago Pool Lakes, comprise 668 km^2 of surface water, situated at the lower end of a 15,540 km^2 watershed through which flow the Wolf and upper Fox River Systems. The lower 200 km of the Wolf River, along with its major tributaries, and 60 km of the upper Fox River contain spawning and nursery grounds for the lake sturgeon population in the Winnebago System.

Known-age fish.— "Known age" in this study refers to lake sturgeon tagged when their age was known or could be reasonably approximated from their size (Campana 2001). "True age" refers to the age determined from years at large of recaptured known age fish and from bomb radiocarbon analysis of otolith cores of individual fish. I examined the accuracy of pectoral fin spine age estimates of known age fish, and of fish whose true ages were estimated by bomb radiocarbon analysis of their otolith cores. I also examined the accuracy of ages estimated for adults from otolith cross sections by comparing these ages to ages determined by the bomb radiocarbon assays. I compared increment formation and estimated age between pectoral fin spines and otoliths of lake sturgeon younger than age 14. All lake sturgeon were sampled during population and harvest assessments conducted on the Winnebago System.

Forty-six juvenile lake sturgeon 60–100 cm were captured, measured to the nearest 1.3 cm, and marked with monel tags attached to the base of their dorsal fins during bottom trawl assessment surveys from 1976 to 1997 on Lake Winnebago. These fish were recaptured in winter spear harvest assessments from 1995 to 2004, 2–25 years

after initial capture and sampled for age (pectoral fin spine). These fish were not sampled for otoliths because only pectoral fin spines were collected at that time as part of annual standardized harvest assessment. Two PIT tagged juvenile lake sturgeon stocked in 2001 and 2004 in the Winnebago System were recaptured in 2007 in trawls and sampled for age (pectoral fin spines and otoliths).

Because pectoral fin spines have been validated for sterlet up to age 10 (Holzmayer 1924) and corroborated for lake sturgeon up to age 15 (Rossiter et al. 1995), I felt we could use mean lengths at age of 868 lake sturgeon 16–122 cm (TL) sampled in the Winnebago System during 1951–2007 with a pectoral fin spine estimated age of ≤14 years to approximate age at initial tagging of the 46 recaptured juvenile fish. Fish 100 cm or less at initial capture were highly likely to be ≤14 years old, which allowed me to estimate their age within ± 1–4 years based upon empirical length-age data (Tables 1 and 2, Figure 2). I calibrated age at capture and recapture to the nearest 0.01 year using year specific hatching dates determined through spawning assessments on the Winnebago System (Folz and Meyers 1985; Bruch and Binkowski 2002). I estimated true age by adding years at large from tagging to recapture to the estimated age at initial capture. I felt that an initial measurement error of ±1–4 years was acceptable given the longevity of lake sturgeon and average of more than 15 years at large between initial tagging and recapture of the 46 known age wild fish. I recognized the limitations of using length to estimate age of fish, primarily due to the multiplicative error associated with length at age data. However, for lake sturgeon from the Winnebago System, I believe my estimated error was within a range that still allowed me to assign an estimate of age at initial capture to juvenile fish in my "known age" sample.

I did not have sufficient length at age data from fish sampled during 1964–2007 to evaluate whether length at age of age 1–14 juveniles declined during 1951 –2007. I was able though to examine lengths at age (pectoral fin spine estimates) of 15 year old fish sampled in the Winnebago lake sturgeon spear harvests during 1953–1959 and 1997–2006, periods with similar fisheries and harvest assessment methodology. I compared lengths of age-15 fish from these periods because fish younger than age 15 were not fully recruited to the fishery. Age 15 was one year older than the target range of juveniles from our original sample (ages 1–14), but should still be representative of overall growth of juveniles up to that age.

At recapture, all fish sampled during harvest seasons were measured in total length to the nearest 1.3 cm, weighed to the nearest 0.23 kg, and sexed and staged for maturity according to criteria developed by Bruch et al. (2001). Pectoral fin spines were collected at time of recapture for age estimation. Known age PIT tagged stocked fish recaptured during August–October 2007 from Lake Winnebago with a bottom trawl during annual fish community assessments were sampled for total length to the nearest mm, weight to the nearest gram, sex, and age (pectoral fin spines and otoliths). After collection and initial cleaning, pectoral fin spines were dried in a cabinet dryer with air circulated at 20–25 °C for one week. A 0.5 mm section was cut using an Isomet Low Speed Saw immediately distal to the basal propterygium, and examined by an experienced sturgeon age reader with reflected and transmitted light under a binocular scope at 7–25X magnification to estimate the number of growth increments present.

Otoliths were extracted from the auditory capsules in the neurocranium by first sawing through the skull plate laterally at a point beginning and ending at the posterior

pointed ends of the postorbital bones, and laterally at a point beginning and ending adjacent to the apices of the subopercle bones (Figure 3a). A Bosch ® Rotozip RZ10 electric circular saw with a 3.5 inch (8.9 cm) RZdia1 wheel blade was used to saw through the skull plate. A stream of water was directed at the cutting edge during sawing to minimize bone dust. After the skull plate section was removed, the auditory capsules were exposed by using a sharp knife to carefully remove slices of the cartilage over the dorsal surface of the brain. When sufficient cartilage had been sliced away to include portions of the semicircular canals of the pars superior, the auditory capsules containing the pars inferiors were exposed allowing removal of the saccular vestibules of the pars inferiors with a forceps (Figure 3b). Each sagittal otolith was then teased from the saccular vestibule (Figure 3c) and carefully cleaned with a small brush, water and tissue. Otoliths were allowed to dry loosely wrapped in tissue for 30 days prior to embedding. Otoliths should not be stored in envelopes such as those used to store fish scales, as pressure from the sides of the envelope will cause otoliths to fracture, but stored instead in vials or capsules after being dried then loosely wrapped in tissue.

Otoliths were embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). A 0.5 mm thin frontal section was cut from the core (Figure 3d) using two blades separated by spacers on an Isomet low-speed diamond-bladed saw. Sections were lightly polished to improve visibility. While under a binocular microscope at 16–40X magnification using reflected light, growth increments were digitally photographed at a resolution of 2048 X 2048 pixels, and then digitally enhanced using Adobe Photoshop CS2. Age interpretation was based on the digital images, whereby each annulus was interpreted as a pair of adjacent opaque and

translucent bands (the opaque bands appeared white under reflected light). Two experienced sturgeon age readers independently estimated age from pectoral fin spines and otoliths from each fish.

Bomb radiocarbon.—Sagittal otolith pairs and pectoral fin spines were collected from 22 of the largest lake sturgeon registered during the 2006 and 2007 winter sturgeon spearing harvest seasons on Lake Winnebago. All fish were measured in total length to the nearest 1.3 cm, weighed to the nearest 0.23 kg, and sexed and staged for maturity. Ages estimated from pectoral fin spines indicated the birth year of the sampled fish was likely prior to 1970. Five of these sturgeon otolith pairs were too porous or crystalline to assay or age, but 17 sturgeon bomb radiocarbon assays were successfully completed, of which 3 were too poor to estimate age accurately from increment counts.

Otolith cores representing what was assumed to be the first 1–6 years of life were isolated from the central section of each otolith pair as a solid piece with a Merchantek computer-controlled micromilling machine using a 300-µm diameter steel drill bit. In some sturgeon, additional core material from the same otolith was isolated from the two adjacent sections, but restricted to the innermost increments around the core to allow for offset of these lateral sections from the primordium. This procedure of obtaining material from both otoliths of the pair, plus from occasional multiple sections per otolith was necessary to obtain at least 3 mg of core sample material for assay from each sturgeon. The date of sample formation was calculated as the year of fish collection minus the age span of the fish from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. Growth increments appeared to be regularly spaced in the first six years of life, thereby indicating that the midpoint of the core

increments was a suitable choice for the mass-weighted midpoint of otolith core deposition. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided $\delta^{13}C$ ($^{0}/_{00}$) values, to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as $\Delta^{14}C$, which is the per mil ($^{0}/_{00}$) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver & Polach (1977). The mean standard deviation of the individual radiocarbon assays was about $5^{0}/_{00}$.

The year of formation of the sturgeon otolith core can be estimated by comparing its radiocarbon content with that of a reference radiocarbon chronology based on known-age material. The marine $\Delta^{14}C$ reference chronologies used in many other otolith studies are not appropriate for use in a freshwater fish species (Kalish 1993), so sturgeon radiocarbon assays were compared with two independent reference chronologies based on otolith cores from freshwater fish: 1) Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*) from the Arctic (Campana et al. 2008); and 2) freshwater drum (*Aplodinotus grunniens*) from Lake Winnebago (Davis-Foust et al., in press). Although the freshwater drum chronology was not a chronology based on known-age material, freshwater drum otoliths are well known for their clear and easily-interpreted growth pattern, which suggests that the date of formation of their cores can be accurately determined (Pereira et al. 1995).

The feature of a bomb radiocarbon chronology that best serves as a stable dated reference mark is the year of initial increase above pre-bomb levels in response to the

period of atmospheric testing of nuclear weapons. Comparison of this year of initial increase in the reference chronology with that of the species being tested (in this case sturgeon) provides the best measure of age-estimation accuracy, because consistent over- or under-estimation of age will shift the calculated year of initial increase in the test chronology to earlier or more recent years. Several possible methods can be used to calculate and compare the timing of increase between reference and test chronologies, including a promising analytical approach by Hamel et al. (2008). A quantitative but simpler approach is to define the year of initial increase, consistent with atmospheric sources, whereby a $\Delta^{14}C$ value 10% above the pre-bomb background as the year of initial appearance of bomb $\Delta^{14}C$ (Campana et al. 2008). The calculation was based on the difference in $\Delta^{14}C$ values between peak and pre-bomb values. Specifically, the value corresponding to the 10% threshold contribution of $\Delta^{14}C$ (C_T) was estimated by subtracting 90% of the range in $\Delta^{14}C$ between its lowest (C_L) and peak (C_P) value from the peak value:

$$C_T = C_P - 0.9(C_P - C_L)$$

where C_L is on or after 1952, the year of initial appearance of bomb radiocarbon in the atmosphere. The year of initial appearance of bomb $\Delta^{14}C$ (Y_T) is then defined as the year in which the loess-fitted $\Delta^{14}C$ chronology first exceeds C_T.

Radiocarbon-based fish age was estimated, independent of any counts of growth increments, for otolith cores with $\Delta^{14}C$ values above the pre-bomb level as the age of the fish required to move the $\Delta^{14}C$ assay value laterally onto the loess fit of the drum reference chronology. I considered radiocarbon-based fish age as true age, although it

includes analytical error around the radiocarbon assay value (of about 5‰, corresponding to ~0.5 year) and assumes a linear increase in radiocarbon through the period of otolith core formation (which would introduce an error of up to one year if the increase was exponential). Several otoliths for which the section image was classified as poor (independent of the radiocarbon assay results) were not included in this calculation.

Early Increment Formation and Corroboration of Age Estimates.—Twelve wild and two stocked juvenile lake sturgeon <90 cm were captured during August–October 2007 from Lake Winnebago with a bottom trawl during standardized annual fish community assessments. Fish were measured to the nearest mm, weighed to the nearest gram, and pectoral fin spines and otoliths were collected for age estimation. Pectoral fin spines and otoliths were prepared and age was estimated using methods described earlier. Four experienced readers examined growth increment formation on pectoral fin spine sections of the juvenile sturgeon and independently estimated increment location and age. All examinations and age estimates were without prior knowledge of fish size or origin.

Data Analysis.—I used known ages and radiocarbon-based ages as true ages in an age bias plot, the method most sensitive to linear and non-linear differences (Campana et al. 1995), to compare mean ages estimated from pectoral fin spines to true ages of individual known age and radiocarbon assayed lake sturgeon. I plotted individual otolith ages against true ages to examine the accuracy of ages estimated from otolith cross sections. I used coefficient of variation to measure precision of otolith and pectoral fin spine age estimates of juvenile lake sturgeon <90 cm, and plotted individual otolith age estimates against pectoral fin spine age estimates to compare ages estimated from both structures for juvenile fish. To examine the potential for correcting historic age estimates

from pectoral fin spines, I fit linear (intercept = zero), exponential, and power function models of true age against estimated age (pooled known age and ^{14}C samples). I examined residuals and r^2 values to select the model with the best fit, and used a likelihood ratio test to determine whether true age-estimated age models differed significantly between male and female lake sturgeon.

Results

I found no significant difference between mean length at age 15 during 1953–1959 (114.3 cm, SD = 8.7) and 1997–2006 (114.3 cm, SD = 8.6; t = 0.049, df = 533). I concluded that growth rates of juveniles were similar during 1951–2007, thereby allowing me to pool length at age data from age 1–14 juveniles sampled during 1951–2007 for estimating age of our 46 "known age" juveniles based on their length.

Estimated age at initial capture of known age fish ranged from 4 ± 1 year to 14 ± 4 years. Years at large between marking and recapture averaged 15.4 years (SD = 6.6) and ranged 2.5–24.8 years (Table 2). Ages estimated from pectoral fin rays were generally less than true age with an average difference of –4.96 years (SD = 4.57) and ranged from +2 to –17 years (Table 2). Ages estimated from pectoral spines of two PIT tagged stocked fish, 6 and 3 years, were the same as the true age of the fish, whereas ages estimated from otoliths were 6 and 3 or 4 (different estimates from the two readers).

The radiocarbon chronology derived from lake sturgeon otoliths closely resembled the $\Delta^{14}C$ reference chronology of Lake Winnebago developed from freshwater drum otolith cores (Davis-Foust et al., in press; Figure 4). Because the lake sturgeon chronology would have been phase-shifted (to the right or left) if growth increment

counts had under- or over-estimated age, these results confirmed that otolith increment counts provided an accurate age estimate, on average. However, the feature of a bomb radiocarbon chronology that best serves as a dated reference mark is the year of initial increase above pre-bomb levels in response to the period of atmospheric testing of nuclear weapons. For the two available freshwater reference chronologies, this period of initial increase was calculated to lie on or around 1957. Calculation of the sturgeon year of initial increase indicated that it first increased one year earlier, on or around 1956. This one year offset is within the 1–3 yr range of uncertainty associated with bomb chronologies, thereby supporting the conclusion that lake sturgeon growth increments must have been interpreted accurately, on average.

Bomb radiocarbon derived ages of assayed lake sturgeon ranged 27–52 ±1-3 years (Table 3). The key samples for comparison were cores formed before 1966, because they were formed during a period when environmental $\Delta^{14}C$ levels changed most rapidly. Cores that formed during the 1940s, and were 67–68 yr old based on increment counts, were clearly pre-bomb based on $\Delta^{14}C$, and so must have been at least 52 yr old. Matching pectoral fin spine cross sections had 47 and 48 annuli, respectively. Four other core samples, dated between 1958 and 1961 based on increment counts of 39–47 yr, were also dated by $\Delta^{14}C$ as having formed between 1960 and 1961, with deviations from the fitted line of 2–4 yr in both directions. Cores formed after about 1964 were characterized by $\Delta^{14}C$ values that were clearly post-bomb, but somewhat lower and parallel to the corresponding freshwater drum reference chronology. Post-bomb $\Delta^{14}C$ magnitudes often differ between water masses due to differences in carbon turnover and water mixing rates, so are difficult to use as indicators of the individual year of formation. However,

the timing of increase or decrease should still parallel that of the reference chronology, which is the case here. Therefore, my results validate the interpretation of sturgeon otolith increments as accurate age indicators to an age of at least 52 yr, but with individual age-estimation error of up to 4 yr.

Ages estimated from pectoral fin spines were generally less than true age after about age 14 with the deviation increasing as fish grew older (Figure 5). Ages estimated from otoliths were strongly correlated to true ages of known age and ^{14}C assayed fish (r^2 = 0.98; Figure 6). Ages estimated from pectoral spines diverged from ages estimated from otoliths older fish (age bias plot not shown but nearly identical to Figure 5). Examples of otolith cross sections showing annual growth increments from a known age 6 year old stocked fish, a 9 year old wild juvenile, and a 34 year old bomb radiocarbon aged fish are illustrated in Figure 7.

Early Increment Formation and Corroboration of Age Estimates

Growth increments were relatively apparent on pectoral fin spine and frontal otolith sections from the 12 wild and 2 stocked juvenile lake sturgeon sampled for age (Table 4; Figure 7). Age-estimation precision was higher for pectoral fin spines (CV = 0%) than for otoliths (14.0%). Identifying the first increment was more difficult in otolith sections. Estimated ages from pectoral fin spines were strongly correlated to ages from otoliths for the 14 juvenile lake sturgeon (Figure 8).

True Age vs. Estimated Age Model

A power function provided the best fit between estimated pectoral fin spine age and true age (r^2 = 0.98; F = 18826.7; df 1, 62; P = < 0.001) and model residuals were randomly distributed around 0 (Figure 9):

$$TrueAge = EstAge^{1.054796}$$

Linear and exponential models also described a high fraction of error in estimated age (r^2 = 0.96 and 0.93, respectively), but residuals were not linearly distributed. The power function model predicted that lake sturgeon of estimated ages of 20, 40, and 60 years were actually of ages 24, 50, and 75 years. Relationships between true age and estimated did not differ significantly between male and female lake sturgeon (F = 1.20; df = 1, 62; P = 0.28).

Discussion

I found that ages of lake sturgeon estimated from pectoral fin spines were accurate up to age 14, but underestimated true age beyond age 14. The belief over the last 100 years that annual growth increments are deposited on pectoral fin spines of sturgeon has been based upon actual age validation of some younger ages (Holzmayer 1924), and other studies that examined primarily young fish (where spines are more likely to be accurate), or reported age corroboration and not age validation (Cuerrier 1951; Probst and Cooper 1954; Brennen and Cailliet 1989; Rossiter et al. 1995; Stevenson and Secor 1999). Using underestimates of true age, especially with long lived species like sturgeon, will result in overestimating total annual mortality rates. If natural mortality is equated to fishing mortality, allowable harvest rates will be set too high,

thereby increasing the risk of overharvest. Given the serious consequences of using underestimates of age in population modeling, I advise caution in the use and application of sturgeon age estimates derived from pectoral fin spines. My true age–estimated age correction model could be applied to pectoral fin spine age estimates from other sturgeon populations or species, although its inter-population and inter-specific relevance will be unknown until other validation studies are completed.

The age at which inaccuracies become problematic may vary among sturgeon species and among populations within species. My results suggest that inaccuracies for lake sturgeon from the Winnebago System begin at the onset of their protracted period of gonadal development (Bruch 1999; Bruch et al. 2001).

Pectoral fin spines may develop a new growth increment every year, but our ability to discern and interpret these increments may be hampered by one or more factors, including slow growth, individual variation, health of an individual or a population, sex, stage of sexual maturity, and short- or long-term environmental conditions. These factors could vary in their individual or combined effects on populations or individuals within a population on growth increment development or our ability to discern increments. Spine collection and processing techniques and the quality of equipment could also affect readability of pectoral fin spine cross sections. Also, sturgeon pectoral fin spines actively resorb materials laid down in previous increments, and may be not be suitable for biochronology (Veinott and Evans 1999). Resorption may be more of a problem as an individual fish grows into maturity and through adulthood, an important consideration when using these structures for estimating ages of long lived species.

Since Schneberger and Woodbury's (1944) efforts, very little work using otoliths to estimate sturgeon age has been reported. Stevenson and Secor (1999) attempted to estimate age of Atlantic sturgeon *A. oxyrinchus* using sagittal sections of otoliths (similar to Schneberger and Woodbury, 1944), but felt that the optical contrast between opaque and translucent zones in the section was not sufficient to confidently assign annual growth increments, especially in sections with more than twenty increments. Wide use of sturgeon otoliths may be limited because the fish needs to be killed to enable collection, the otoliths are very fragile, and 10–20% of otoliths may be too porous to section and read. Despite these difficulties, I encourage researchers to use otoliths (frontal section) for sturgeon age estimation when possible, because these are likely the only structures in the sturgeon that can provide an accurate age estimate throughout the lifetime of an individual.

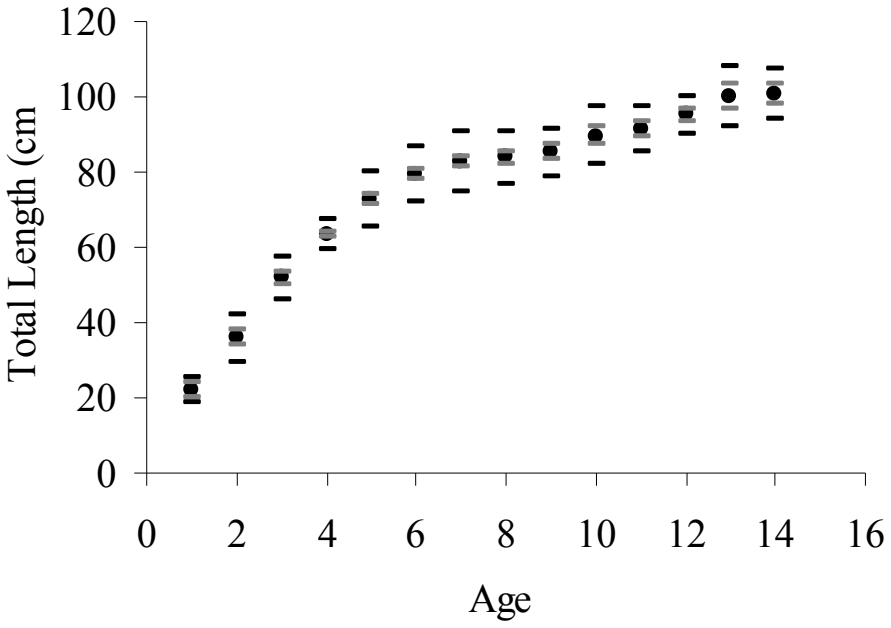

FIGURE 2. —Estimated length at age 1-14, juvenile lake sturgeon, Winnebago System, Wisconsin, 1951-2007. Grey bars are 95% confidence intervals of the mean; black bars are ± 1 standard deviation.

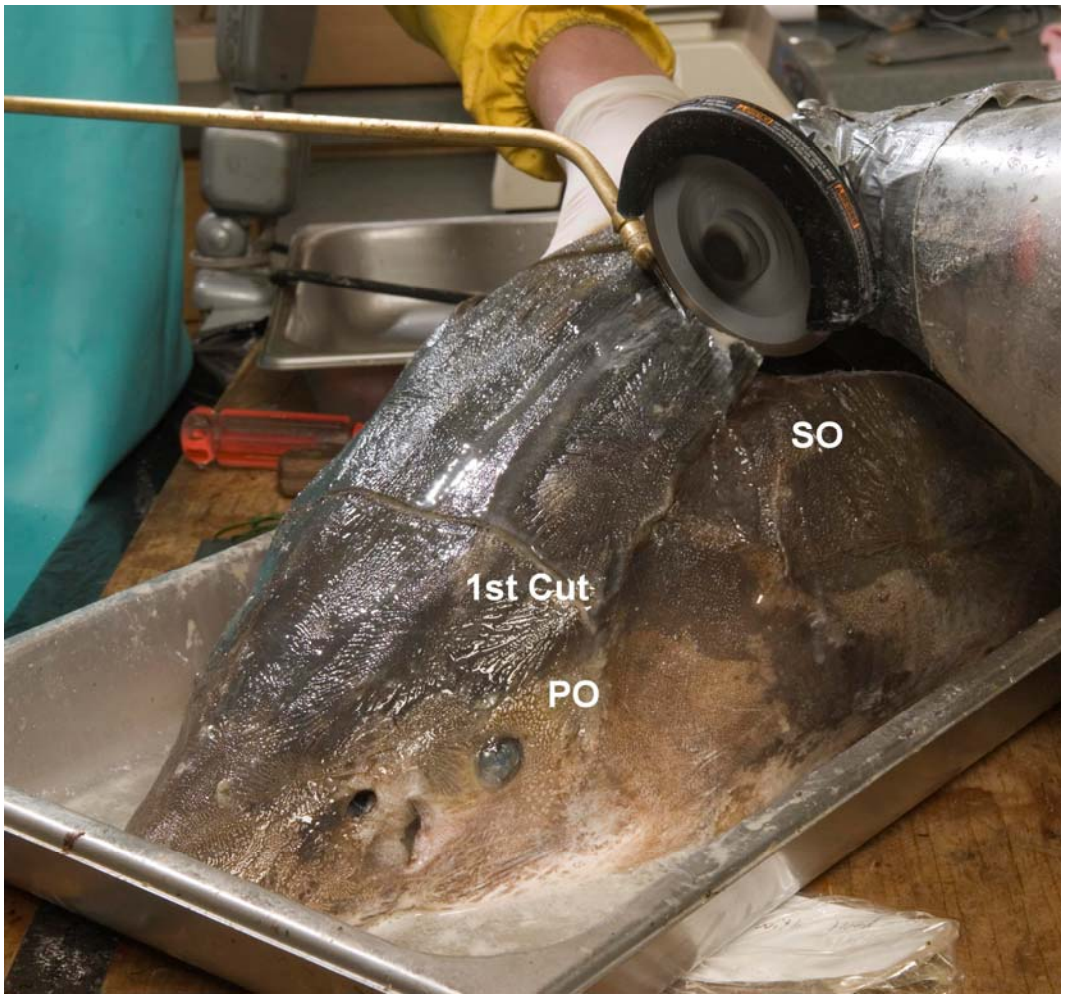

FIGURE 3a.—Location of cuts through lake sturgeon skull plate for otolith extraction. First cut is made laterally at a point beginning and ending at the posterior pointed ends of the postorbital bones (PO). Second cut is made laterally at a point beginning and ending adjacent to the apices of the subopercle bones (SO).

FIGURE 3b.—Removal of the left inner ear of a lake sturgeon from the auditory capsule.

FIGURE 3c.—Lake sturgeon left inner ear showing sagittal otolith in saccular vestibule of pars inferior.

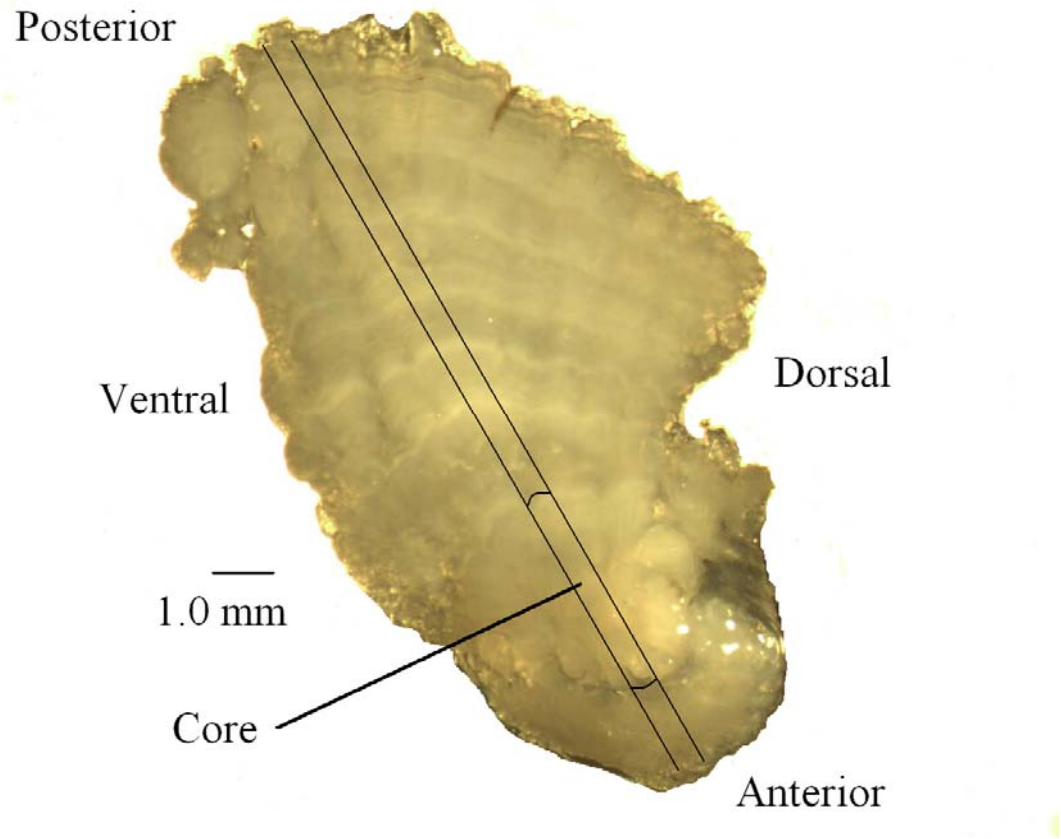

FIGURE 3d. —Lake sturgeon sagittal otolith showing orientation, and location of frontal section removed for age estimation, and the core removed for ^{14}C assay.

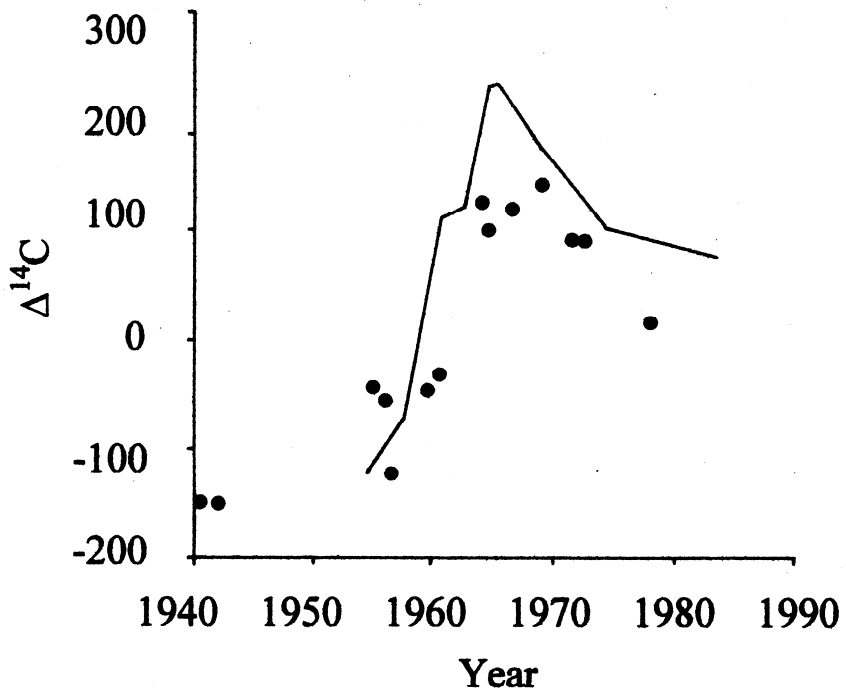

FIGURE 4. —$\Delta^{14}C$ Values of otolith cores, lake sturgeon and year of formation based on otolith age estimates (filled circles), 2006–2007, Lake Winnebago, Wisconsin; $\Delta^{14}C$ reference chronology for freshwater drum (solid line fit through loess procedure) from Lake Winnebago (Davis-Foust et al. in press).

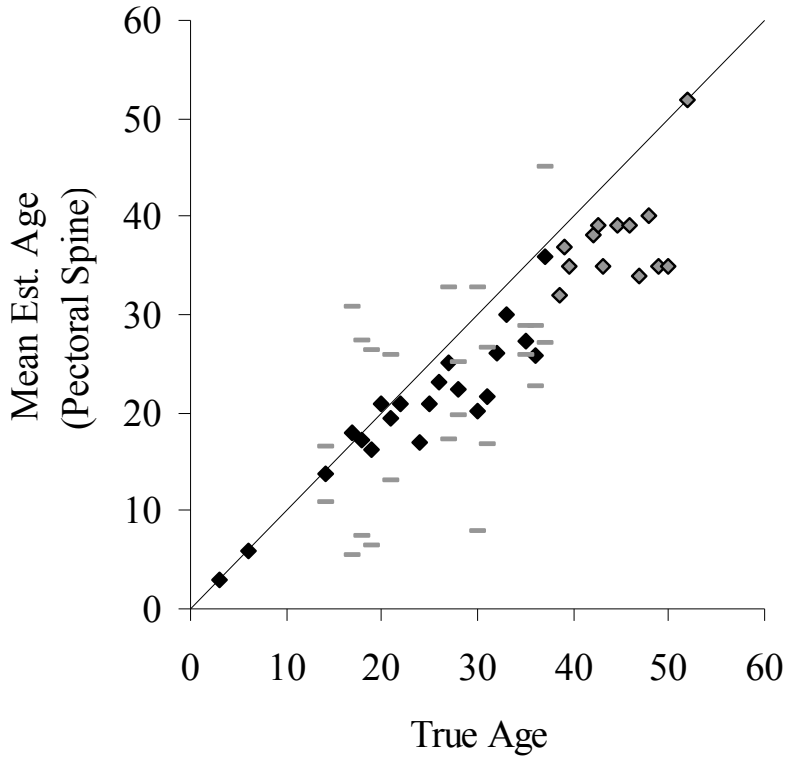

FIGURE 5.—Age bias plot comparing age estimates from pectoral fin spines to true age of known age lake sturgeon 1995–2004 (black diamonds), and to true age determined through bomb radiocarbon assays of lake sturgeon otolith cores 2006–2007 (grey diamonds), Winnebago System, Wisconsin. Grey bars delineate 95% confidence intervals around mean estimated ages of true ages sampled more than once. One to one line also illustrated.

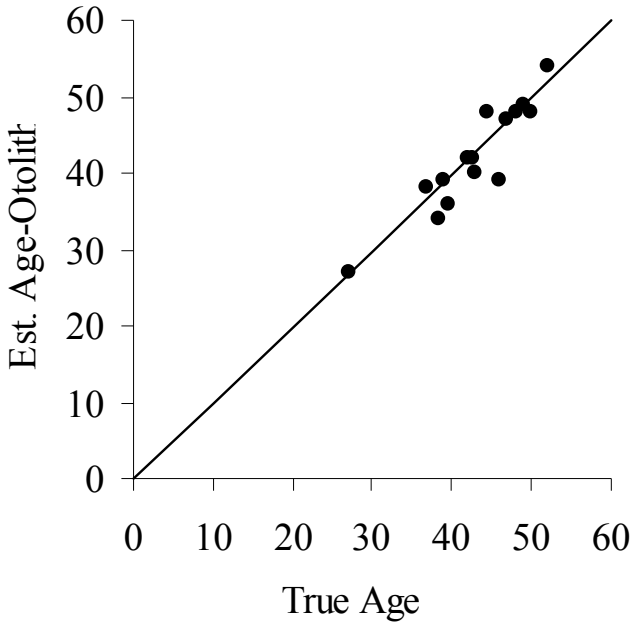

FIGURE 6.—Age of lake sturgeon estimated from frontal otolith cross sections compared to true age derived from known age fish 1995–2004, and bomb radiocarbon assays of otolith cores 2006–2007, Winnebago System, Wisconsin. One to one line also illustrated.

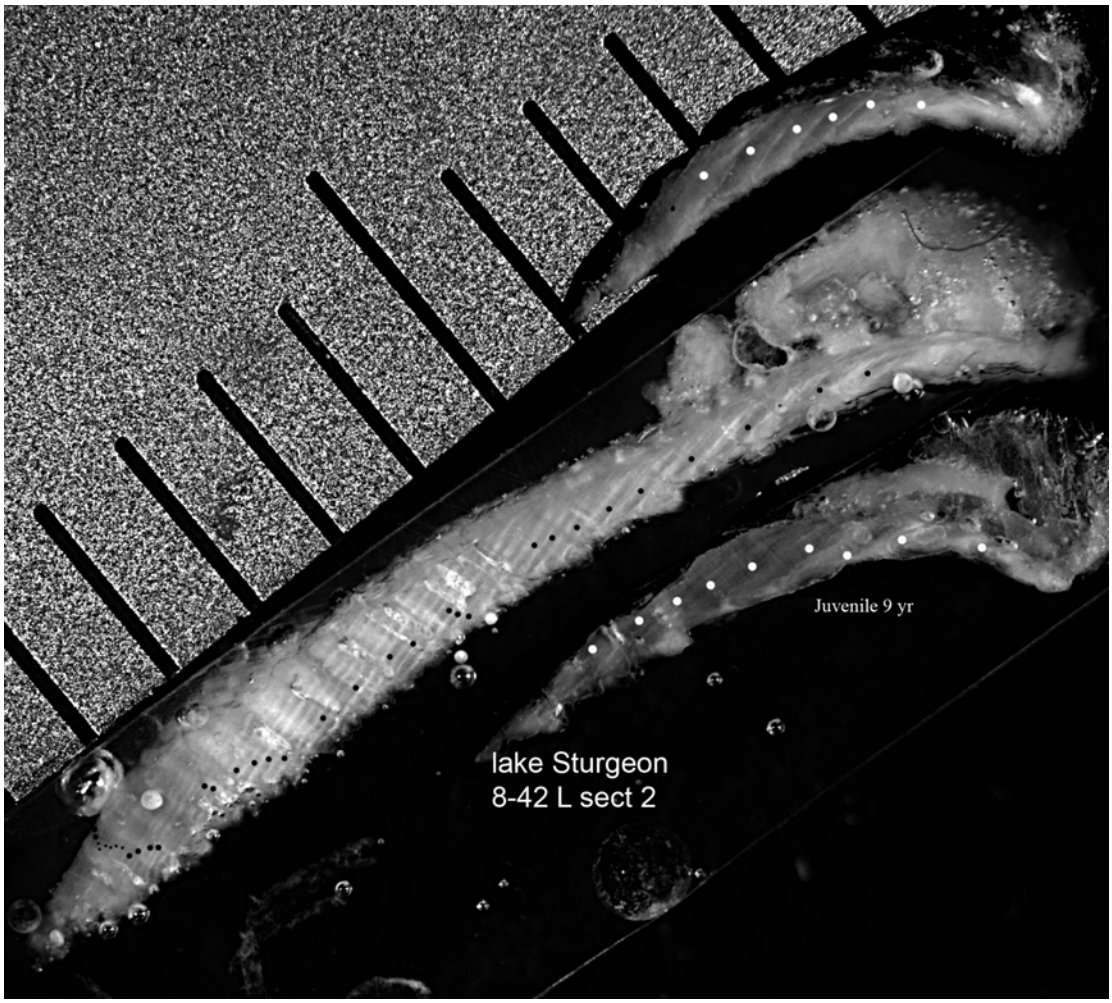

FIGURE 7.—Adult and juvenile lake sturgeon otolith cross-sections showing growth increments, Winnebago System, Wisconsin. Age estimates are 34 (bomb radiocarbon aged fish sampled February 2006 – large section), 9+ (wild juvenile sampled August 2007– bottom section), and 6+ (known age stocked sampled August 2007 – top section) years. Rule is in mm.

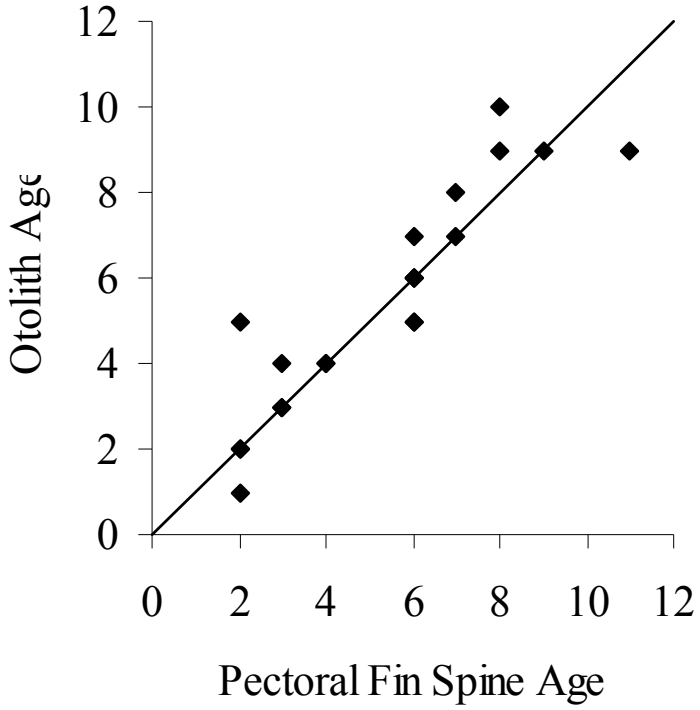

FIGURE 8.—Age of juvenile lake sturgeon estimated from otolith cross sections compared to age estimated from pectoral fin spine sections, August–October 2007, Winnebago System, Wisconsin. One to one line also illustrated.

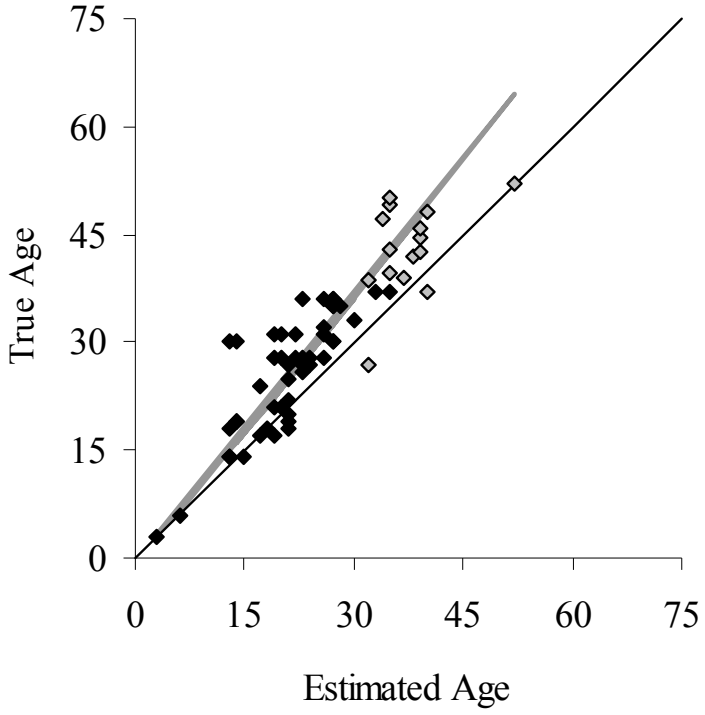

FIGURE 9.—True age vs. estimated age regression, lake sturgeon, Winnebago System, Wisconsin. Black diamonds are true age (known age fish) vs. pectoral fin spine estimated age; grey diamonds are true age (bomb radiocarbon assayed fish) vs. pectoral fin spine estimated age. Grey line is model: *true age = estimated age^1.054796*. One to one line also illustrated.

TABLE 1.—Estimated mean total length at ages 1–14, number sampled (N), standard deviation of lengths, range of lengths, and 95% confidence intervals of mean lengths for juvenile lake sturgeon in the Winnebago System, Wisconsin, during 1951–2007. Ages were estimated from pectoral fin spine sections.

Age	Mean TL (cm)	N	Std. Deviation	Range (cm)	L95%CI	U95%CI
1	22.2	13	3.2	16.0-26.2	20.3	24.1
2	35.8	46	6.3	23.9-49.8	33.9	37.7
3	51.8	49	5.9	38.6-71.1	50.1	53.4
4	63.3	126	4.3	49.5-73.7	62.6	64.1
5	72.8	136	7.3	50.5-86.4	71.5	74.0
6	79.3	103	7.6	63.5-96.5	77.8	80.8
7	82.7	92	7.7	68.8-99.1	81.1	84.3
8	83.7	78	7.3	71.1-99.1	82.0	85.3
9	85.3	55	6.3	73.7-102.6	83.6	87.0
10	89.6	48	7.6	74.9-111.8	87.4	91.8
11	91.3	36	6.2	81.3-108.5	89.2	93.4
12	95.0	36	5.1	84.6-103.5	93.3	96.7
13	100.0	26	8.0	86.4-122.4	96.7	103.2
14	100.7	24	6.4	89.2-121.9	98.0	103.4

TABLE 2.—Original tagging date, sex, total length and assigned age at tagging, recapture date, total length at recapture, years at large, estimated true age at recapture, and pectoral fin spine estimated age of juvenile lake sturgeon in the Winnebago System, Wisconsin, tagged during 1976–1997 and recaptured during 1995–2004. Assigned ages based on within year birth date determined from spawning survey data.

Original Tagging Date	Sex	TL (cm) at Tagging	Assigned Age at Tagging	Recapture Date (when aged)	TL (cm) at Recapture	Years at Large	True Age at Recapture	Pectoral Age at Recapture
18-Apr-1976	♀	94.0	11.95	10-Feb-2001	165.1	24.82	36.77	32.77
8-May-1978	♀	99.1	13.01	17-Feb-1995	162.6	16.78	29.79	26.79
16-May-1978	♂	96.5	12.03	9-Feb-2002	143.5	23.74	35.77	25.77
10-Jul-1978	♀	68.6	4.18	18-Feb-1995	124.5	16.61	20.79	18.79
12-Jul-1978	♀	83.8	8.19	13-Feb-1997	141.0	18.59	26.78	22.78
12-Jul-1978	♂	88.9	10.19	11-Feb-1996	125.7	17.58	27.77	18.77
12-Jul-1978	♀	91.4	11.19	26-Feb-1995	152.4	16.63	27.82	25.82
31-Aug-1978	♀	91.4	11.32	12-Feb-1995	152.4	16.45	27.78	23.78
19-Oct-1978	♂	69.9	4.46	16-Feb-1995	129.5	16.33	20.79	19.79
25-Sep-1979	♀	92.7	12.39	12-Feb-2000	154.9	20.38	32.78	29.77
27-Sep-1979	♂	99.1	13.40	10-Feb-2001	156.2	21.37	34.77	27.77
10-Oct-1979	♂	100.3	14.43	15-Feb-1996	134.6	16.35	30.78	21.78
11-Oct-1979	♂	100.3	14.44	10-Feb-2001	146.1	21.34	35.77	26.77
11-Sep-1980	♀	95.3	12.35	15-Feb-2004	135.9	23.43	35.78	26.78
18-Sep-1980	♂	81.3	6.37	12-Feb-2000	132.1	19.40	25.77	22.77
8-Oct-1980	♀	96.5	12.43	14-Feb-2004	133.4	23.35	35.78	22.78
10-Oct-1980	♀	97.8	13.43	15-Feb-2004	154.9	23.35	36.78	34.78
28-Oct-1980	♀	91.4	11.48	14-Feb-2004	144.8	23.30	34.778	26.78
4-Nov-1980	♂	96.5	12.50	13-Feb-1999	111.8	18.28	30.776	25.78
5-Nov-1980	♀	88.9	10.50	17-Feb-1998	149.9	17.28	27.788	22.79
28-Sep-1981	♂	99.1	13.40	12-Feb-2000	124.5	18.37	31.773	25.77
29-Sep-1981	♀	90.2	11.40	14-Feb-1998	127.0	16.38	27.780	21.78
12-Oct-1981	♂	83.8	8.44	14-Feb-2004	120.7	22.34	30.779	19.78
12-Oct-1981	♂	90.2	11.44	12-Feb-2000	102.9	18.34	29.773	12.77
12-Oct-1981	♂	90.2	11.44	12-Feb-2000	96.5	18.34	29.773	13.77
13-Oct-1981	♂	95.3	12.44	14-Feb-2004	146.1	22.34	34.779	26.78

16-Oct-1981	♀	91.4	11.45	15-Feb-1998	115.6	16.33	27.783	19.78
21-Oct-1981	♂	86.4	8.46	15-Feb-2004	118.1	22.32	30.782	18.78
21-Oct-1981	♀	91.4	11.46	18-Feb-1995	132.1	13.33	24.791	20.79
18-Oct-1982	♂	76.2	5.45	15-Feb-2004	123.2	21.33	26.782	23.78
7-Oct-1983	♀	95.3	12.43	15-Feb-1998	129.5	14.36	26.784	20.78
26-Sep-1984	♂	99.1	13.39	11-Feb-1995	121.9	10.38	23.771	16.77
14-Sep-1987	♂	80.0	6.36	13-Feb-2000	96.5	12.42	18.778	13.78
14-Sep-1987	♀	99.1	13.36	15-Feb-2004	133.4	16.42	29.783	26.78
2-Aug-1994	♂	84.6	8.24	12-Feb-2000	95.3	5.53	13.774	12.77
3-Aug-1994	♂	94.5	12.25	14-Feb-2004	129.5	9.53	21.780	20.78
3-Aug-1994	♂	99.6	13.25	13-Feb-1999	121.9	4.53	17.778	20.78
4-Aug-1994	♀	91.9	11.25	13-Feb-2003	114.3	8.53	19.778	20.78
9-Aug-1994	♂	79.2	6.26	10-Feb-2002	101.6	7.51	13.770	12.77
10-Aug-1994	♂	97.8	13.27	12-Feb-2000	109.2	5.51	18.774	13.77
11-Aug-1994	♂	94.0	12.27	12-Feb-2000	104.1	5.51	17.774	12.77
23-Aug-1994	♂	88.9	10.30	10-Feb-2001	124.5	6.47	16.771	16.77
23-Aug-1994	♂	91.4	11.30	10-Feb-2001	114.3	6.47	17.771	17.77
11-Aug-1997	♀	90.2	11.27	13-Feb-2000	91.4	2.51	13.776	14.78
11-Aug-1997	♂	92.7	12.27	15-Feb-2004	120.7	6.51	18.782	20.78
13-Aug-1997	♀	100.3	14.27	12-Feb-2000	110.5	2.50	16.773	18.77

TABLE 3.—Sample date, sex, total length, pectoral fin spine age, otolith age, ^{14}C (true) age, $\Delta^{14}C$ value, year of otolith formation based on increment counts and $\Delta^{14}C$ values of adult lake sturgeon of the Winnebago System, Wisconsin, 2006–2007. Two fish (*) could not be assigned a year of formation based on $\Delta^{14}C$ value of otolith core as values pre-dated 1958 levels.

Sample Date	Sex	TL (cm)	Pectoral Spine Age	Otolith Age	^{14}C (True) Age	$\Delta^{14}C$ Value	Year of Formation (based on increment counts)	Year of Formation (based on $\Delta^{14}C$ Value)
Feb-06	♂	137.2	32	27	27.0	16.6	1978	1978
Feb-06	♀	162.6	40	38	37.0	126.4	1964	1965
Feb-06	♂	162.6	32	34	38.5	91.4	1972	1968
Feb-06	♀	161.3	37	39	39.0	84.3	1968	1968
Feb-06	♀	166.4	35	36	39.5	91.3	1971	1968
Feb-06	♂	153.7	38	42	42.0	101.6	1964	1964
Feb-06	♀	167.6	39	42	42.5	120.6	1966	1966
Feb-06	♀	161.3	35	40	43.0	141.4	1969	1966
Feb-06	♂	146.1	39	48	44.5	-42.7	1955	1958
Feb-06	♀	176.5	39	39	46.0	-44.2	1967	1960
Feb-06	♀	162.6	34	47	47.0	-45.9	1959	1959
Feb-06	♀	165.1	40	48	48.0	-30.5	1960	1960
Feb-06	♀	160.0	35	49	49.0	-122.1	1956	1956
Feb-06	♀	165.1	35	48	50.0	-117.5	1959	1957
Feb-07	♀	188.0	52	54	52.0	-54.0	1956	1958
Feb-06	♀	179.1	47	67	>52	-149.9	1940	*
Feb-06	♀	170.2	48	68	>52	-149.8	1942	*

TABLE 4.—Collection date, total length and estimated age of juvenile lake sturgeon sampled for growth increment formation and corroboration using pectoral fin spines (PFS) and otoliths from Lake Winnebago, Wisconsin, during August–October 2007. *Italics* = known age fish. Asterisk = otolith was too porous to age. All ages are estimates counting the last visible annuli, not including growth to the edge.

Date Collected	Total Length (cm)	PFS Reader 1	PFS Reader 2	Otolith Reader 1	Otolith Reader 2
1-Aug-2007	86.0	9	9	9	9
8-Aug-2007	*74.9*	*6*	*6*	*6*	*6*
8-Aug-2007	59.9	3	3	3	3
29-Aug-2007	63.8	4	4	4	4
29-Aug-2007	76.2	7	7	8	7
31-Aug-2007	76.5	6	6	7	6
4-Sep-2007	88.9	9	9	*	*
4-Sep-2007	79.5	11	11	9	9
4-Sep-2007	*64.0*	*3*	*3*	*4*	*3*
5-Sep-2007	51.6	2	2	5	2
4-Sep-2007	72.6	6	6	5	5
5-Sep-2007	52.8	2	2	1	2
5-Sep-2007	65.5	6	6	6	5
1-Oct-2007	80.3	8	8	10	9

CHAPTER 2

Population Dynamics of Lake Sturgeon in the Winnebago System: Long-Term Impacts of Harvest Management Policies, Environmental Changes, and Public Involvement

Introduction

One of the cornerstones in fisheries management decision making is evaluation of the impact of past harvest management strategies on a fishery. Inconsistencies in data collection or quality, changes in personnel or program priorities, and environmental stochasticity can hinder meaningful long-term evaluations. Changes in abundance, growth, or distribution of a fish population over time can be observed in population and harvest assessments; and management actions such as size limits, bag or harvest limits, and season lengths are often prescribed in reaction to positive or negative changes in the fishery. While prescriptive management actions can be modeled to predict their potential impact on future fish populations (Chapter 3), the hindsight of trends and parameters developed from historic data are useful for evaluating the effectiveness of past management actions. A lack of quality historic long-term population and fishery assessment data often leaves managers with only their professional opinion to determine whether a past management action or regulation was effective.

The impact of past management actions on a fish population can be especially difficult to understand for long-lived, late-maturing species. Long-lived, late-maturing species exemplifying a periodic life history pattern (Winemiller and Rose 1992) are

typically slow growing, have a low intrinsic rate of population increase, and experience greater population declines at a given fishing mortality rate (Adams 1980, Trippel 1995). Based on phylogenetic comparisons of 18 intensively exploited fish stocks in the north-east Atlantic, after accounting for differences in fishing mortality, species that decreased in abundance over time were those that attained a larger maximum size and exhibited lower potential rates of population increase (Jennings et al 1997).

Sturgeon species are well-known periodic life history strategists that have tended to decline in abundance over the last 100 years (IUCN-Sturgeon Specialist Group 2006). With the exception of a few populations, sturgeon world-wide have generally not yet responded well to management actions and regulations designed to protect or restore stocks. While the response of sturgeon populations to negative anthropogenic factors is exemplified by reduced harvest rates throughout the northern hemisphere, positive responses of populations to management measures have not been realized for most species (Rosenthal et al. 2002, Rosenthal et al. 2006). Due to their low intrinsic rate of population increase, evaluation of sturgeon population response to management actions designed to increase abundance will require consistent long-term data that span many decades.

The population of lake sturgeon (*Acipenser fulvescens*) in the Winnebago System has been actively managed to sustain a viable population and fishery for over 100 years and population and harvest assessment data have been consistently collected for over 60 years. Harvest was estimated through creel surveys during 1941-1954 (except for 3 years during WWII). Harvest and effort were enumerated during 1955–2007 through mandatory registration of all harvested fish, and through aerial counts of spearing shanties. Catch at age data have been collected for harvests during 1954-1969, 1976, 1981, 1991, 1993-2007.

Sex and maturity of harvested fish have been collected in 1954 and during 1991-2007. Sex and total length have been collected and tagging studies have been conducted on lake sturgeon captured in the upper Fox and Wolf Rivers and their tributaries during spawning runs out of Lake Winnebago during 1954-1964 and 1975-2007. Total length and CPE were collected and tagging studies were conducted on lake sturgeon captured in fyke and trap nets on Lake Winnebago and the three small lakes upstream (the Upriver Lakes) during 1951-1964, and on lake sturgeon captured in trawls used on Lake Winnebago for sheephead (*Applodinotus grunniens*) removal operations during 1971-1990. These data provide a unique opportunity to examine the long-term population dynamics of lake sturgeon in the Winnebago System, and assess the impact of harvest management strategies, environmental changes, and social events that occurred over a century, on these dynamics.

My objectives were to: (1) estimate age and growth, size and age at maturity, weight-length relationships, relative condition, fecundity, eggs per recruit, recruitment, mortality, abundance, intrinsic rate of population growth, and yield per recruit of lake sturgeon in the Winnebago System during 1941-2007; and (2) assess the potential impact of harvest management policies, environmental changes, and public involvement on the population dynamics of lake sturgeon in the Winnebago System during 1874-2007.

Age and Growth.—Previous studies indicate that lake sturgeon grow slowly (Harkness 1923; Schneberger and Woodbury 1946; Cuerrier and Roussow 1951; Probst and Cooper 1954; Priegel and Wirth 1977; Folz and Meyers 1985; Rossiter et. al 1995; Bruch 1999). Some of the pioneering work on estimating lake sturgeon age and growth was completed on the Winnebago System using otoliths (Schneberger and Woodbury 1946) and pectoral fin-ray sections (Probst and Cooper 1954). For example Schneberger

and Woodbury (1946) estimated male lake sturgeon 107-152 cm (42-60 inches) in total length were 14 to 31 years old, and females 122-170 cm (48-67 inches) in length 21 to 40 years old. Probst and Cooper (1954) estimated age of lake sturgeon for both genders combined, 20-201 cm (7.7-79 inches) in total length, to be 1 to 82 years. Male and female lake sturgeon have also been reported to exhibit sexual dimorphism in growth after reaching sexual maturity (Bruch 1999). None of the previous lake sturgeon age and growth studies validated the accuracy of the structures used to estimate age, so validation of lake sturgeon age estimation (Chapter 1) was critical to developing meaningful estimates of growth, mortality, recruitment and yield.

More than 14,000 pectoral fin-ray sections have been collected from sturgeon in the Winnebago System since the late 1940s (Schneberger and Woodbury 1946; Probst and Cooper 1954; Priegel and Wirth 1975, 1978); Folz and Meyers 1985; Bruch 1999). The age validation work reported in Chapter 1 showed that ages estimated from pectoral fin spine sections generally underestimate true age and therefore needed to be corrected prior to their use in other population dynamics models.

Size and Age at Maturity.— Maturity, generally a function of the sex and the size of individuals, is usually modeled as logistic function of size or age. Lake sturgeon and most other sturgeon species mature later in life and generally do not spawn every year. Most of the literature on lake sturgeon age and size at maturity focuses on gonadal condition, and often the length, weight, or minimum estimated age of fish observed with fully developed gonads in a particular sample (Harkness 1923; Currier 1949; Dubreuil and Currier 1950; Cuerrier and Roussow 1951; Roussow 1957; Sunde 1961; Priegel and Wirth 1975; Dumont et al. 1987; Nowak and Jessop 1987). Male lake sturgeon have

been reported to mature at lengths of 76-114 cm (30-49 inches) and ages of 12-20 years, whereas female lake sturgeon have been reported to mature at lengths of 83-140 cm (33-55 inches) and ages of 14-33 years (Table 1). In the Winnebago System, female lake sturgeon have been reported to mature at total lengths of 130-140 cm (51-55 inches) and ages of 20-25 years (Priegel and Wirth 1975; Folz and Meyers 1985, Bruch 1999). Female lake sturgeon in the Winnebago System generally spawn every 3-5 years, but one spawning female was captured that had spawned two years earlier (R.M. Bruch, WI DNR, Oshkosh, unpublished data). In the Winnebago System, male lake sturgeon have been reported to mature at total lengths of 83-114 cm (32-45 inches) and ages of 12-15 years. Males sometimes spawn in consecutive years, but more often spawn every other year (Priegel and Wirth 1975; Folz and Meyers 1985). The wide range of reported ages of maturity of male and female lake sturgeon could reflect latitudinal differences in growth rates, and may also be an artifact of erroneous age estimation.

The harvest management system for lake sturgeon in Lake Winnebago has been based on an assumed size of 50% maturity for adult females at 55 inches (139.7 cm) total length since implementation of a harvest cap to control exploitation in 1999. All female lake sturgeon 55 inches and longer in the spear harvest are considered adult and all female sturgeon less than 55 inches are considered immature (Bruch 1999). The daily tally of numbers harvested during the season is critical for determining season length because the harvest is controlled through harvest limits set separately for juvenile females, adult females, and males. Caps are set to minimize the risk that annual harvest exceeds 5% of the estimated standing stock of each category. The spearing season is closed at the end of a spearing day when 100% of any one of the three harvest caps is

reached or exceeded, or 24 hours after the end of a spearing day when 90-99% of any one of the three harvest caps is reached. An average size of maturity of females less than 55 inches might shorten the season, whereas an average size of maturity greater than 55 inches might lengthen the season. Given this harvest management system, a clear understanding of size of maturity of adult female lake sturgeon in the Winnebago System is essential.

The long-term Winnebago lake sturgeon spawning and harvest assessment data can be used to quantify the dynamics of size at maturity of lake sturgeon. Clarification of the age of maturity using Winnebago data will provide insight into the dynamics of maturity for lake sturgeon in the Winnebago System that is critical to harvest management and general understanding of population dynamics of the species.

Weight-Length Relationships and Relative Condition.—There have been numerous reports published on the weight-length relationships of lake sturgeon from throughout the species' range (Probst and Cooper 1954; Priegel 1973; Threader and Brousseau 1986; Dumont, et al 1987; Ecologistics Ltd 1987; Nowak and Jessop 1987; Sandilands 1987; Larson 1988; McDonald 1998; Craig et al. 2005; Smith and Baker 2005; Huges et al 2005; Adams et al. 2006; Lallaman et al 2008). Most of these authors though reported no or limited data on sex and none on stage of sexual maturity. The availability of long term Winnebago System lake sturgeon length, weight, and sex data, along with validated age-length data, provides an opportunity to examine trends in Winnebago lake sturgeon growth and relative condition over the last 60 years. This is the first description of lake sturgeon weight-length relationships that can account for sex and stage of sexual maturity.

Relative condition of sturgeon, as with many fish species, is highly variable for individuals and the population because of seasonal changes in gonadal development, temporal variability food supply, or temperature fluctuation. Because of sturgeon longevity and life history, the species may be more apt to exhibit relatively wide variance in its condition. Also, the impact of density dependent factors on the mean relative condition of sturgeon populations would likely require decades of data, including lengths and weights (as well as sex and gonadal stage), and a time-series of population density estimates (possibly estimates by sex and maturity). Most fish show a tendency towards allometric growth or an increase in relative body thickness or plumpness as they get older (Froese 2006). Sturgeon also exhibit this pattern (Quist et al. 1998, Craig et al. 2005), but individuals within populations can vary widely in relative condition within and among years.

Understanding the dynamics of growth and relative condition of lake sturgeon, and how they may relate to long-term changes in density and harvest will provide insight into the dynamics of sturgeon in the Winnebago and elsewhere, contributing to a more complete understanding of the life history characteristics required for the development and implementation of sturgeon management and recovery plans.

Fecundity.—Understanding fecundity is critical to calculation of a fish species' eggs per recruit ratio (Boreman 1997). Sturgeon species are well known for being highly fecund with a strong relationship between the body weight and numbers of fully developed eggs (Hochleithner and Gessner 1999). Fecundity reported in the literature for various sturgeon species ranges from as few as 8,000 eggs in an *Acipenser ruthenus* specimen (Berg 1948) to as many as 7,700,000 eggs in a *Huso huso* specimen (Babushkin

1947), though the number of eggs an adult female sturgeon carries has been traditionally reported as the number of eggs per kg of body mass.

Fecundity of lake sturgeon *(Acipenser fulvescens)* has been studied by Cuerrier (1949; cited in Harkness and Dymond, 1961), Dubreuil and Currier (1950), Harkness and Dymond (1961), and Sandilands (1987), but these studies examined relatively few fish, and did not account for ovarian tissue mass or volume or ovaries in an F4 (black egg) development stage, as classified by Bruch et al. (2001).

Eggs per Recruit.—Eggs per recruit (EPR) is defined as the potential lifetime egg production of an age-1 female, or the sum of the products of the estimated number of eggs a female will produce at each age in her lifetime and the probability that she will survive to that age (Boreman 1997). The probability that she will survive to a specific age depends on the fishing and natural mortality rates she is experiencing. The EPR ratio is the ratio of the eggs per recruit of a fished population to the eggs per recruit of an un-fished population. The EPR ratio at various fishing mortality rates provides insight into the risk of recruitment overfishing. Goodyear (1993) recommended maintaining an EPR ratio of at least 20% of the maximum when fishing mortality is zero. Boreman et al. (1984) recommended maintaining an EPR ratio of 50% for rebuilding (as opposed to maintaining) the stock of shortnose sturgeon (*Acipenser brevirostrum*) along the US Atlantic coast. Quist et al. (2002) found that recruitment overfishing may occur on shovelnose sturgeon in the Missouri River System with a target EPR ratio of 40-50%, with no minimum length limit in the commercial fishery and exploitation rates of ≤10%. Boreman (1997) reported an estimated 50% reduction in the EPR ratio of white and Atlantic sturgeon with a fishing mortality rate (F) of 5-6%.

Estimating the eggs per recruit ratios for Winnebago lake sturgeon at different fishing mortality rates allowed development of minimum the EPR ratio needed to sustain the stock, develop harvest caps for the Winnebago sturgeon spear fishery, and provide guidance for other lake sturgeon fisheries.

Recruitment, Mortality Rates, and Abundance.—Understanding recruitment rates, mortality rates, and abundance is key to effectively managing an exploited fish population. Stock assessments provide biological information on these metrics that resource managers integrate with social and economic factors to make recommendations on sustainable yield, maximum fishing mortality rates, regulations, and habitat protection and enhancement. Assessing recruitment, mortality, and abundance of sturgeon populations is generally difficult due to their late age of maturation, relatively low stock densities, complex migration patterns, and capture difficulty.

Ricker (1954) and Beverton and Holt (1957) developed the two classic density dependent Stock Recruitment models with recruitment diminishing to zero with maximum stock size in the Ricker model, for example with walleye (*Zander vitreum*) (Hansen et al 1998), or building to an asymptotic plateau at maximum stock size with the Beverton-Holt model, for example with plaice (*Pleuronectes platessa*) (Beverton and Holt 1957). If fish populations can increase towards some system-specific carrying capacity, then adult stock size should affect subsequent recruitment of eggs, larvae, juveniles, or adult recruits that in turn may be part of the density dependent mechanisms eventually limiting population growth. Large variation in recruitment over a wide range of parental stock sizes results from complex interactions of stochastic density independent environmental factors and

deterministic density dependent biotic factors (Walters et al. 1986; Madenjian et al. 1996; Hansen et al. 1998).

Stock-recruit relationships have not been reported in the literature for sturgeon despite the high importance of this relationship to effective long-term fishery management, likely because of the difficulty in quantitatively assessing sturgeon stocks, especially juveniles, and the potential long lag between measurable stock and recruitment events. Although lake sturgeon in the Winnebago System have been the subject of intensive stock and fishery assessments since the 1940's, no S-R model has been developed for this stock. Given the unique life history traits of most sturgeons, it is difficult to project the type of S-R relationship their populations would exhibit. While lake sturgeon on the Winnebago System regularly consume fish, no juvenile sturgeon have ever been found in adult sturgeon stomachs (Stelzer et al 2008; R.M. Bruch, unpublished data 2007). Lake sturgeon, primarily males, prey on their own eggs while they are at their spawning sites (Bruch et al. 2001; Bruch and Binkowski 2002) which might lead to a Ricker type stock-recruit relationship. This egg eating behavior, on the other hand, may actually improve conditions for egg incubation, because many of the eggs fall into interstitial spaces below the surface of the rocky spawning substrate, and the constant grazing of surface eggs by sturgeon and other fish (suckers and redhorse) may help maintain hyporhehic flows and control disease (fungus) on subsurface eggs (Johnson et al. 2006). Developing a stock-recruitment model for lake sturgeon is important for understanding lake sturgeon S-R dynamics and potential optimal stock size, for determining stocking rates for rehabilitation projects, and for modeling long-term trends in sturgeon populations.

Estimation of fishing and natural mortality rates relies on accurate estimates of exploitation and ages of harvested fish. Fish ages, used to estimate mortality, are likely the most important data collected in stock assessments, and accurate estimates of exploitation require tag and recapture programs that mark adequate numbers of fish, suffer no (or at least measurable) tag loss, and do not miss recaptured marks.

Sturgeon are commonly recognized as having relatively low natural mortality (Beverton and Holt 1959), and as such, are able to tolerate only low levels of fishing mortality or exploitation (Preigel and Wirth 1975, Taghavi, 2001). Historic estimates of mortality rates of sturgeon based on pectoral fin spine age estimates though may have significant error. Lake sturgeon age validation results from Chapter 1 showed that interpretations of growth increments from cross sections of pectoral fin spines of lake sturgeon from the Winnebago System significantly underestimated the age of fish older than 13-15 years. Use of mortality rates estimated from erred age data in fisheries models can result in harvest management strategies that lead to stock overexploitation.

Catch at age data are often used to build age structured models that estimate trends in recruitment, mortality, and abundance (Quinn and Deriso 1999, Hilborn and Walters 2001, Haddon 2002). Statistical catch at age (SCAA) models are forwarding projecting; N_{t+1} is predicted from N_t (Hilborn and Walters 1992; Haddon 2001). SCAA analysis integrates several population dynamics models to estimate vital statistics for exploited fish stocks based on principals of catch curve analysis, but over many cohorts and years. An objective function, either maximum likelihood or least squares, is used to optimize the fit of the SCAA model to the available catch at age data. Effort (or catch rate), and

stock-recruit data are also used in the analysis to help constrain fishing mortality and recruitment parameters to reasonable values.

SCAA models have been used extensively as a tool for understanding the dynamics of a wide range of commercial and recreational fisheries. Wilberg et. al (2005) used an SCAA to hypothesize that excessive commercial and recreational fishing mortality rates, in the face of successive year class failures, was likely the primary cause of the collapse of the yellow perch (*Perca flavescens*) fishery in southern Lake Michigan during the mid to late 1990's. Wilberg et al. (2005) recommended conservative harvest regulations remain in effect despite renewed requests from user groups to increase harvest targeting a strong 1998 year class of perch. Linton (2002) used an SCAA model to estimate recruitment, mortality, and abundance of a recovering lake trout (*Salvelinus namaycush*) population in Lake Superior, finding that natural mortality was the largest mortality component for wild lake trout while mortality from commercial fishing was the largest mortality component for stocked lake trout. His model suggested that, despite total mortality rates being below target rehabilitation levels, lake trout recruitment was still below the levels necessary to sustain the population. Ebener et. al (2005) used an SCAA model to estimate stock specific maximum allowable total annual mortality rates for commercially fished lake whitefish (*Corregonus clupeaformis*) populations in Michigan (USA) Native American Treaty waters of Lakes Huron, Michigan and Superior.

While SCAA models have been used successfully to better understand the population dynamics and set harvest limits for species such as yellow perch, lake trout and lake whitefish, they do not appear to have been used as a tool to better understand or

manage sturgeon populations or harvest. Pine et al. (2001) used an age structured cohort analysis model to examine population growth and mortality trends of the Gulf sturgeon during a ten year period, 1986-95, estimating a total annual mortality rate of 16%. I found no other references in the literature of age structured analysis on sturgeon, likely due to the lack of long term catch at age data for sturgeon fisheries, and because most sturgeon fisheries, at least those in North America and western Europe, have been shut down. SCAA analysis requires data from the number of years an individual fish could potentially be subject to harvest. In the case of lake sturgeon, 50 to 60 years of catch at age data are necessary.

The Winnebago sturgeon spear harvest catch at age data, while not available for every year over the last 50 to 60 years, is available for substantial blocks of time over the last 55 years, and were adequate to run an SCAA model. This is the first use of SCAA analysis to estimate recruitment, mortality, and abundance for any species of sturgeon, and the first opportunity to evaluate the usefulness of SCAA modeling for understanding sturgeon stock dynamics and for sturgeon population and harvest management.

Fish stock assessments often begin with the desire to determine abundance or some relative measure of abundance of the stock in question. Developing abundance estimates for sturgeon is difficult for many of the same reasons determining the stock-recruit relationship for sturgeon is difficult including low densities, capture difficulties, and unique and complex migration patterns of the various sturgeon life stages. These factors often confound sampling efforts and may violate assumptions of the abundance estimator models.

Sturgeon population densities have been estimated by a variety of models including

the relationship between exploitation rate and harvest levels for Atlantic Sturgeon in the Hudson River (Kahnle et al. 2007), and an open population Jolly-Seber model for Gulf sturgeon (Berg et al. 2007). Estimates of lake sturgeon abundance in the Winnebago System were developed historically using Chapman's modification of the Peterson closed population model (Priegel and Wirth 1975, Folz and Meyers 1985, Bruch 1999). Lake sturgeon on the Winnebago System have been captured and tagged during their annual spawning run up the Wolf and upper Fox Rivers and tributaries during 1953-1963, and 1975-2007. Fish were marked with Petersen disc tags in 1953, monel metal jaw tags in 1954, plastic dart tags during 1958-1963, monel metal dorsal fin tags during 1955-1957, 1975-2005, and PIT tags during 1999-2007.

Estimates of the harvestable stock (sturgeon larger than the minimum size limit in effect at the time) were developed during the mid 1950s to 1990 using sturgeon tagging data collected during freshwater drum (*Aplodinotus grunniens*) removal operations on Lake Winnebago and the Upriver Lakes, and recapture data collected during the ensuing winter spear fishery. After drum removal operations ceased in 1991, separate estimates of adult male and female sturgeon were developed with a Chapman modification of the Peterson estimator using tagging data from annual spring sturgeon spawning assessments on the Wolf and Upper Fox River systems, and recapture data from the ensuing winter spear fishery (Bruch 1999).

Lake sturgeon density estimates for the Winnebago System are used to set harvest caps each year for the sturgeon spear fishery to ensure the annual harvest does not exceed 5% of the estimated harvestable stock, so measurement error must be minimal to ensure harvest does not exceed the sustainable harvest level (Bruch 1999). Since 1991,

estimates were often difficult to develop because of the difficulty of capturing and tagging enough fish during the short spawning season, tag loss, and the small number of recaptures in some low harvest seasons. Although historical estimates have been used to set harvest caps to maintain annual exploitation at or below 5%, alternative abundance estimators were needed to corroborate previous estimates and ensure harvest caps are set that will adequately control exploitation.

Intrinsic Rate of Population Growth.—The intrinsic rate of increase (r) is one of the most important parameters to understand about the population. Many important attributes of animals and their life history parameters are tied to the intrinsic rate of increase, including natural mortality rates (M), Brody's growth coefficient (K from the von Bertalanffy length-age model), L_∞ and W_∞ (from the vB length-age model), and α (per capita recruitment rate from the Ricker and Beverton-Holt stock-recruit models). Many factors can affect the intrinsic rate of increase including fishing and natural mortality, density, relative condition of individuals in the population, growth rate, age of maturity, fecundity, and environmental and demographic stochasticity. The extent to which each of these factors affect the intrinsic rate of increase would be difficult to discern, but an estimate of the intrinsic rate of increase provides insight into the long-term stability of the population and how fishing mortality, habitat change or other perturbations may affect the population.

The intrinsic rate of increase has rarely been estimated for sturgeon species. A discrete rate of increase (λ) of 1.05 (equal to an r of 0.0488) was estimated for Gulf Sturgeon, a protected species from the Gulf of Mexico, during 1986-1995 using an age-structured model (Pine et al. 2001). Others only mentioned the general but reasonable belief that sturgeon species have low intrinsic rates of increase (Waldman and Wirgin 1998;

Wirgin et al. 2002). Unfortunately *r* is difficult to measure for species like sturgeon because of difficulties estimating abundance of this low-density animal, and because few established sturgeon assessment programs have sufficient data to estimate *r* at this time.

The sturgeon management and assessment program on the Winnebago System is one of the longest running assessment programs on any sturgeon species in the world and should provide sufficient data to estimate *r* for both adult males and females during 1954-2007. Estimates of *r* would be the first for any sturgeon species by sex, which should provide important insight into lake sturgeon life history.

Yield per Recruit.—The yield per recruit (Y/R) model is a tool often used by Fisheries Managers to help set size limits for fisheries, and is the foundation of the FAST model (Fishery Analysis and Simulation Tool) (Slipke and Maceina, 2006) used by the Wisconsin Department of Natural Resources to support fisheries regulation decisions. The parameters used in the Y/R model include several from the Von Bertalanffy length-age model so errors in age estimation will cause problems with the reliability of the model output. Despite the assumptions in Y/R models of isometric growth (sturgeon growth is likely allometric) and constant recruitment, the model can still be a useful tool in estimating sturgeon yield per recruit for different harvest mortality rates to evaluate effort and minimum size limits.

The literature on use of yield per recruit models for management of sturgeon fisheries, while somewhat limited appears to be increasing since the mid 1990's. Maximum yield per recruits (Y/R) for white sturgeon populations on the lower Columbia River system, Washington, USA was estimated to occur with exploitation rates of 5-15% (Beamesderfer et al. 1995). Maximum sustainable Y/R was estimated at instantaneous

fishing mortality rates of 0.16 for male and 0.07 for female beluga sturgeon (*Huso huso*) inhabiting the Caspian Sea (Taghavi 2001). The FAST model was used to simulate the impact of various size limits on Y/R of commercially harvested shovelnose sturgeon populations in the Missouri River System suggesting that shovelnose sturgeon are more sensitive to overharvest than previously thought (Quist et al. 2002). The FAST model was also used to conclude that paddlefish (*Polyodon spathula*) harvest regulations in the lower Tennessee River system, Tennessee, USA were ineffective at controlling growth overfishing occurring in the commercial paddlefish fishery (Scholten and Bettoli 2005).

The lake sturgeon spear fishery on the Winnebago System has been regulated with various minimum size limits since 1932: 30 inches (76.2 cm) during 1932-1958, 40 inches (101.6 cm) during 1959-1973, 45 inches (114.3 cm) during 1974-1995, and 36 inches (91.4 cm) during 1996-present (2008). Modeling yield per recruit for Winnebago lake sturgeon will provide insight into the appropriateness and effectiveness of the various minimum size limits implemented on the Winnebago System over the years, as well as potentially providing insight into the usefulness of using yield per recruit model output to set size limits for lake sturgeon fisheries.

Long-Term Impact of Harvest Management, Environmental Change, and Public Involvement on Lake Sturgeon Population Dynamics.—The earliest attempts to manage sturgeon harvest were policies enacted by the Wisconsin Fisheries Commission after their creation by the Wisconsin Legislature in 1874 (Wisconsin Commissioners of Fisheries, 1878), and included size limits and seasons, followed by a total harvest ban in 1915 (Wisconsin Fish and Game Laws, 1900-1915). The modern-day management program for lake sturgeon in the Winnebago System has used estimates of age, growth, mortality,

and abundance to develop harvest policies since the 1940's. Lake sturgeon in the Winnebago System were considered faster growing and earlier maturing than lake sturgeon from other populations following an examination conducted during a period with a 30 inch (76.2 cm) minimum length limit out of concerns about recruitment over-fishing (Schneberger and Woodbury 1946). In the 1950s, length at age estimates failed to show a difference in growth rates between the sexes, supporting continuing liberal harvest regulations (Probst and Cooper 1954). Priegel and Wirth (1975) used estimated ages of 7,013 lake sturgeon harvested during 1955-1967 to estimate total annual mortality at 0.054, and average an annual recruitment rate of age 15-19 year old sturgeon at 4.7%. Priegel and Wirth (1975) subsequently recommended a 4.7% annual harvest limit (later rounded to 5%, Personal communication, D. Folz, WI DNR, Oshkosh, retired) which has since been a cornerstone of the Wisconsin Lake Sturgeon Management Plan (Wisconsin DNR, 1998).

Age estimates of lake sturgeon harvested from the Winnebago System during 1955-1983 were used to show a reduction in the relative proportion of fish ≥ 20 years old in the harvest, and an increase in total annual mortality from 5.4% (Priegel and Wirth 1975) to 10.5%, following an increase in the minimum length limit from 40 inches (101.6 cm) to 45 inches (114.3 cm) in 1974. Changes in age structure and mortality rates were attributed to increased recruitment, and the 45 inch minimum length limit was retained (Folz and Meyers 1985). Age estimates of sturgeon harvested during 1991-1997 were used to estimate a further increase in total annual mortality rates from 10.5 to 18.6% of the legal stock, and to justify a reduction in the minimum length limit from 45" (114.3

cm) to 36” (91.4 cm) to reduce the harvest of adult females and to reduce the risk of recruitment overfishing (Bruch 1999).

Environmental changes and public involvement also likely played a role in shaping the lake sturgeon population in the Winnebago System over time. The pool lakes of the Winnebago System, Winnebago, Butte des Morts, Winneconne, and Poygan were impounded in the late 1800s with an additional increase in the early 1900s. This impoundment, amounting to about 1 meter, set into motion environmental changes that likely physically affected the system’s fish community, but also affected the sturgeon spearing public’s perception of the status of that fish community, especially sturgeon, for decades.

Examining trends in the population dynamics of lake sturgeon in the Winnebago System over the last 60 years in relation to management actions, harvest regulations, environmental changes, and public involvement will allow a thorough evaluation of sturgeon management strategies that should be useful for developing future management policies for sturgeon in the Winnebago System and elsewhere.

Methods

Age and Growth.—I determined the mean lengths at age, mean annual growth increments, growth patterns, and parameters for von Bertalanffy growth models for juvenile, male, and female lake sturgeon in the Winnebago System using length and age data from juveniles and adults collected during winter harvest seasons, from juveniles sampled during a variety of surveys on the Wolf River and Winnebago Pool Lakes during 1953-2007, and from newly hatched larvae sampled at the University of Wisconsin-Milwaukee Great Lakes WATER Institute in 2007.

Adult and juvenile lake sturgeon (>76.2 cm) harvested during the annual winter spear fishery on Lake Winnebago and the Upriver Lakes during 1953-1959, 1991, and 1993-2007 were measured in total length to the nearest 1.3 cm, sampled for age (pectoral fin spine), and sexed. Juvenile lake sturgeon were also captured with 3.8 cm stretch mesh fyke nets set under the ice in Lake Poygan and the lower Wolf River during the winters of 1952-65, with an 8.2 m headrope (6.4 mm bobbin weave cod-end insert) trawl during September and October 1983, 1992, and 2007, with seines (3.6-15 m long, 1.2-1.8 m deep, stretch mesh ranging from 1.5-12 mm) in the Wolf River during the summer and fall of 1985-1987, with hand dip nets in the Wolf River during the summer of 1982, and with 230 V, 10 amps AC and DC pulse electrofishng equipment during June – October of 1980-1987 and 1992. All non-harvest juveniles were sampled for age (pectoral fin spine) except for larvae and fingerlings where age was determined by size. Non-harvest juveniles captured in 1992 and 2007 sampling were sexed. Larvae were sampled with a larvae D-net (1 meter maximum throat width, 100 micron mesh) in the Wolf River during May 2006, and at hatching at the University of Wisconsin-Milwaukee Great Lakes WATER Institute in 2007.

After collection and initial cleaning, pectoral fin spines were dried in a cabinet dryer with air circulated at 20-25 °C for one week. A 0.5 mm-thick section was cut using an Isomet Low Speed Saw immediately distal to the basal propterygium, and examined by an experienced sturgeon age reader with reflected and transmitted light under a binocular scope at 7-25X magnification to estimate the number of growth increments present.

I used the power function:

$$TrueAge = EstimatedAge^{1.054796} * e^{\varepsilon}$$

(where ε is stochastic multiplicative error) developed from validated lengths at age reported in the Chapter 1 to correct ages of 4248 male and 5016 female lake sturgeon whose pectoral fin spine estimated age was >14. I fit the corrected ages and pectoral fin spine estimated ages from 622 juvenile lake sturgeon ages 2-14, seventy-nine known age 1 fish, and 50 newly hatched larvae to estimate mean lengths at age for males age 0-69 and females age 0-96. I pooled all juveniles <15 regardless of sex assuming no sexual growth differentiation at this size (Bruch 1999).

I fit von Bertalanffy growth models (von Bertalanffy 1938):

$$L_t = L_\infty * (1 - e^{-K*(t-t_o)}),$$

where: : L_t = length at time t; L_∞ = length infinity (model parameter); K = Brody's growth coefficient (model parameter); and t_0 = time of zero length or fertilization (model parameter) to mean length at age data to estimate model parameters L_∞, K, and t_0 for males and females. I conducted a likelihood ratio test to test for differences between male and female models.

I examined annual growth increments and lifetime growth patterns by calculating the mean annual growth increments for age groups 0, 1 and 2; for groups of 3 successive age classes for ages 3 to 14; and for groups of 5 successive age classes for ages 15 to 54 for each sex. I combined groups of age classes for mean increment calculations to account for error and to allow better discernment of the trends between annual growth increment and age. Limited sample size prevented calculation of estimated annual growth increments beyond age 54. I also estimated annual growth increments by examining capture recapture records of 2062 male and 279 female lake sturgeon tagged and recaptured within the period 1975-2007. Fish were captured with dip nets during

spawning assessments on the Wolf and upper Fox Rivers in 1975-2006, measured to the nearest 1.3 cm, sexed, and marked with monel metal tags attached to the base of the dorsal fin (1975-1999), monel and PIT tags inserted behind the base of the skull adjacent to the 1st dorsal scute (1999 (1999-2005), and PIT tags 2005-2007. Double tagging from 1999-2005 provided data to examine tag loss. Fish were recaptured during spawning assessments 1976-2007, identified by individual tag, sexed, and measured to the nearest 1.3 cm.

I also estimated growth parameters using life history invariates:

$$L_{\infty} = L_{\max} / 0.985 ,$$

where: L_{∞} = length infinity; and L_{max} = maximum length (Pauley 1980);

$$LogT_{\max} = 0.5496 + (0.957 * LogT_m) ,$$

where: T_{max} = maximum age; and T_m = mean age of first maturity (Froese and Binohlan, 2000);

$$K = Ln(1 + L_m / L_{\infty}) / T_m$$

where: K = Brody's growth coefficient; L_m = average length of first maturity; and L_{∞} = length infinity; and T_m = age of first maturity (Froese and Binohlan, 2000); and

$$K = 3 / T_{\max}$$

where: K = Brody's growth coefficient; T_{max} = maximum age (Taylor, 1958).

I addition to estimating the growth parameters t_0 (time of zero length or fertilization) from the von Bertalanffy models, I also estimated t_0 from empirical data on

lake sturgeon spawning and incubation time periods on the Winnebago System (Bruch and Binkowski 2002).

I modeled continuous growth in total length of lake sturgeon from hatching through their first year with a logistic model:

$$L_t = ((L_0 * e^{(k*t)})/((1 + (L_0 / L_{\max}) + ((L_0 / L_{\max}) * e^{(k*t)}))) * e^{\varepsilon}$$

where: L_t = total length at time t (days post hatch); and L_0 = total length at hatching, k = intrinsic rate of increase in length, t = time in days post hatch, L_{max} = maximum total length, and e^{ε} = stochastic multiplicative error.

I used paired t-tests to compare lengths at age of males vs. females sampled during harvest seasons 1953-1959 to lengths at age of males and females sampled during harvest seasons during 1991-2007.

Size and Age at Maturity.—Sturgeon registered during annual spear harvests in 1953-1956 and 1991-2007, and sturgeon captured in annual spawning assessments during 1954-64, and 1975-2007 were sexed and staged for maturity. Sex and stage of fish examined during 1991-2007 were based on criteria by Bruch et al. (2001). Sex and stage of fish sampled in 1953-1956 were classified according to Bruch et al. (2001) criteria using original notes on gonadal development of sampled fish compiled by G. Priegel (Retired Fisheries Research Biologist, WI Dept. of Natural Resources, Oshkosh).

I modeled maturity using three different approaches:

1) as a logistic function of total length and age using ratios of immature and mature male and female sturgeon by total length and age:

$$M = 1/(1 + e^{-r(X - X_m)}),$$

where: X = total length (or age); X_m = total length (or age) at 50% maturity; and r = slope parameter; estimating model parameters using non-linear least squares;

2) by examining length frequencies of adult female and male sturgeon captured in spawning assessments during 1954-64 and 1975-2006 to determine minimum size and size of full recruitment to the spawning stock; and

3) by using invariate relationships suggested by Froese and Binohlan (2000):

$$LogL_m = (0.8979 * LogL_\infty) - 0.0782 \text{ (unsexed mean length of maturity);}$$

$$LogL_m = (0.9469 * LogL_\infty) - 0.1162 \text{ (female mean length of maturity);}$$

$$LogL_m = (0.8915 * LogL_\infty) - 0.1032 \text{ (male mean length of maturity);}$$

where: L_m = mean length of first maturity; and L_∞ = length infinity.

I also estimated total lengths of males and females at first maturity and at full recruitment to the adult stock by calculating the mean minimum value and mean mode of 10 year groups of the total length frequencies of fish sampled during spawning assessments conducted during 1953-1964, and 1975-2007.

Weight-Length Relationships and Relative Condition.—I used weight-length data pairs from the Winnebago lake sturgeon harvest database and the population assessment database collected from 1951-2007 in the model:

$$W_t = \alpha * L_t^{\beta} * e^{\varepsilon_i},$$

to determine weight-length relationships for unsexed, male, and female lake sturgeon, and male and female lake sturgeon by stage of sexual maturity where: W_t = *Weight at age*

t; L_t = *Length at age t*; α = parameter or condition factor; β = shape parameter that describes the departure from linearity, and e^{ε_i} = stochastic multiplicative error.

Assuming allometric growth, I estimated relative condition (K_n)

$$K_n = \frac{W}{\alpha L^{\beta}}$$

to compensate for allometric growth by comparing observed weight (W) to that predicted from weight-length relationship (L^{β}), and examine trends of harvested fish during 1951-2007. To examine trends through time, I calculated mean annual K_n for all fish in the harvest >114.2 cm to minimize any influence on the mean by the various minimum size limits in effect during 1951-2007. I examined trends by lake (Lake Winnebago vs. Upriver Lakes) by calculating mean relative condition for fish in each lake's respective harvest in years when a fishery occurred on both waters. I calculated mean annual relative condition by year for each sex to examine the sex effect for all years that sex data were available from harvested fish.

Fecundity.—I estimated average fecundity at age from the fecundity-length relationship developed as part of this study. Forty seven F4 stage (Bruch et al. 2001) adult female lake sturgeon were sampled from Lakes Winnebago, Poygan and Winneconne during the winter sturgeon spear fisheries during February 2005 - 2008. One F4 stage known age adult female was sampled from captive rearing at the University of Wisconsin-Milwaukee Great Lakes WATER Institute. Fish were measured in total length to the nearest 1.27 cm and weighed to the nearest 0.227 kg. Both gonads were carefully dissected and weighed separately to the nearest gram. Weights of right and left ovaries were distinguished for the last 37 of the 48 fish sampled after a consistent pattern

of a substantial difference in weights between the two ovaries was noticed while initially collecting individual ovary weight in 2005.

Three sub-samples of eggs were removed from each ovary in the anterior, middle and posterior regions, using a tablespoon to scrape a spoon-sized quantity of eggs from between ovarian folds without also collecting ovarian tissue. Egg sub-samples were weighed to the nearest 0.01 gram and all subsample eggs were counted. Average diameter of eggs from each sub-sample was determined by lining up 10 randomly selected eggs along a metric ruler, measuring the total distance to the nearest 0.5 mm, and dividing the total distance by 10.

Thirteen ovaries from fish sampled in 2005 and 2007 were processed into caviar to separate eggs from residual ovarian tissue and to estimate the weight of ovarian tissue in each ovary. These data were combined with data previously collected during the production of caviar from two fish sampled in 2004. The leading ray of the left pectoral fin was removed from 40 of the 48 fish sampled, and following dehydration in a spine drying cabinet, cross-sectioned proximal to the base of the fin ray with a Buehler isomet low-speed saw for age estimation. Estimated ages were corrected for error using the formula Ln True Age = Ln Estimated Age^1.054796 derived from the age validation reported in Chapter 1.

Eggs per Recruit.—I estimated eggs per recruit (EPR) or the number of eggs produced by an average recruited adult female lake sturgeon in the Winnebago population using:

$$P = \sum_{i=1}^{n} \rho_i \varphi_i \prod_{j=0}^{i=1} e^{-(F_{j+} M_j)},$$

where: n = number of ages in the unfished population; ρ_i = proportion of females mature at age *i*; φ_i = average fecundity of females of age *i*; F_j = instantaneous fishing mortality rate of females during period *j*; and M_j = instantaneous natural mortality rate of females during period *j*.

The EPR Ratio = 100 * ($EPR_{fished}/EPR_{unfished}$) and reflects the fraction of future egg production that is lost due to fishing mortality where maximum EPR=100 when fishing mortality is zero. I applied a selectivity curve from the current 91.4 cm minimum size limit in the winter spear fishery (developed for the statistical catch at age model) to the model.

I ran the model with instantaneous fishing mortality rates (*F*) ranging from 0 to 1.5 (0 to 76% exploitation) to assess the impact of harvest on future egg production by sturgeon in the Winnebago System, assuming instantaneous natural mortality (M) was constant at 0.055.

Recruitment, Mortality Rates, and Abundance. — I developed a statistical catch at age (SCAA) model for 1-80 year old lake sturgeon in the Lake Winnebago System using corrected catch at age data from annual spear harvests during 1954-1969, 1976, 1981, 1991, and 1993-2007 to estimate year and age specific lake sturgeon recruitment, mortality, abundance, and harvest.

I used the age validation true age-estimated age correction model reported in Chapter 1 to develop an age-error key to correct the age composition samples from annual spear harvests in the analysis using age samples collected in a random sampling design during the spear harvest seasons. The age error key consisted of true age and pectoral fin spine estimated age data for all fish examined as part of the age validation study, comprising

an initial matrix of true ages 1-80 heading each column and estimated ages 1-80 heading each row. Each cell in this first matrix contained the number of fish with a true age that had a specific estimated age of the corresponding row. I calculated the mean, standard deviation, and coefficient of variation (CV) of true age for each estimated age, and then the mean CV for all estimated ages in the sample. I used this mean CV along with the power function relationship between estimated age and true age (Ln True Age = Ln Estimated Age^1.054796), and the Excel function NORMDIST(x,mean,SD) to construct a second 125 x 125 matrix with a normal distribution of the proportion (0 to 1) of true age fish for each estimated age (for each row). The column headings in the second matrix were also true ages 1-125 and the row headings were also estimated ages 1-125. Multiplying the uncorrected pectoral fin spine age frequency of a harvest age composition sample by the proportions in each row of cells in the second matrix produced a third matrix that contains the corrected number of fish at true ages in each of the uncorrected age rows. The sum of the quantities in the cells within each true age column produced the corrected age frequency for the sample. I used the corrected age frequencies in the statistical catch at age model.

Total actual annual harvest was estimated in 1954 through creel census, and directly enumerated during 1955-2007 through mandatory registration. In the SCAA model I estimated spear harvest using Baranov's equation (Baranov 1918; Quinn and Deriso 1999):

$$C_{ij} = (F_{ij} / Z_{ij}) * N_{ij} * (1 - e^{-Z_{ij}}),$$

where: C_{ij} = Estimated catch in year i of age class j; F_{ij} = Estimated instantaneous fishing mortality in year i of age class j; Z_{ij} = Estimated total instantaneous mortality in year if of age class j; and N_j = Estimated abundance in year i of age class j.

I estimated abundance (N) in year i +1 of age j + 1 from instantaneous fishing and natural mortality, and abundance in year i of age j:

$$N_{i+1,j+1} = N_{ij} * e^{-F_{ij}*-M_{ij}} .$$

To parameterize the initial model, I initially estimated Natural mortality M_{ij} using Pauly's equation (Pauly 1980):

$$Log_{10}(M) = -0.0066 - 0.279 * Log_{10}(L_\infty) + 0.6543 * Log_{10}(K) + 0.4634 * Log_{10}(T)$$

where L_∞ and K = parameters from the Von Bertalanffy length-age model; and T = the mean annual air temperature for the region in which the fishery is located, 6.4 °C (www.answers.com); and then derived the best fit M through a sensitivity analysis by running the SCAA model at different values for M and comparing the predicted annual F's for the period 1999-2007 to empirical F's calculated from tag return data for the same period. I chose the M that resulted in the highest correlation between empirical and estimated F's as the best fit M for the final SCAA runs. I selected the period 1999-2006 to compare empirical to estimated F values as PIT tags were used during this time and tag loss was measured based on double tagging of each fish.

I modeled age-specific selectivity s_j as function of age for each period of a different minimum length limit: 1954 – 76.2 cm; 1954-1973, 101.6 cm; 1974-1996, 114.3 cm; 1997-2006, 91.4 cm. I developed selectivity curves by examining corrected age frequencies from spear harvests within each size limit period, calculating the proportion each partially recruited age comprised of the total proportion of fish at age of full recruitment (mode); modeling these proportions with the logistic model (Haddon 2001):

$$S_a = 1/1 + e^{-Ln(19)*((a-a^{50})/(a^{50}-a^{95}))},$$

where: s_a = selectivity at age *a*; a^{50} = age of 50% selectivity; and a^{95} = age of 95% selectivity. The model requires $s_a = 1.0$ for at least one age to ensure estimates are well defined.

To constrain the SCAA model, I used an empirically derived relationship between winter water clarity (WC) and instantaneous fishing mortality rates (estimated from tag returns), and an assumed Ricker stock-recruit relationship. Water clarity was recorded with a secchi disc at the same general location in 5 m of water (Lake Winnebago maximum depth is 6 m) off the southeast shore of Lake Winnebago each winter spearing season from 1948 to 2007 (Data from Lloyd Lemke, sturgeon spearer, Sturgeon for Tomorrow, Fond du Lac, WI). F is typically modeled as a function of effort in SCAA models, but in the Winnebago sturgeon spear fishery, effort has a weak relationship with harvest. Winter water clarity has a close relationship with harvest and proved to be a good surrogate for effort. I first converted empirical exploitation rates (u) from tag return data to F using a derivation of Baranov's equation assuming a constant natural mortality rate (M) of 0.055:

$$F_i = (u_i * Z_i) / A_i$$

where F_i = estimated instantaneous fishing mortality in year *i*; u_i = estimated exploitation rate in year i; Z_i = estimated total instantaneous mortality in year *i*; and A_i = estimated total annual mortality in year *i*. I then modeled the relationship between F (dependent variable) and WC (independent variable) as an exponential function.

I modeled errors as sum of squares and treat predicted catch as lognormal error:

$$SS_{catch} = \lambda_1 \sum_{i=1}^{m} \sum_{j=1}^{n} (\log_e C'_{ij} - \log_e C_{ij})^2$$

where C' = observed catches in each year i (m years) at age j (n ages) (from the catch-at-age matrix); and C = predicted catches in year i at age j (from Baranov's equation in the model). I initially specified lambda (λ_1) as 1 and then varied λ_1 in subsequent runs to determine the best fit.

I treated predicted fishing mortality as log-normal deviations and estimated observed fishing mortality F_i in year i in the catch-at-age model and predicted fishing mortality in year i from winter water clarity (WC):

$$SS_{WWC} = \lambda_2 \sum_{i=1}^{m} (Log_e F - Log_e (A * \exp(b * WC_i))$$

where I initially specified Lamda (λ_2) according to the assumed tightness of the relation $F_i = A*exp(b*WC_i)$, varied λ_2 in subsequent runs to determine the best fit.

I treated predicted recruitment of yearling lake sturgeon as log-normal deviations and estimated observed recruitment $N_{i,1}$ in year i in the catch-at-age model, and predicted recruitment $N_{i,1}$ in year i from spawner abundance S_i. I initially specified Lambda (λ_3) according to the assumed tightness of the stock-recruit relation (Ricker S-R model):

$$SS_{spawn} = \lambda_3 \sum_{i=1}^{m} (\log_e N_{i,1} - \log_e (\alpha S_i e^{-\beta S_i}))^2 ,$$

And then varied the values of λ_3 in subsequent runs to determine best fit.

I chose lambda vales and parameter estimates that minimized the sum of the component errors:

$$\min(SS_{catch} + SS_{waterclarity} + SS_{spawn})$$

I completed all calculations in Excel. The layout of the Excel spreadsheet showing the relationships between model parameters, observed and estimated catches,

recruitment, winter water clarity and fishing mortality is based on a layout suggest by Haddon (2001).

I parsed SCAA abundance estimates into juvenile, adult male, and adult female by considering all fish >25 years old as adults. Mean proportion of adult females of total estimated adult stock is 0.323 based on sexed Chapman model abundance estimates derived from sexed tagging and recapture data, 1978-2007. Age of 50% maturity is 27 for females and 20 for males and total number of fish estimated in stock >25 years best approximated density of adult stock.

To model recruitment I fit a Ricker stock-recruitment model:

$$R = \alpha * S * e^{-\beta * S} + \varepsilon$$

to two data sets with appropriate time lags from the SCAA modeling results (additive error): estimated adult females as stock (*S*) and estimated yearlings as recruits (*R*), and estimated adult females (*S*) and estimated 21 year old females as recruits (*R*) (assuming a 50:50 female to male sex ratio of all 21 year old fish estimated to be in the population; females first recruit to the adult stock at approximately age 21) as replacement adult females (Myers 2001, 2002).

In addition to within year total abundance estimates by age class derived from the SCAA model, I used the Jolly-Seber open population density model to estimate densities of adult male and female lake sturgeon in the Winnebago System during 1955-2007, and the Chapman modification of the Peterson model to estimate adult male and female densities during 1978-2007.

Tag and recapture data were available from 1955-1963, and 1975-2004 to develop adult male and female abundance estimates using the Jolly Seber model:

$$\hat{N}_t = \frac{(n_t + 1)\hat{M}_t}{(m_t + 1)} \text{ and } \hat{M}_t = \frac{(s_t + 1)Z_t}{(R_t + 1)} + m_t;$$

where $\hat{N}_t$ = number of animals in population at time t; m_t = number of marked animals captured at time t; $n_t = m_t + u_t$ = total number of animals captured at time t; u_t = number of unmarked animals captured at time t; s_t = number of animals released at time t (n_t – accidental deaths); $\hat{M}_t$ = number of marked animals in population M_t at time t: R_t = number of s_t animals released at time t and caught again later, and Z_t = number of animals marked before t, not caught in sample t, but caught again later.

Assumptions of the Jolly Seber model include: (1) every animal has the same probability of capture: $p_t = m_t/M_t = n_t/N_t$; (2) every marked animal has the same survival probability; (3) marked individuals do not lose their marks and are all recognized upon recapture; and (4) sampling and releases are instantaneous.

I estimated confidence limits and variance $\hat{N}_t$ of the Jolly-Seber estimates using:

$$T_1(\hat{N}_t) = \log_e(\hat{N}_t) + \log_e\left(\frac{1 - \frac{n_t/\hat{N}_t}{2} + \sqrt{1 - \frac{n_t}{\hat{N}_t}}}{2}\right)$$

, and

$$Var\left[T_1(\hat{N}_t)\right] = \left(\frac{\hat{M}_t - m_t + s_t + 1}{\hat{M}_t + 1}\right)\left(\frac{1}{R_t + 1} - \frac{1}{s_t + 1}\right) + \frac{1}{m_t + 1} + \frac{1}{n_t + 1}$$

$$T_{1L} = T_1(\hat{N}_t) - 1.6\sqrt{Var[T_1(\hat{N}_t)]}$$
$$T_{1U} = T_1(\hat{N}_t) + 2.4\sqrt{Var[T_1(\hat{N}_t)]} \quad .$$
$$\frac{\left(4e^{T_{1L}} + n_t\right)^2}{16e^{T_{1L}}} < \hat{N}_t < \frac{\left(4e^{T_{1U}} + n_t\right)^2}{16e^{T_{1U}}}$$

Because female lake sturgeon spawn once every 3-5 years and male lake sturgeon spawn once every 1-2 years (Bruch and Binkowski 2002), density estimates developed using a Jolly Seber model would not be valid for the first two and the last two years for females and the first and last years for males. Telemetry and tag-recapture data have shown that individual female and male sturgeon do not consistently follow a regular pattern of spawning periodicity (R.M. Bruch, unpublished data 2006), which suggests that individual migration patterns should not violate the model assumption of every animal having the same probability of capture.

Data were available to develop adult male and female abundance estimates for the years 1978-2007 using the Chapman modification of the Peterson Model:

$$\hat{N} = (((M+1)*(C+1))/(R+1)) - 1$$

where: $\hat{N}$ = abundance estimate; M = number initially marked; C = number in capture sample; and R = number of recaptures in capture sample. Assumptions of the Chapman model include: (1) every animal has the same probability of capture: $p_t = m_t/M_t = n_t/N_t$; (2) No immigration or emigration; and (3) marked individuals do not lose their marks and are all recognized upon recapture.

I estimated upper and lower 95% confidence limits based on the R/C ratio. For an R/C ratio >0.10 I used the binomial proportion:

$$L_1 = R/(R+(C-R+1))F_{\alpha(2),v1,v2}$$
$$v1 = 2*(C-R+1)$$
$$v2 = 2*R$$
$$L_2 = (R+1)F_{\alpha(2)v1',v2'} / C-R+(R+1)F_{\alpha(2),v1',v2'}$$
$$v1' = 2*(R+1) = v2+2$$
$$v2' = 2*(C-R) = v1-2$$
$$L95\%CI = (((M+1)*(C+1))/((L_2*C)+1))-1$$
$$U95\%CI = (((M+1)*(C+1))/((L_1*C)+1))-1$$

For an R/C ratio <0.10 when R <50 I used the Poisson confidence limits:

$$L_1 = \chi^2{}_{(1-\alpha/2),v}/2$$
$$v = 2*R$$
$$L_2 = \chi^2{}_{\alpha/2,v'}/2$$
$$v' = 2*(R+1)$$
$$L95\%CI = (((M+1)*(C+1))/(L_2+1))-1$$
$$U95\%CI = (((M+1)*(C+1))/(L_1+1))-1$$

For an R/C ratio <0.10 when R >50 I used the normal approximation for Chapman's formula:

$$CI = \hat{N} \pm z_\alpha * \sqrt{V*\hat{N}}$$
$$V*\hat{N} = ((M+1)^2*(C+1)*(C-R))/((R+1)^2*(R+2))$$

When running the Chapman model I maintained instantaneous natural mortality at a constant of 0.055 (annual conditional rate of 5.4%). I calculated recaptures by summing all of the recaptures in a given harvest season from the pool of fish marked from the previous 10 spring spawning assessments that were still at large minus annual loss from natural and fishing mortality. Mandatory registration provided an accounting of all marks previously removed from each cohort of marked fish through fishing mortality. I incorporated tag loss using results of double tagging experiment conducted from 1999-2005.

Department of Natural Resources Fisheries staff inspected all registered fish from 1955-1960, and 1996-2007, and a subsample of registered fish from 1991-1995 for marks. From 1965-1995 local taverns were responsible for conducting registration including looking for recaptures. To account for marks missed by citizen run registration stations, fisheries staff registered a random sub-sample of the harvest during the 1991-1995 seasons allowing a correction factor to be calculated and used to adjust recapture numbers from the 1965–1995 harvest seasons.

Intrinsic Rate of Population Growth.—I estimated intrinsic and discrete rates of population increase and carrying capacity of male, female, and adult stock by fitting continuous logistic models:

$$N_t = (N_0 * e^{(r*t)}) / ((1 + (N_0 / K) + ((N_0 / K) * e^{(r*t)})))$$

to abundance estimates for adult male and female lake sturgeon developed from Chapman, Jolly-Seber, and SCAA models; where: N_t = number at time *t*, N_0 = number at time zero, *r* = intrinsic rate of increase, *K* = carrying capacity, and *t* = time (year). The periods modeled were 1958-2004 for abundance estimates from the Jolly-Seber model, 1954-2007 for estimates from the SCAA model, and 1978-2007 for estimates from the Chapman model.

Yield per Recruit.—I used a yield per recruit model to examine the combinations of fishing mortality rates and age of entry into the spear fishery at which the lake sturgeon population could be harvested to maximize yield under an annual exploitation limit of 4.7%:

$$Y_t / N_0 = F * e^{-M*(t_r - t_0)} * W_\infty * (1/Z - (3e^{-K*(t_r - t_0)} / Z + K) +$$

$$(3e^{-2K*(t_r - t_0)} / Z + 2K) - (e^{-3K*(t_r - t_0)} / Z + 3K)$$

where: F = fishing mortality set up as variable from 0 to 1.0; N_0 = number that recruit to the population (set to 1 to eliminate it from equation); t_r = a variable; t_0 = a constant from vB length-age model; W_∞ = a constant from vB length-age model; K = a constant from vB length-age model; M = a constant; and $Z = M + F$. I used M = 0.055 (from SCAA sensitivity analysis), t_0 = -3.506 and K = 0.0485 (parameters from a combined male and female von Bertalanffy model), and W_∞ = 44.7 kg (estimated from weight-length model using L_∞ from female vB model).

I also estimated size group with maximum biomass using an invariant suggested by Froese and Binohlan (2000):

$$L_{opt} = (1.042 * LogL_\infty) - 0.2742$$

$$L_{opt} = (1.053 * LogL_m) - 0.0565$$

where: L_{opt} = Total length corresponding to age group with the maximum biomass (equivalent of generation time); L_∞ = length infinity; and L_m = average length of maturity

Long-Term Impacts of Harvest Management, Environmental Changes, and Public Involvement on Lake Sturgeon Population Dynamics.—I examined historical Wisconsin fish and game laws and regulations, and Wisconsin Department of Natural Resources archived resource monitoring and management files on the Winnebago System and the Winnebago lake sturgeon population and fishery. I interviewed current and former Wisconsin fisheries researchers and managers, and fish and game law enforcement officers, and Winnebago sturgeon spearers about the Winnebago sturgeon population and fishery, environmental changes, and public involvement. I used the information gathered to develop a chronology of the major lake sturgeon harvest management policies and

strategies, known major environmental or habitat perturbations, and known public involvement events related to the Winnebago sturgeon fishery that occurred on the Winnebago System during 1874-2007 and examined trends in Winnebago System lake sturgeon population dynamics in relation to these policies, strategies, environmental changes, and events to discern any correlative patterns, and potential relationships.

Results

Age and Growth.—Mean lengths at age ranged from 1.2 cm (SD 0.03) at hatching to 163.8 cm (SD 7.73) at age 55 for male, to 181.1 cm (SD 12.18) for age 70 female (Table 5). Older ages were represented in the sample, males to age 69 and females to age 96, but sample sizes at ages older than 55 and 70 were relatively small. Sturgeon growth occurred in two stanzas, from hatching to 96.25 cm (age 12) for juveniles, and for fish larger than 96.25 cm (age 13 and older) as separate curves for males and females. Von Bertalanffy (vB) growth curves fit well to mean length at age data within each of these stanzas describing the relationship between mean length at age and age for each of these three groups (Figure 10). VB growth parameters for juveniles from hatching to age 12 were L_∞ = 98.1 cm, K = 0.230, and t_0 = -0.070. VB growth parameters for males age 13-69 were L_∞ = 166.4 cm, K = 0.052, and t_0 = -4.527, and for females age 13-96, L_∞ = 188.9 cm, K = 0.045, and t_0 = -2.485. A likelihood ratio test found a significant difference between the male and female growth models for fish ≥13 years of age (F = 102.8; df = 3, 100; P < 0.001).

Growth parameters estimated by invariate models were relatively comparable to parameters estimated by von Bertalanffy models. Table 6 lists growth parameters from

the fitted von Bertalanffy growth curves, and from invariate models (Taylor 1958, Pauly 1980, Froese and Binohlan 2000).

Length at age of male and female lake sturgeon did not appear to have changed overall during the period from 1953 to 2005. T-tests between mean lengths at age for male lake sturgeon age 15 to 35, and females age 15 - 48 sampled during Upriver Lakes harvests in 1953-57 and 2000-2005 failed to show a significant difference between mean length at age for all ages evaluated except age 21 for males and ages 19 and 20 for females where mean lengths at ages in the 1950s was found to be significantly greater than mean lengths at ages in the 2000s (Figures 11 and 12, Tables 7 and 8).

Mean annual growth increments were 7.79 cm yr^{-1} (SD 5.96) for fish from hatching to age 12, 1.50 cm yr^{-1} (SD 2.00) for age 13 to age 55 males, and 1.61 cm yr^{-1} (SD 3.67) for age 13-70 females (Table 9). A t-test between mean annual growth increments of male and female lake sturgeon ≥13 years failed to show a significant difference between means (p=0.831), although female growth increments were substantially more variable than those for males. Mean annual growth increments diverged between males and females after age 25 (Figure 13) with males exhibiting an annual mean increment of 0.98 cm (SD 1.71) and females 1.31 cm (SD 3.99). I found significant relationships between mean annual growth increment and age of female lake sturgeon ages 25-54 described by the power function (r^2 = 0.991; F = 205.26; df = 1, 4; P < 0.001):

$$MAI_i = 2093.6 * (Age_i^{-1.991}) * e^{\varepsilon_i} \ ,$$

where: *MAI* = mean annual increment (Figure 14) and ε = stochastic error. The male model, also illustrated in Figure 14 did not result in a significant relationship at the 0.05

level (r^2 = 0.607; F = 6.19; df = 1, 4; P = 0.068). Likely due to the weaker male model, a likelihood ratio test failed to show a significant difference between the two models (F = 3.67; df = 2, 8; P=0.074) resulting in acceptance of the combined partial model for lake sturgeon age 25-54 (r^2 = 0.573; F = 13.43; df = 1, 4; P = 0.004):

$$MAI_i = 3088.51 * (Age^{-2.176}) * e^{\varepsilon_i} \quad .$$

Age as a function of length was best described by a power function for juvenile lake sturgeon from hatching to 96.25 cm (r^2 = 0.70; F = 3911.2; df = 1, 1665; P < 0.001) (Figure 15):

$$Age_i = 0.000279 * (TL_i^{\ 2.3336}) * e^{\varepsilon_i} \ ;$$

by an exponential function for males >96.25 cm (r^2 = 0.62; F = 7381.8; df = 1, 4564; P < 0.001) (Figure 16):

$$Age_i = 3.6945 * (e^{(TL_i * 0.01476)}) * e^{\varepsilon_i} \ ;$$

and by an exponential function for females >96.25 cm (r^2 = 0.77; F = 17768.1; df = 1, 5386; P < 0.001) (Figure 17):

$$Age_i = 4.1931 * (e^{(TL_i * 0.01356)}) * e^{\varepsilon_i} \ ;$$

A likelihood ratio test found a significant difference between the male and female models (F = 74.3, df = 2, 9950, P < 0.001).

Continuous growth in length of lake sturgeon from hatching through the first year fit well to a logistic model (Figure 18). Model parameters were L_{max} = 21.7 cm, k = 16.7, and L_0 = 1.3 cm.

Size and Age at Maturity.—Maturity stages observed in males in winter were Mv (immature), M1 (immature or mature but not developed), and M2 (fully developed).

Males examined during spawning assessments exhibited stages M2, and M3 (spent). Maturity stages observed in winter sampled females were FV (immature), F1 (immature or mature but not developed), F2 (early vitelogenesis), F4 (fully developed – black egg fish), and F6 (spent). Females examined during spawning assessments exhibited stages F4, F5 (ovulating), and F6 (spent).

The logistic models based on maturity and length data from harvested fish for:

males, $M = 1/(1+e^{(-0.209*(YL-119.775))})$; and females $M = 1/(1+e^{(-0.345*(TL-138.69))})$ estimated that males begin to mature at 102 cm (about age 14) with 50% maturity occurring at 120 cm (about age 20), and 100% maturity occurring at 142 cm (about age 30); and that females begin to mature at 122 cm (about age 21), with 50% maturity occurring at 139 cm (about age 27), and 100% maturity occurring at 152 cm (about age 33) (Figures 19 and 20).

Length frequencies of spawning lake sturgeon from 1954-2007 estimated a size of first spawning for males of 97.9 cm and for females 121.9. Sizes of full recruitment to the spawning stock were estimated at 139.7 cm for males and 157.5 cm for females.

Invariate models (Froese and Binohlan 2000) estimated the sizes of first spawning of male and female lake sturgeon at total lengths of 93.6 and 121.1 cm (Table 6).

Weight-Length and Relative Condition.—The general weight-length relationship of lake sturgeon of the Winnebago System ranging from 3.3-210.8 cm total length and 0.00011-85.275 kg is expressed by the Log10 power function ($r^2 = 0.950$; F = 951927.0; df = 1, 50013; P = 0) (Figure 21):

$$W_i = 0.000001396 * (L_i * 3.3065) * e^{\varepsilon_i} .$$

The weight-length relationship of lake sturgeon from the Winnebago System is best expressed in two stanzas based on total length. The weight-length relationship of young juveniles from hatching to 71 cm (age 0 to 6) is the first stanza and is best expressed by the Log10 power function ($r^2 = 0.997$; F = 85415.4; df = 1, 287; P = 0) (Figure 22):

$$W_i = 0.000002258 * (L_i^{3.1875}) * e^{\varepsilon_i}.$$

Although sexed weight-length data were limited for fish less than 71 cm, there appears to be no difference between weight –length plots for these fish (Figure 23). Figure 23 clearly shows a divergence of male and female weight-length relationships after 71 cm initiating the second stanza. The weight-length relationship for males > 71 cm is best expressed by the Log10 power function ($r^2 = 0.887$; F = 62804.4; df = 1, 7998; P = 0) (Figure 24):

$$W_i = 0.000001797 * (L_i^{3.2453}) * e^{\varepsilon_i};$$

and for females > 71 cm, the Log10 power function ($r^2 = 0.930$; F = 122924.1; df = 1, 9292; P = 0) (Figure 25):

$$W_i = 0.00000076 * (L_i^{3.4223}) * e^{\varepsilon_i}$$

Likelihood ratio tests found significant differences between male and female (> 71 cm) models (F = 62.97, df = 2, 17290, P = 5.65E-28); juvenile (≤ 71 cm) and male (> 71 cm) models (F = 5.31, df = 2, 8285, P = 0.005); and juvenile (≤ 71 cm) and female (> 71 cm) models (F = 181.89, df = 2, 9579, P = 2.95E-78).

Weight-length models for stages of maturity of males and females > 71 cm show an isometric relationship for males in an Mv stage, and allometric relationships for M1 and M2 stage males; and isometric relationships for females in stages F4, and F6, and

allometric relationships for Fv, F1, and F2 stages. All weight-length model parameters and regression information are listed in Table 10.

Relative condition (K_n) across all sizes and sampling methods without regard to sex or maturity stage, during the period 1951-2007 was the highest for lake sturgeon fingerlings followed by fish from 25 to 71 cm, then fish 120-180 cm (Figure 26). Lake sturgeon in the size ranges 71-140 cm, and > 200 cm generally had the lowest relative condition of all the fish sampled. T-tests showed that relative condition of fingerlings was significantly higher than 25 – 71 cm fish (ages 2- 6) (t = 5.60, crit t = 1.97, df = 284, p = 5.14E-08), and significantly higher than 160-180 cm fish (~age 38-60 females, and age 55+ males) who had the third highest mean *K* (t = 12.62, crit t = 1.96, df = 7162, p = 3.90E-36).

Mean annual relative condition of harvested fish > 114.2 cm from 1951-2007 plotted against year shows an abrupt downward trend around 1980 followed by relatively lower, more variable condition factors in the 1990s and 2000s (Figure 27). The means of annual mean relative condition factors for the periods 1951-1980 and 1981-2007 are 1.08 (SE 0.008) and 0.973 (SE (0.009). A t-test between these means found the mean annual relative condition during 1951-1980 to be significantly higher than the mean annual relative condition during the period 1981-2007 (t = 8.37, df = 55, P = 2.16E-11).

Mean relative condition of lake sturgeon >114.2 cm harvested from the Upriver Lakes trended opposite from condition of fish harvested from Lake Winnebago during the period 1951-2007 (Figure 28). T-tests showed that the mean relative condition of all fish harvested from the Upriver Lakes during 1952-1976 was significantly lower than the mean relative condition of fish harvested in the same years from Lake Winnebago (t = -

51.29, critical t = 1.96, df = 17360, P = 0), but failed to find a difference between mean condition of fish harvested from both waters during the period 1981-2007 (t = 0.04, critical t = 1.96, df = 32547, P = 0.48). Also, t-tests showed that fish harvested from Lake Winnebago during 1981-2007 had a significantly lower mean relative condition than fish harvested from Winnebago during 1952-1980 (t = 79.73, critical t = 1.96, df = 42946, P = 0). Finally, t-tests showed that fish harvested from the Upriver Lakes during 1951-1976 had a significantly lower mean relative condition than fish harvested from the same waters during 1981-2007 (t = -7.91, critical t = 1.96, df = 6961, P = 3.05E-15).

Mean relative condition of females in the harvest was greater than males in 13 of the 16 years with sexed data that were examined, with t-tests within years showing females having significantly better relative condition in 7 of 8 years examined during 1991-2002. Mean relative condition of males was never found to be significantly greater than females within any year examined (Table 11).

Fecundity and Eggs per Recruit.—Fecundity of the 48 lake sturgeon sampled averaged 445,703 eggs (SE = 33716; range = 81,540 – 1,273,307) and the mean number of eggs per kg of body weight was 12767 (SE = 360; range = 7,515-18,261). The 48 lake sturgeon averaged 163.0 cm in total length (SE = 1.92 cm; range = 116.0-193,0 cm), 33.7 kg in weight (SE = 1.72 kg; range = 10.8-73.0 kg), and 47.6 years of age (SE = 2.07 years; range = 20-95 years). The mean GSI was 24.49 (SE = 0.69; range = 14.23-34.69) and the mean gonad weight (combined weight of both ovaries) was 8587 grams (SE = 660.6 grams; range = 1543 – 24861 grams).

Eggs comprised an average of 87.7% of the mass of lake sturgeon ovaries (SE = 0.150; range 75.0%-93.5%) and ovarian tissue comprised an average of 12.3%. Ovaries

from individual fish differed consistently in size, with the weight of one ovary averaging 15.5% larger than the other (range = 0.4-69.3%). Left ovaries were heavier in 55.8% of the fish sampled.

The mean diameter of eggs from the 288 sub-samples was 2.77 mm (SE = 0.013 mm, range 2.57-2.97 mm). The mean diameter of eggs did not differ between large (2.733 mm) and small ovaries (2.771 mm) for individual fish (t-test, t = 0.123, df = 94, p=0.903). Mean egg weight was 16.93 mg (SE = 0.19; range = 13.22 – 27.16 mg) and the mean number of eggs per gram was 59.6 (SE 0.58; range = 36.8 – 75.7 eggs per gram).

Weight was the best predictor of fecundity ($r^2 = 0.91$; F = 451.8; df = 1, 46; P < 0.001) as a linear function (Figure 29):

$$Fecundity = (W * 18683.6) - 183527 .$$

Age was also a reasonable predictor of fecundity ($r^2 = 0.65$; F = 69.7; df = 1, 38; P < 0.001) as a power function (Figure 30):

$$Fecundity = 1169.198 * (Age^{1.15124}) .$$

Total length, although the poorest predictor of fecundity of the three tested, was also a reasonable predictor ($r^2 = 0.58$; F = 64.3; df = 1, 46; P < 0.001) as a power function (Figure 31):

$$Fecundity = 0.000176 * (TL^{4.2315}) .$$

The maximum potential lifetime egg production per recruit (EPR_{max}) of a female lake sturgeon from the Winnebago System, assuming a maximum age of 100 years,

M=0.055, at 0% exploitation is estimated to be 394,976,072 eggs. An exploitation rate of 25.3% would result in a lifetime egg production of 1.8% of the EPR_{max} (Figure 32). The exploitation limit used to manage the Winnebago sturgeon spear fishery since 1970 (Priegel and Wirth 1975), 4.7%, would result in a value 31.7% of the EPR_{max}, while the actual estimated mean exploitation rate of adult females in the fishery during the period 1982-2007, 3.62% (SD = 2.25%) , results in a value of 45.6% of the EPR_{max} (assuming a 92.4 cm minimum size limit). A 7.1% exploitation rate would result in a value of 20% of EPR_{max}.

Recruitment, Mortality Rates, and Abundance.—SCAA estimated mean annual recruitment to the lake sturgeon stock in the Winnebago system during 1954-2007 was 9002 (SD 7119.18) yearlings. Mean annual recruitment by decade showed a decline in yearling recruits as the adult stock increased over the 54 year period (Table 12). The stock-recruitment relationship between adult females and yearling recruits was best defined by a Ricker model:

$$R_i = 20.07706 * S * e^{\wedge}(-0.000445 * S) + \varepsilon ,$$

where model parameters α = 20.07706, and β = 0.000445, and R = the number of yearling recruits produced by S, the number of adult females in the stock the year prior, and ε is stochastic error (Figure 33).

The stock-recruitment relationship between adult females and 21 year old female recruits was best defined by a Ricker model:

$$R_i = 2.99395 * S * e^{\wedge}(-0.000436 * S) + \varepsilon ,$$

where model parameters α = 2.99395, and β = 0.000436, and R = the number of 21 year old female recruits produced by S, the number of adult females in the stock 21 years prior, and ε is stochastic error.

Instantaneous natural mortality (M) and conditional natural mortality (n) for age 1 and older lake sturgeon, developed through the sensitivity analysis using results of the SCAA model, were estimated to be 0.055 and 5.4%. Pauly's (1980) equation estimated instantaneous and conditional natural mortality to be 0.0715 and 6.9%.

The SCAA estimated mean instantaneous fishing mortality (F) of the winter sturgeon spear fishery for adults and juveniles in the harvests during 1954-2007 to be 0.027 (SD 0.024), and the mean exploitation rate for the period to be 2.9% (SD 0.024). Mean fishing mortality and exploitation rates by decade peaked in the 1950s at 0.072 or 7.5% (SD 0.042, 0.044), followed by a quick decline to their lowest levels in the 1970s and 1980s at 0.018 or 1.9% (SD 0.005, 0.006), and an increase in the 1990s and 2000s to 0.023 or 2.4% (SD 0.011, 0.012) (Figure 34, Table 13).

Instantaneous fishing mortality and exploitation rates of adult stock estimated from empirical tag return during 1979-2007 averaged 0.024 or 2.3% (SD 0.021, 0.020) for males, and 0.037 or 3.5% (SD 0.023, 0.022) for females. Rates for both sexes increased from the 1980s to the 1990s, followed by decreases in the 2000s (Table 14).

Mean abundance of adult male lake sturgeon in the Winnebago System during 1995-2004, the most recent decade of the present study with data available for all three estimators, was estimated at 23134 (SD 3727) (Chapman model), 22501 (SD 6902) (Jolly-Seber Model), and 28006 (SD 984) (SCAA Model). Mean abundance of adult female lake sturgeon in the Winnebago System for the period 1995-2004 was estimated

at 10877 (SD 2278) (Chapman model), 11491 (SD 4479) (Jolly-Seber Model), and 13347 (SD 377) (SCAA Model). All three models showed an increase in estimated abundance of adult stocks during the period 1954-2007 (Figures 35 and 36).

Ninety five percent confidence intervals around abundance estimates were generally relatively wide at the onset of intensive tagging in the late 1970s for the Chapman estimates, but became narrower through time as the number of marked fish grew in the population (Figures 37 and 38). Intervals around estimates developed from the Jolly-Seber model were quite variable throughout the period surveyed (Figure 39 and 40). Male data out numbered female data by an order of magnitude and subsequently produced the narrowest confidence intervals for abundance estimates from both models.

Intrinsic Rate of Population Growth.—Estimates of intrinsic (r) and discrete (λ) rates of increase of the adult stock during 1954 – 2007 ranged from 0.049 to 0.138 (r), and 1.050 to 1.148 (λ). Estimated rates of increase of adult females and males were similar for logistic models from Jolly-Seber and SCAA abundance estimates, but substantially higher for males and lower for females from models developed using Chapman abundance estimates (Table 14).

Abundance of all ages 1 through 80 were estimated to peak in the mid 1970's declining by 2000 to levels comparable to those seen in the 1950s. Abundance of ages 26-80 increased from the 1950s to the 1990s reflecting the rise in adult densities during the 54 year period (Figure 41).

Yield per Recruit.—Maximum yield per recruit in the lake sturgeon spear fishery on the Winnebago System, while also maintaining exploitation (t_{rmax}) at or below the recommended 4.7% (F = 0.05) annual limit (Priegel and Wirth 1975), is estimated at 3.03

kg per recruit for fish recruited at age 13, 96.5 cm total length, 5.09 kg (Figures 42 and 43). Maximum yield per recruit without regard to the maximum exploitation limit (F_{max}) was estimated to be 3.93 kg/recruit harvesting fish first recruited at age 22, 126.4 cm and 11.87 kg, and at an annual exploitation rate of 61.8% (F = 1.0). Yield per recruit at the more conservative fishing mortality rate $F_{0.1}$ (10% of F_{max}) is estimated to be 2.83 kg/recruit at a recruitment age and size of 12 years, 94.7 cm, 4.79 kg, and an annual exploitation rate of 3.8% (F of 0.04).

Maximum yield per recruit for males vs. females in the lake sturgeon spear fishery on the Winnebago System, while also maintaining exploitation (t_{rmax}) at or below the recommended 4.7% (F = 0.05) annual limit (Priegel and Wirth 1975), is estimated at 2.16 kg per recruit for males recruited at age 12, 94.7 cm, 4.79 kg; and 2.75 kg per recruit for females recruited at age 15, 107.5 cm, 6.81 kg . Maximum yield per recruit without regard to the maximum exploitation limit (F_{max}) would be 2.82 kg/recruit harvesting males first recruited at age 21, 123.3 cm and 11.87 kg, and at an annual exploitation rate of 61.8% (F = 1.0); and 3.52 kg/recruit harvesting females first recruited at age 24, 127.8 cm and 12.31 kg, and at an annual exploitation rate of 61.8% (F = 1.0).

The size group with maximum biomass, L_{opt}, calculated as an invariant function of L_∞ (Froese and Binohlan 2000), is estimated to be 121 cm, 19 years for males, and 140 cm, 27 years for females. As a function of f L_m or size of first spawning (Froese and Binohlan 2000), maximum biomass is estimated to occur at a size of 105 cm, age 13, for males, and 137 cm, age 26, for females.

Long-Term Impact of Harvest Management, Environmental Change, and Public Involvement on Lake Sturgeon Population Dynamics.—Dozens of regulations and laws have been enacted since the late 1800s to manage the lake sturgeon population and fishery in the Winnebago System. Laws prior to the 1940s were enacted with little to no biological data to support the decision making process. Wisconsin created its first Fisheries Commission in 1874 to survey the status of declining fisheries throughout the state, and most importantly to build fish hatcheries. Fishery regulations were created and passed by the state legislature at this time and the state superintendant of fisheries called for an end to the "nefarious practice" of spearing and spears were outlawed as a legal harvest method in 1878 (Wisconsin Commissioners of Fisheries, 1878). In 1887 though spears were again made legal on Lake Winnebago, and the Fox and Wolf Rivers for sturgeon (Wisconsin Fish and Game Laws, 1887). Also, in 1892, when all varieties of nets were made illegal statewide in Wisconsin, gill nets were still allowed in the Winnebago System (Wisconsin Fish and Game Laws, 1892). Ice shanties were made illegal in Wisconsin in 1897, although in 1899 Lake Winnebago was granted an exemption to the law. In 1915, the Wisconsin legislature created the Conservation Commission to conduct forestry, fisheries, and wildlife management in the state, which, in one of its first acts, enacted a ban on all sturgeon harvest. The ban remained in effect until January 1932 on the Winnebago System when a sturgeon spearing season was reopened as part of an economic relief bill passed to alleviate some of the hardships brought on by the Great Depression (Wisconsin State Historical Society Archives).

In the 1940s fisheries biologists began collecting biological and harvest data on the Winnebago lake sturgeon population and fishery (Schlumpf 1941, Schneberger and

Woodbury 1946) and by the late 1950s a series of sweeping regulation changes were enacted in an attempt to prevent overexploitation and to prevent sturgeon from being harvested until after they were large enough to spawn (Priegel and Wirth, 1975; personal communication, G. Priegel and T. Wirth, WI DNR fisheries research biologists, Lake Winnebago System, Oshkosh, retired). Key components of the new regulations was the elimination of a set-line fishery and the creation of a winter spear fishery on the Upriver Lakes, increasing the minimum size limit from 76.2 cm to 101.6 cm, and reducing the bag limit from 5 to 1 fish per person per year. Throughout this period illegal harvest of sturgeon during their spawning migrations up and down the Wolf and upper Fox Rivers was a serious concern and often blamed by spearers for any perceived problems with the sturgeon stock (Personal communication, Ken Corbett, WI DNR Game Warden, Wolf River, Clintonville, retired). The late 1950s and early 1960s also were a period of dramatic ecological changes on the Winnebago System, especially the lakes, as 1000's of acres of emergent and submergent wetlands in the lakes disappeared, initiating a 30 year period of extensive lakewide turbidity (Wisconsin Department of Natural Resources 1989, Kahl 1993).

The new sturgeon harvest rules enacted in the 1950s were not significantly modified until 1974 when the minimum size limit was increased from 101.6 to 114.3 cm after new data indicated the size and age of sturgeon maturity was greater than previously thought (Priegel and Wirth, 1975). The 1970s also saw a rise in concern by sturgeon spearers over a perceived decline in the lake sturgeon population, based on numerous poor harvest seasons in the late 1960s and early 1970s. This concern led to the founding in 1977 of Sturgeon for Tomorrow, a citizen's based sturgeon conservation organization

whose initial primary goal was to develop the technology to artificially rear sturgeon so they could be stocked to replenish the Winnebago sturgeon population. Sturgeon for Tomorrow contributed significantly to the development of the sturgeon aquaculture program in Wisconsin, but no sturgeon were stocked at the time due to concerns expressed by the sturgeon biologists of the Wisconsin Department of Natural Resources about whether there actually was a need to stock. Also, in 1977, the increased public involvement in sturgeon management resulted in the initiation of the Sturgeon Guard program, funded by Sturgeon for Tomorrow, designed to use citizen volunteers to protect spawning sturgeon 24 hours a day from poaching at sites when they were most vulnerable to illegal harvest. An addendum to this action was the increase in fines levied on a person in possession of an illegally harvested sturgeon to $1500 in 1985.

The completion of the Winnebago Comprehensive Management Plan in 1989 (Wisconsin Department of Natural Resources 1989) was followed by implementation of rigorous non-point pollution controls throughout the Winnebago watershed, as well as by a significant increase in fisheries management activities including sturgeon population and harvest assessments. By the mid 1990s improved winter water clarities resulted in several record sturgeon spearing harvests and rising concern by WI DNR about overexploitation of the stocks. In 1992, WI DNR fisheries staff, Oshkosh, formed the Winnebago Sturgeon Citizens Advisory Committee, to advise the Department on sturgeon management. The committee met regularly to work with local fisheries biologists to identify sturgeon management issues and recommend actions to ensure the spear harvest was maintained at a safe level. A primary concern was the suspected overharvest of adult female sturgeon, realized when Department fisheries staff began

sexing and staging harvested fish in 1991. This concern was fueled in part by the significant reduction of fish over 100 pounds (45.5 kg) in the harvest between 1974 and the mid 1990s. Between 1993 and 2007 the Sturgeon Advisory Committee, together with the DNR, developed and worked to secure passage of 23 new regulations and laws designed to limit harvest to no more 5% annually, while maintaining an open sturgeon spear fishery on the Winnebago System.

The new laws and regulation included several new innovations in sturgeon harvest management including annual harvest limits set by fish sex and maturity, a reduction in the maximum season length, a 67% reduction in the daily spearing hours, a reduction in the minimum size limit from 114.3 cm to 91.4 cm, a limited effort fishery on the Upriver Lakes, a 100% increase in the cost of a Winnebago sturgeon spearing license, and a statutory requirement that all sturgeon spearing license funds be used only to manage the Winnebago lake sturgeon population and fishery. At the same time, harvest and population assessments were increased and improved including the replacement of metal monel dorsal fin tags with PIT tags in 1999 to eliminate tag loss and provide a means to more accurately estimate densities and exploitation. Assessment efforts expanded again in 2002 with the implementation of extensive long term radio and sonic telemetry studies designed to document migration patterns of juvenile and adult lake sturgeon and to more accurately identify the components of the harvestable stock that were in Lake Winnebago and the Upriver Lakes during the February spearing season.

In addition to improvements in water clarity, other important changes in the Winnebago System aquatic ecosystem occurred during the late 1980's and 1990's. After a series of very mild winters in the late 1980's, the heretofore low density gizzard shad

population exploded in the Winnebago System and were heavily preyed upon by various piscivores as well as by lake sturgeon. Lake sturgeon were foraging heavily upon dying and dead gizzard shad during the shad's annual winter die-off (Stelzer et al. 2008). In 1998, zebra mussels were found in Lake Winnebago and by 2002 were extremely abundant throughout the lake system, likely contributing to increased water clarity, but also by 2005 potentially negatively interacting with the chironomidae larvae population in Lake Winnebago, the lake sturgeon's traditional primary year-round forage item (Stelzer et al. 2008). In this same time period spearers began to note the highly variable relative condition of the sturgeon they were harvesting. In 2005 following a year of exceptionally low abundance of chironomid larvae, gizzard shad, and zebra mussels (K. Kamke and A. Techlow, WI DNR, Oshkosh, unpublished data), harvested lake sturgeon exhibited the poorest condition observed in spearers' memories.

Despite the environmental perturbations taking place in the Winnebago System and the high variability seen on sturgeon condition in some years during the late 1990s and early 2000s, by 2004 greater numbers of trophy size adult females began to show up in the spawning stock and the harvest. A new record fish, 85 kg (188 pounds) was speared in 2004 breaking the previous record of 83 kg that had stood since 1953. During the 2008 spearing season, a new record of 46 fish over 45 kg were registered in the harvest. During 2003-2008 spawning assessments, adult females were routinely captured that exceeded 80 kg, with some in excess of 100 kg.

A chronology of sturgeon management actions, harvests, regulations and laws, significant environmental changes, and public involvement events are listed in Table 15.

Discussion

Age and Growth.—Lake sturgeon in the Winnebago System exhibit growth in total length in two distinct stanzas: from hatching to 96 cm (age 12), and >96 cm. Males and females have similar lengths at age until they reach 130 cm in total length or about age 25, after which growth in total length at age diverges with females attaining larger sizes at age and also living longer, thus attaining a larger asymptotic length. Females can likely reach at least 100 years in age, while males can reach at least 70. Probst and Cooper (1954) also noted growth of lake sturgeon from the Winnebago System in two stanzas delineating the inflexion point between the stanzas at 103 cm after age 13. Given the results of the age validation work reported in Chapter 1, the Probst and Cooper (1954) age estimates of lake sturgeon in their sample < 14 years were likely accurate and therefore comparable to the samples in the current study. Probst and Cooper (1954) speculated that, although they had "limited data on the age of lake sturgeon at sexual maturity from the Lake Winnebago area", the change in growth occurring between stanza 1 and stanza 2 could be attributed to "alteration in the general metabolism due to the development of the gonads". Taghavi (2001) modeled growth of beluga sturgeon (*Huso huso*) in the Caspian Sea in three stanzas: hatching to age 8 (~150 cm), age 8-24, and > age 24; separating male and female growth models for the 2nd and 3rd stanzas. While his data were very limited for fish less than 8, and greater than 28 (females) and 17 (males), the data still showed a distinct break in growth patterns at a late juvenile stage following the very fast growth of the first 6 to 8 years of life, identical to the pattern displayed by the Winnebago lake sturgeon.

Length at age plots for other sturgeon species show an inflexion point generally between ages 6 and 14 delineating what could be called the end of the first growth stanza: white sturgeon (*Acipenser montanus*) (Everett and Tuell 2002); Atlantic sturgeon (Van Eenennam and Doroshov 1998); Gulf sturgeon (*Acipenser oxyrinchus desotoi*); shovelnose sturgeon (*Scaphirhynchus platorynchus*) (Kennedy et al. 2007); Siberian sturgeon (Ruban 2005); Atlantic sturgeon (Stevenson and Secor 1999).

Declines in growth rate of lake sturgeon in the Moose River, Ontario, Canada at age 8-9, 64 cm (Threader and Brousseau 1986), and of shortnose sturgeon (*Acipenser brevirostrum*) at age 7-10, approximately 50 cm, from the Saint John River estuary, New Brunswick, Canada (Dadswell 1979), were attributed to diet and habitat changes at the onset of gonadal maturation. A change in reliability of annuli seen on the scutes of European sturgeon species at age 6 or 7 was attributed to "an abrupt change in the metabolism at a time at which the sexual organs begin to develop, that is, at the time of preparation from the onset of sexual maturity" (Classen 1949). The observed age and size of first maturity of lake sturgeon in the Winnebago System was age 13, 97 cm for males and age 21, 121 cm for females. The onset of 1st maturation for males matches well with the growth inflexion point for males, but not for females, although the gonads of females at an age of 13 and size of 97 cm have moved from an Fv into an F1 stage of development (Bruch et al 2001) that, despite not experiencing 1st maturity until 7 or 8 years later, indicates 13 year old females are directing energy away from somatic towards gonadal growth.

With the exception of Taghavi (2001), authors have typically reported sturgeon length at age, and the estimated parameters of the length-age relationship after fitting a

single von Bertalanffy (or other) model to the full range of estimated ages, or estimated mean lengths at age present in their samples (Dadswell 1979; Baker 1980; Stevenson and Secor 1999; Quist et al. 2002; Ceapa et al. 2002; Kennedy et al, 2007; Pine et al. 2001; Smith and Baker 2005; Johnson 2005; Everett and Tuell 2000). Brody (1927, 1945) (namesake of the Brody growth coefficient, K, a parameter in the von Bertalanffy growth model) in his original modeling of animal growth, divided his growth data at an inflexion point and calculated two separate curves. Although Brody was fitting two halves of a logistic model, I suggest a similar approach be used to model sturgeon growth to estimate mean length at age and growth parameters. This approach provides a more realistic estimate of t_0 (time at length zero, or fertilization), and provides an estimate of Brody's growth coefficient (K) for juveniles, as well as length at the inflexion point using the parameters from the juvenile or 1st growth stanza model. The parameters L_∞ and K would be equally as useful for the 2nd stanza models for males and females, while t_0 from the second growth stanza model would likely be best utilized in further modeling applications such yield per recruit.

The general 1st and 2nd stanza models characterize growth within each respective stanza over the range of ages above and below the growth inflexion point. Within the first year of life, and possibly within other early years, a separate logistic model can also be developed to characterize weekly or monthly growth as shown by the excellent fit of the total length at age data of age 0 lake sturgeon from hatching to 280 days post hatch.

Species of the family *Acipenseridae* are commonly believed to be slow growing fish. The low mean annual growth increments of Winnebago lake sturgeon are a testament to this life history characteristic with some tagged and recaptured adult males

and females showing no growth in length for up to 16 and 22 years. This slow to no-growth pattern emphasizes the need to minimize measurement error when measuring sturgeon lengths. Historically spawning and harvested lake sturgeon on the Winnebago System have always been measured to the nearest 0.5 inch (1.27 cm) which, given the low mean annual growth increments, resulted in measurement error that could have been avoided had the fish been measured more accurately. Lake sturgeon should be measured in total length (in lieu of fork length) in a consistent manner on a measuring board to the nearest mm to minimize measurement error and maximize precision.

Size and Age at Maturity.— The results of the maturity modeling of lake sturgeon from the Winnebago System are the first reporting of the full range of lengths and ages at which both male and female lake sturgeon of any population become mature for the first time. Male and female lake sturgeon from the Winnebago System reach maturity for the first time, 102 cm (age 14), and 122 cm (age 21), at smaller sizes and younger ages than previously thought (Priegel and With 1975). Maturity modeling also revealed that the population of males in the Winnebago System requires 16 years (age 14-30) to become fully recruited to the adult stock, while females require 12 years (age 21-33). Female lake sturgeon from the St. Lawrence River in Quebec were also found to exhibit a protracted age of first maturity with fish first recruited to the adult stock at age 15 with 100% recruitment at age 32, a span of 17 years (Fortin et al. 1992)

The wide range of sizes and ages at first maturity may help explain, in addition to latitudinal differences in growth, the wide range of size and age of maturity of lake sturgeon reported in the literature. Male lake sturgeon have been reported to first mature at 76 cm (age 19-20) (Dubreuil and Currier 1950), 83 cm (age 14-15) (Probst 1954,

Currier 1966), 85-95 cm (ages 18-20) (Magnin 1966), and 114 cm (ages 14-16) (Priegel and Wirth 1971). Female lake sturgeon have been reported to first mature at 84 cm (age 26) (Dubreuil and Currier 1950), 90-100 cm (age 20-30) (Magnin 1966), 127 cm (age 22-25) (Probst 1954, Currier 1966), and 139 cm (ages 24-26) (Priegel and Wirth 1971). While variation in reported size at first maturity is not surprising for a slow growing, late maturing, and wide ranging fish like lake sturgeon, it is likely that some of the spread in sizes and ages could be attributed to limited sample sizes of fish from within a protracted size range of fish maturing for the first time and ageing error.

Estimates of size of first maturity of male and female lake sturgeon from the Winnebago System calculated as a function of L_∞ from invariate formulas, 94 cm for males, and 121 cm for females (Froesse and Binohlan 2000), matched both maturity model estimates, 102 cm and 122 cm, and empirical data from spawning assessments, 98 cm and 122 cm, quite well. In the models suggested by Froese and Binohlan (2000) (based on 467 pairs of L_m and L_∞ encompassing 265 species of fish from 3 classes, 27 orders, and 88 families including 2 species of sturgeon) asymptotic length explained 85% of the variation of length at first maturity in males and 91% in females.

The protracted age of first maturity found for lake sturgeon of the Winnebago System and the St Lawrence River, Quebec, Canada (Fortin et al. 1992) suggests a life history trait common for the species. A protracted age of first maturity has also been suggested for shortnose sturgeon (*Acipenser brevirostrum*) in the Saint John River estuary, New Brunswick, Canada (Dadswell 1979), Kaluga sturgeon (*Huso dauricus*) in the Amur River, Russia (Krykhtin 1986), and Atlantic sturgeon in the Hudson River, New York, USA (Van Eenennaam et al. 1996) indicating this life history trait may be

common to many of the species within the family Acipenseridae. Literature citations, when reporting size and age of maturity of sturgeon typically provide estimates of size and age of first maturity, but rarely provide the size and age of full recruitment of males and females to the mature stock. The long span of time from earliest to latest maturation of individuals in a sturgeon stock, and relatively old age of 50% maturity provides additional insight into the vulnerability of sturgeon stocks to recruitment overfishing and to why so many stocks have quickly collapsed from high harvest rates.

Weight-Length and Relative Condition.— Martin (1949) concluded changes in weight-length relationships of fishes reflect different stanzas of growth associated with different life stages and recommended W-L model parameters should be calculated by stanza. The weight-length relationship for lake sturgeon from the Winnebago System using unsexed data, is best described, similar to its length-age relationship, in two growth stanzas based on total length: fish ≤ 71 cm, and fish > 71 cm. LeCren (1951) found significant differences in W-L model parameters for yellow perch (*Perca fluviatilis*) from Lake Windemere, UK, at different life stages, and stages of gonadal development. The most accurate descriptions of weight-length relationships of lake sturgeon > 71 cm from the Winnebago System were attained by models based on sexed and maturity staged data.

Although the inflexion in dimorphic growth in length at age for lake sturgeon from the Winnebago System occurs at approximately 131 cm (age 25), the dimorphic split in the weight-length relationship occurs at 71 cm (age 6) with males possibly displaying greater variation in their weight-length relationship between 71 and 96 cm total length than females (Figure 23). This apparent higher variation could be caused by the onset of gonadal development occurring more rapidly in some of the males compared

to most of the females between 71-96 cm in total length. While annual growth increments in total length for males and females appear to be similar for fish age 6-25, the weight-length relationships are not. Females older than age 6 generally display more allometry although the degree of allometric growth expressed by an individual depends heavily on its stage of gonad development.

The weight-length relationship of immature sub-adult males (Mv stage) is isometric, but the relationship for similar sized sub-adult females (Fv stage) is allometric indicating the body shape of females in this life stage is changing more rapidly than males the same length and age. Although males and females share similar patterns in total length growth increments up to age 25, more than 50% of females at age 25 are still in the Fv stage, compared to less than 15% of males in an Mv stage at age 25, perhaps allowing the Fv females to express more allometry in their weight-length relationship at this age. The display of weight-length isometry by F4 and F6 stage adult females likely reflects the tight relationship between weight and fecundity displayed in an F4 stage fish completely full of eggs and an F6 stage fish completely spent and remaining in this condition for nearly a year prior to recovery.

The parameters α (log10) and β are the respective slope and intercept of the log transformed power function linear regression of $\log_{10}$Wt on $\log_{10}$L. A decrease or increase in slope (log10 α) results in increase or decrease respectively in the intercept (β). The plot of log10 α against β from weight-length models from populations within a species forms a straight line, and the slope of the resultant line can be used to calculate the form factor ($a_{3.0}$) for a specific population (Froese 2006):

$$a_{3.0} = 10^{\log 10\alpha - S*(\beta - 3)},$$

where α = alpha parameter from W-L model, β = beta parameter from W-L model, and S = slope of the log10 α on β regression for the species. To compare W-L models of lake sturgeon sampled among various populations, and from various sex and staged data sets within populations, alpha parameters must be standardized to consistent measurement units for length and weight (beta does not change). I used conversion equations from Froese(2006) to standardize alpha to total length in mm and weight in grams for the 12 W-L models I developed for lake sturgeon using unsexed, sexed, and maturity staged data, and for 20 other W-L models developed for other lake sturgeon populations from throughout the species' range (Probst and Cooper 1954; Priegel 1973; Threader and Brousseau 1986; Dumont, et al 1987; Ecologistics Ltd 1987; Nowak and Jessop1987; Sandilands 1987; Larson 1988; McDonald 1998; Craig et al. 2005; Smith and Baker 2005; Huges et al 2005; Adams et al. 2006; Lallaman et al 2008). I regressed log10α on β from the 32 W-L models to produce the regression:

$Log10\alpha = 4.40309 - 2.1949 * \beta$, ($r^2 = 0.85$; F = 168.6; df = 1, 29; P = 1.31E-13), (Figure 44).

I then used the slope of this regression (-2.1949) to calculate, and then rank the form factor for the 32 populations sampled (Table 17). The mean form factor of all populations sampled was 0.007289 (SD 0.004643), and the median form factor was 0.00657.

Form factors for various unsexed and sexed samples of lake sturgeon from the Winnebago System averaged 0.006328 (SD 0.000521) with a median of 0.006233, ranging from a low of 0.005749 for F6 (spent) females to a high of 0.007529 for F4 (gravid) females. Both males and females in the progression of gonadal development

exhibited sequentially increasing plumpness, Mv (immature) through M2 (fully developed) and F6 through F4. Winnebago lake sturgeon in their first W-L growth stanza (≤ 71 cm), as would also be expected, exhibited a lower form factor than fish> 71 cm; and finally among fish in their second W-L growth stanza, > 71 cm, males exhibited a lower ranked form factor than females.

The ranking of Winnebago samples shows the impact of gonadal development and spawning condition on body shape, and thus on the weight-length model parameters, and that the Winnebago population exhibits a body shape or overall plumpness slightly below average, although still within the bounds of the 95% CI of the mean of all samples. The ranking also shows general latitudinal and density dependent trends with fish from relatively robust populations in northern Ontario exhibiting a lower plumpness, and fish from more southern, or diminished and recovering populations exhibiting a higher plumpness. The form factor statistic could potentially be used as an additional tool in the overall status evaluation of a lake sturgeon population, providing adequate data are available, through a comparison with the form factors of other lake sturgeon populations whose status and weight-length relationships have already been well described.

Fecundity.—My sample of 48 female lake sturgeon is the largest fecundity sample ever examined for the species with good contrast in the data including fish from 11-73 kg, 116-193 cm total length, and age 20-95 years, providing useful models to estimate fecundity from weight, length, or age. These results provide a solid base of information for use in modeling lake sturgeon population dynamics.

The mean fecundity of lake sturgeon from the Winnebago System is similar lake sturgeon fecundity reported in previous studies (Cuerrier 1949; Dubreuil and Currier

1950; Harkness and Dymond 1961; and Sandilands 1987) (Table 16), although the wide range of size of fish I examined provides more reliable fecundity estimators, especially for weight and length. Despite the limited sample sizes and wide variation in the mean size of fish examined in previous studies, which also likely accounts for the wide range in mean fecundity reported, mean numbers of eggs per kg of fish are relatively consistent among studies.

The estimate of mean egg diameter for fully-developed eggs from lake sturgeon of the Winnebago System is within the range of mean egg diameters found by other investigators (von Bayer 1910 (cited in Harkness and Dymond 1961); Harkness and Dymond 1961; Sandilands 1987). In addition, our estimate of mean egg weight (58.53 eggs per gram) is similar to the estimate of mean egg volume found by Fred Binkowski (50 ovulated, unfertilized eggs per ml; University of Wisconsin-Milwaukee Great Lakes WATER Institute, unpublished data).

The number of eggs per kg of body weight for Winnebago lake sturgeon was similar to estimates from other studies of lake sturgeon fecundity (Table 16). Our estimate of the fecundity-weight relationship for lake sturgeon indicates that fecundity of lake sturgeon would be overestimated for fish lighter than 27 kg and underestimated for fish heavier than 28 kg using an estimate of 12767 eggs per kg of fish body weight. To avoid such bias, my linear model using weight as the independent variable is the best estimator of fecundity. If weight is not available, total length and age were reasonable predictors of fecundity, although age may have limited application to other lake sturgeon populations due ageing error, and due to potential differences in growth rates and age of maturity.

The mean proportions that eggs and ovarian tissue comprise of the mass of lake sturgeon ovaries in a pre-spawn F4 stage (87.7% and 12.3%) are the first such reported for the species and possibly for any sturgeon species allowing the development of more accurate fecundity estimates for the species. I was not able to find such metrics reported for any other sturgeon species in the available literature.

Eggs per Recruit.—Goodyear (1993) recommended, for fish stocks in general, maintaining levels of spawning stock biomass per recruit that are at least 20% of the biomass present at zero exploitation to prevent recruitment overfishing or the harvest of spawners below the replacement level of their offspring. For shortnose sturgeon, Boreman et al. (1984) recommended a level of 50% of the biomass present at zero exploitation to rebuild the population. Since lake sturgeon fecundity is a linear function of body weight, and by extension, of female spawning stock biomass, the 20% and 50% target levels recommended by Goodyear (1993) and Boreman et al (1984) should apply to potential lifetime egg production per recruit, EPR_{max} of lake sturgeon. Assuming an instantaneous natural mortality rate of 0.055, and applying the selectivity curve present in the Winnebago spear fishery with a 91.4 cm minimum size limit, an annual exploitation rate of 7.1%, 2.4% higher than the 4.7% exploitation limit recommended by Priegel and Wirth (1975), would result in 20% of EPR_{max}. An annual exploitation rate of 4.7% is estimated to result in 31.7% of EPR_{max} well above the 20% minimum suggested by Goodyear (1993), but below the 50% minimum for sturgeon stock recovery recommended by Boreman, et al. (1984). Following relatively high exploitation in the 1950s (mean of 6.7%), the mean exploitation rate in the Winnebago System sturgeon spear fishery for the period 1960-2007 was 2.1% resulting in an estimated 57.5% of

EPR_{max}, well above the 50% level recommended by Boreman et al (1984) to allow stock recovery. Although the EPR ratio model is not stochastic and does not account for any potential density dependent mechanisms, it may provide important metrics for low density sturgeon stocks still subject to exploitation that can be used to help set harvest limits. The population of lake sturgeon in the Winnebago System experienced high harvest rates in the 1950s, considered overexploitation at the time (Priegel and Wirth 1975), but after annual exploitation decreased to an average of 2.1% and 57.5% of EPR_{max}, during 1960-2007, the stock recovered well beyond the densities of the 1950's supporting the effectiveness of Boreman et al.'s (1984) 50% EPR_{max}, recommendation for sturgeon population recovery.

Recruitment.—Young sturgeon are often difficult to capture in a consistent and reliable manner (Kempinger 1996, Kennedy et al. 2007; Paragamian and Hansen 2008) and as such recruitment estimates and stock recruitment models for sturgeon are lacking in the literature. Recruitment estimates for sturgeon populations have typically been made through hindcasts of age estimates, assuming age estimation error is low enough to allow accurate identification of birth years of the fish aged (e.g. Quist et al. 2002; Woodland and Secor 2007; Thomas and Haas 2001), or through the number or catch rate of first recruits to a fishery (e.g. Priegel and Wirth 1975; Baker 1980). Age estimation error, as shown in Chapter 1, calls into question all estimates of recruitment through hindcasts of age estimates. While age estimates determined from pectoral fin spine cross sections for other sturgeon species and populations may not exhibit the same error as I found for lake sturgeon from the Winnebago System, the likelihood of significant error existing for at least most adult aged sturgeon of various populations and species is high

and therefore needs to be considered when using ageing data to estimate recruitment. Estimating recruitment through the number or catch rate of new recruits into a fishery is also prone to error if the ages of the new recruits place them into the time of their life when pectoral fin spine age estimates may begin to show significant error.

In the present study, I estimated the number of lake sturgeon yearling recruits and 21 year old female recruits in the Winnebago System, and the adult females that produced them, from a statistical catch at age (SCAA) model based on age data that I corrected for age estimation error for the years 1954 - 2007. Prior to producing the SCAA model output, I anticipated that the stock-recruitment relationship of lake sturgeon in the Winnebago System would likely show moderate S-R density dependence, given the relatively high abundance of adults. I did not expect though to see the strength of the inverse S-R relationship indicated by the SCAA model results since, to date, we had not found adult lake preying on their own young (Stelzer et al 2008), although we had seen them preying on their own eggs (Bruch and Binkowski 2002).

The mean yearling recruitment level during 1955-2007 for lake sturgeon of the Winnebago System, as estimated by the SCAA model, was 0.941 (SD .974) yearlings/adult, although the rate was highly variable (dependent upon adult stock density) ranging from 0.011 to 2.597 yearlings/adult. Paragamian and Hansen (2008) used a stochastic density dependent simulation model to estimate a level of recruitment of 0.4 yearlings/adult was needed for recovery of the Kootenai River white sturgeon population in Idaho, USA. If other sturgeon species or populations also have an intrinsic wide ranging recruitment rate and strong density dependent Ricker stock-recruit relationships similar to those suggested by the Winnebago System lake sturgeon SCAA

model, it, may be difficult to discern these relationships for stocks at low adult densities, or for populations with insufficient data to model recruitment. On the other hand, a sturgeon population with a Ricker style stock-recruit relationship, but at low densities and being managed for recovery, should have good potential to produce large numbers of yearling recruits, providing spawning and nursery habitat is still adequate, and the adult stock has not dropped below some effective population threshold. The greatest yearlings/adult production for the Winnebago stock, 2.59, is estimated to have occurred in 1968 at a point of the lowest adult density of 7302 (out of which 2213 estimated to be adult females). This low point in adult stock occurred after overexploitation in the legal winter spear fishery in the 1950s and early 1960s, and the unknown impact of suspected excessive illegal poaching occurring in the same time period during spring spawning runs.

The slope at the origin of the spawner-recruitment curve, if both axes are in the same units, as the maximum reproductive rate (Myers 2001, 2002). The alpha parameter from the stock-recruitment model (2.99) developed with estimates of adult females as stock and 21 year old females as recruits would be a minimal estimate of the maximum annual rate that adult female lake sturgeon in the Winnebago System replace themselves falling well within the range of 1 to 7 that many fish species exhibit (Myers et al. 1999).

The density dependent parameter (β) of both stock-recruit models I developed were similar and within each other's 95% confidence intervals (0.000445 and 0.000436) which was not surprising since both used recruit estimates from the same SCAA model. What was surprising originally was the strong signal of density dependence exhibited by the original catch at age data in the SCAA model. While lake sturgeon in the Winnebago

System have not been found to prey upon their own young, the demographic mechanisms of a Ricker style density-dependent stock-recruit relationship could possibly include increased egg mortality due to fungal infection as egg densities increase at spawning sites, and increased egg predation by sturgeon and other predators (e.g. Catostomids, Cyprinids, crayfish) with increased egg densities. Extrinsic factors could include limited or diminished interstitial spaces in spawning substrates, marginal or diminished water velocities during egg incubation or pre-larvae stage, or dehydration of eggs or pre-larvae due to a drop in water levels during incubation and pre-larvae stages.

Mortality.—The estimate of instantaneous natural mortality (M) of 0.055 developed from the SCAA sensitivity analysis is the first such estimate for any sturgeon species using validated age data. Natural mortality is generally estimated for most fish species by subtracting an estimate of instantaneous fishing mortality (F) from total instantaneous mortality (Z) originally estimated as the negative slope of the descending arm of a catch curve (Ricker 1975). The catch curve is only as reliable as the age estimates that produced it, and given the age validation results from Chapter 1, it is possible that all catch curves previously developed for sturgeon using un-validated age estimates could produce inaccurate estimates of Z. Instantaneous natural mortality rates (M) of lake sturgeon populations, developed from catch curves and estimates of Z based on un-validated age data and independent estimates of F, have been estimated at 0.076 (Black Lake, MI, Baker, 1982), 0.072 (Groundhog and Mattagami Rivers, Ontario, Nowak and Jessop, 1987), and 0.12 – 0.20 (St. Lawrence River, Quebec, Dumont et al. 1987).

Estimates of M of other sturgeon species derived from catch curves include 0.020 for shortnose sturgeon in the Hudson River, New York, USA (Woodland 2005), 0.108-0.138 for shortnose sturgeon in the St. John River Estuary, New Brunswick, Canada, 0.07 for pallid sturgeon (*Scaphirhynchus albus*) in the Mississippi River, USA (Killgore et al. 2007), 0.10 for white sturgeon in the lower Columbia River, Oregon and Washington, USA (DeVore et al. 1995), and 0.092 for white sturgeon in the Kootenai River, British Columbia, Canada, and Montana and Idaho, USA (Paragamian et al. 2005). As mentioned earlier, estimates of instantaneous natural mortality rates of other sturgeon species developed from estimates of total instantaneous mortality from catch curves and independent estimates of instantaneous fishing mortality rates are also likely prone to being inaccurate due to the use of un-validated age estimates to build the catch curves.

Using von Bertalanffy growth parameters developed from validated age estimates for Winnebago lake sturgeon > 96 cm in Pauly's equation, which derives M from L_∞ and mean air temperature, produced estimates of M = 0.081 for males, and 0.071 for females. Pauley's equation (Pauley 1980), has been used to produce estimates of M of 0.049-0.70 for white sturgeon in the lower Columbia River, Oregon and Washington, USA (Beamesderfer et al. 1995), and 0.04 for beluga sturgeon (*Huso huso*) in the southern Caspian Sea, Iran (Taghavi 2001).

Taghavi (2001) also used a model suggested by Richter and Efanov (1976) using age of 50% maturity to estimate M:

$$M = (1.521 / t_{50\%Mat}{}^{0.72}) - 0.155,$$

where: $t_{50\%Mat}$ = age of 50% maturity, which provided estimates of M for male and female beluga sturgeon of 0.05 ($t_{50\%Mat}$ = 16) and 0.03 ($t_{50\%Mat}$ = 18). I used the $t_{50\%Mat}$

for male and female lake sturgeon from the Winnebago System (19 and 27) in Richter and Efanov's (1976) formula to derive estimates of M of 0.028 and -0.013 (a negative M for females).

Finally, Kennedy and Sutton (2007) used a model suggested by Hoenig (1983) relating total instantaneous mortality to fish maximum age:

$$LnZ = 1.46 - 1.01 * Lnt_{\max},$$

where: maximum age of fish in the population (or sample), to estimate an M of 0.115 for shovelnose sturgeon (*Scaphirhynchus platorynchus*) in the upper Wabash River, Indiana, USA. Applying this model to lake sturgeon demographics from the Winnebago System results in an estimated M's of 0.035 for males and 0.001 for females (given empirical estimates of F and t_{max} for males and females of 0.024, 70, and 0.040, 100).

Despite potential error from use of un-validated age data, and the potential shortcomings of generic mortality models, nearly all of the estimates of natural mortality for the various sturgeon species listed above are low and within a range that would be expected for slow-growing, late maturing, and long-lived animals exhibiting a k-selected or periodic (Winemiller and Rose 1992) life history strategy. My estimate of M of 0.055 for the Winnebago lake sturgeon population should be fairly solid given its development through an SCAA model based on validated age data, although estimation of M by sex would be an important further improvement. Estimates of M of other lake sturgeon populations based on catch curve analysis were generally higher than 0.055, possibly an artifact of age error. If the age estimates from pectoral fin spines of other lake sturgeon populations, and other sturgeon species have error similar to the error in the fin spine

estimates for lake sturgeon from the Winnebago System, their respective catch curves will generally overestimate Z, and subsequently overestimate M (if F was accurately estimated). Furthermore, if underestimates of ages are used in a catch at age analysis, Z and F would be overestimated and M could be underestimated (while recruitment would be overestimated). Estimates of Z for protected or unexploited sturgeon populations are typically equated to M, assuming F=0, although if the catch curves used to estimate Z were developed with under-estimates of true age, Z and M will be overestimated.

Obviously the generic formulas for estimating M have important utility in the absence of other data for a particular fish stock, but their utility is somewhat limited, and until independent estimates of M are developed for various species and stocks, it is probably prudent to be careful about application of M estimates from these formulas, especially for species with intrinsically low M's.

The SCAA model estimate of 0.055 was developed using unsexed catch at age data. Given the differences in life history and growth patterns between males and females after they reach the growth inflexion point (for length) of 96 cm, it is reasonable to suspect that male and female lake sturgeon experience different natural mortality rates. We have been collecting catch at age data by sex from the Winnebago sturgeon spear harvest annually since 1993, but 15 years of data are insufficient to build a sex based SCAA model. By the year 2050 the minimal required catch at age data will have been collected to allow a SCAA model to be built by sex and an opportunity to evaluate differences in natural mortality between male and female lake sturgeon in the Winnebago System. An additional attribute of M more difficult to evaluate is its variability. The current Winnebago lake sturgeon SCAA and all other models requiring an estimate of M,

assume M is constant. This is a relatively reasonable assumption given the extremely low M of lake sturgeon, although there is likely some variability in M from year to year or decade to decade. Catch curve analysis could potentially provide some insight into M's variability, but, despite being able to correct inaccurate age estimates using the age validation results, the error inherent in the corrected data may mask our ability to confidently determine the potentially narrow range of natural variation in M.

Total annual mortality rates (A) of lake sturgeon on the Winnebago System, based on empirical tag return data (corroborated by SCAA model estimates based on validated age data) have averaged 8.8% during 1977-2007. Estimates formerly developed for A for the Winnebago System lake sturgeon population were 5.4%-13.4% during 1955-1967 for Lake Winnebago (Priegel and Wirth 1975), 8.8%-22.2% during 1952-1976 for the Upriver Lakes (Priegel and Wirth 1978), 10.5% during 1975-1981 (Folz and Meyers 1985), and 9.8%-18.6% during 1975-1996 (Bruch 1999). All of the former estimates were developed from catch curve analyses based on un-validated age data and those from the period 1976-1996 are generally substantially higher than the estimate based on validated age data used in the SCAA model and corroborated by empirical tag return data for the same period. Underestimates of true age due to error of pectoral fin spine ages would result in an overestimation of total instantaneous mortality (as the negative slope of the descending arm of a catch curve) and subsequently also overestimate total annual mortality.

The total annual mortality of 8.8% experienced by the lake sturgeon population in the Winnebago System during 1977-2007 allowed the adult population to grow and sustain at a relatively high level. Recruitment did experience a decline during the period,

but not due to recruitment overfishing, but instead more likely due to the estimated inverse relationship between adult female stock and yearling recruits. Assuming an annual conditional natural mortality rate of 5.4%, total annual mortality averaged 6.8% during 1978-1989, increasing during 1990-1996 to an average of 9.2% (before new regulations imposed in the late 1990s were enacted to bring down the harvest rate) resulting in a continued robust adult stock plus an SCAA model estimated improved recruitment rate in the 2000s. Preigel and Wirth's (1975) recommendation of an annual exploitation limit of no more than 4.7% to sustain a robust lake sturgeon stock in the Winnebago System appears to be very appropriate for long term effective management of the population and the spear fishery.

Abundance.— Sturgeon abundance in North America is typically estimated using mark and recapture data in a closed population model (e.g. Peterson or Schnabel estimator) or an open population model (e.g. Jolly-Seber estimator) (Ricker 1975, Priegel and Wirth 1975; Priegel 1973; Scholl 1986; Baker and Borgenson 1999; Bruch 1999; McLeod et al. 1999). Caspian Sea sturgeon stock abundance has been estimated using area swept estimates from trawl catch per effort data (Ivanov et al. 1999; Khodorevskaya and Krasikov 1999). Developing reliable estimates with either methodology can be confounded by varying assessment capture success due to behavioral changes that may be associated with different growth stanzas or life history stages, complex migrational patterns of adults and sub-adults (R.M. Bruch, WI DNR and F.P. Binkowski, UW-Milwaukee WATER Institute, unpublished data), gear limitations, or low population densities.

The population of lake sturgeon in the Winnebago System is the largest stock of the species remaining in the Great Lakes basin. The current estimated adult stock of 34000 adults in the Winnebago System is 3 to 2050 times larger than the 17 known successfully spawning populations of lake sturgeon, out of an original estimated 107 populations, that once used rivers tributary to the Great Lakes and St. Lawrence River systems (Holey et al 2000).

The earliest estimates of lake sturgeon abundance in the Winnebago System, developed in the 1950s, indicated the stock of legal fish (≥ 102 cm) was approximately 10000 (Preigel and Wirth 1975). Estimates developed in the 1980s and then in 1990 indicated the legal stock at the time (fish ≥ 114 cm) had increased to 36000-40000 (Folz and Meyers 1985; Bruch 1999). Adult stock in 1995 was estimated to be approximately 8000 females and 40000 males (Bruch 1999). A Peterson model was used to develop original abundance estimates in the 1950s-1990s. Estimates developed as part of the current study, using Peterson (Chapman's modification), Jolly-Seber, and SCAA estimators, matched the historical Peterson estimates quite well and also showed a significant increase in abundance from the 1950s to the 1990s. All three models also showed a leveling off of stock abundance in the 1990s and 2000s suggesting that either carrying capacity had been reached, or increased fishing mortality in the 1990s had quelled stock growth.

The SCAA model using catch at age data produced smoothed and consistent estimates through the entire period 1954-2007, although the Chapman modified Peterson estimate produced extremely accurate estimates in the most recent years, especially for adult male stock, using empirical tag and recapture data. The use of PIT tags, along with

accurate tag loss data, dramatically improved the accuracy of the Peterson population estimates. The SCAA model also showed that while the adult population was increasing, the overall abundance of all ages in the Winnebago stock was decreasing due to the estimated inverse relationship between yearling recruits and adults.

Intrinsic Rate of Population Increase.—One of the most important population parameters to know about a fish population is its intrinsic rate of population increase, a direct measure of a species' or population's ability to sustain itself or to recover from excessive losses due to overharvest or catastrophic environmental events. Sturgeon are commonly recognized as a group of species that typify long-lived, late-maturing periodic strategist fish (Winemiller and Rose 1992) with low intrinsic rates of increase. Despite this common recognition, very few populations have had their intrinsic rate of population increase quantitatively estimated. Population trends of the Gulf sturgeon over a 10 year period were used in an age structured model to estimate a discreet rate of population increase (λ) of 1.05, equivalent to an intrinsic rate of increase (r) of 0.049 (Pine et al. 2001). Priegel and Wirth (1975) equated their estimate of the annual recruitment rate of age 15 to 19 year old lake sturgeon in the Winnebago System winter spear fishery during 1955-1967, 4.7%, to a 1.047 discrete rate of population growth (equivalent to an intrinsic rate of increase of 0.046), and used this number to set the now famous exploitation limit of 4.7% used since to manage all of Wisconsin's lake sturgeon fisheries.

I estimated intrinsic rates of increase of the adult lake sturgeon population in the Winnebago System in the current study using long term estimates of abundance calculated by three different estimators for a 54 year period. The resultant estimates ranged from 0.049 (discrete of 1.050) developed from the statistical catch at age model to 0.138 (discrete of

1.148) developed from Chapman density estimates. While the Chapman density estimates are currently the most accurate estimates due to the large number of tagged adult sturgeon now in the Winnebago System, low tagging numbers or absence of tagging in the 1960s and 1970s diminishes the reliability of the early estimates and thus the reliability of rates of population increase developed from these or the Jolly-Seber data. The SCAA model provided the most complete analysis of long term trends and I suggest that the rates of population increase from this model (r of 0.049, λ of 1.050) be used as the most accurate estimate for lake sturgeon of the Winnebago System.

Yield per Recruit.—Yield per recruit (Y/R) modeling of the lake sturgeon population in the Winnebago System estimated maximum yield would be 3.05 kg/per recruit under a 4.7% annual exploitation limit as recommended by Priegel and Wirth (1975), with fish recruited to the spear fishery at age 13, and 98 cm in total length. The Y/R model assumes knife-edge selectivity and constant recruitment, and while these do not occur in the Winnebago sturgeon spear fishery, the size and age of initial recruitment to the fishery is 91 cm and age 11. Fifty percent recruitment to the fishery occurs at 115 cm, age 18, and full recruitment to the fishery occurs at 138 cm, age 28. The sizes and ages of maximum yield per recruit of lake sturgeon from the Winnebago System developed from invariant models (Froese and Binohlan 2000) were 105-121 cm, ages 13-19 for males, and 137-140, ages 26-27 for females, which fall into the selectivity model's 0-100% recruitment range of fish into the Winnebago spear fishery, and, for males, very close to the size and age of entry into the fishery recommended by the Y/R model (Figure 45). The Y/R model used in this exercise predicts size of maximum yield per recruit regardless of sex, while the invariant models predict size of maximum yield per recruit

based on size of fist spawning and L_∞ by sex, which likely accounts for the disparity between the optimum size ranges suggested by the two approaches. Both approaches indicate that the current 91.2 cm (36 inch) minimum size limit in the spear fishery is likely providing close to maximum yield per recruit under an annual 4.7% exploitation limit.

The yield per recruit model uses an estimate of natural mortality, and estimates of parameters from the von Bertalanffy growth model, and is subject to error if mortality and age estimates are not accurate. Use of an instantaneous natural mortality rate higher than the true rate results in a decrease in the recommended age of recruitment and a reduction in maximum yield per recruit, while use of a lower than true rate has the opposite effect. Use of higher or lower W_∞ and K results in a proportional change in the estimated yield per recruit, but not in the estimated age and size of entry into the fishery required to maximize yield. Errors in t_0 result in a substantial shift in the recommended age and size of entry into the fishery. An erroneous increase in t_0 results in an increase in the age of entry, increasing the risk of recruitment overfishing, while a decrease in t_0 suggests that fish should recruited at a younger age to maximize yield, increasing the risk of growth overfishing. Pectoral fin spine age estimates for lake sturgeon of the Winnebago System tended to underestimate true age that would, when used to develop von Bertalanffy growth parameters, result in a smaller t_0, as well as a higher K and possibly a higher L_∞ (and subsequently a higher W_∞). A Y/R model run with these erroneous parameters, evaluated as $t_{r\text{-}max}$ (at a specific exploitation rate) or F_{max} would tend to suggest higher yields per recruit and recommend a younger age and size of entry into the fishery. Use of an overestimate of instantaneous natural mortality, which would

be the case if Pauley's equation were used to estimate M for the Winnebago lake sturgeon population, would exacerbate the tendency of the Y/R model to estimate higher than realistic Y/R and recommend younger size and age of entry into the fishery to maximize yield.

The sturgeon population in the Winnebago System has experienced a long term average annual exploitation rate of 2.6% (SD 2.3%) during 1954-2007 producing a total yield in the 54 year period of 1,034,845 kg or an average yield of 19,164 kg/yr (SD 15,074 kg). The size and age of 50% recruitment during this period ranged from 88 cm, age 10, to 115 cm, age 18, dependent upon which of four different minimum size limits was in effect at the time. Given the Y/R modeling results discussed above it is reasonable to say that the Winnebago winter sturgeon spear fishery was producing close to, but likely somewhat below maximum yield for the period 1954-2007 at an average exploitation rate of 2.6%. Beamesderfer et al. (1995) predicted maximum yield per recruits (Y/R) for white sturgeon populations on the lower Columbia River system, Washington, USA with exploitation rates of 5-15%. Taghavi (2001) estimated maximum sustainable Y/R at instantaneous fishing mortality rates of 0.16 (10.7% exploitation rate with an M=0.05) for male and 0.07 (6.7% exploitation rate with an M=0.03) for female beluga sturgeon (*Huso huso*) inhabiting the Caspian Sea. Given the potential impact of pectoral fin spine ageing error on estimates of mortality rates, growth model parameters, and Y/R model output, it is possible that the exploitation limits recommended by Beamesderfer et al. (1995) and Taghavi (2001) could be set too high. Quist et al. (2002) used the FAST model to simulate the impact of various size limits on Y/R of commercially harvested shovelnose sturgeon populations in the Missouri River System

suggesting that shovelnose are more sensitive to overharvest than previously thought. Scholten and Bettoli (2005) also used the FAST model to conclude that paddlefish (*Polyodon spathula*) harvest regulations in the lower Tennessee River system, Tennessee, USA were ineffective at controlling growth overfishing occurring in the commercial paddlefish fishery. Yield per recruit models are useful for the development of size limit regulations on sturgeon fisheries but should be applied selecting the optimal age to maximize yield, at a conservative exploitation rate likely 5% or less.

Impact of Harvest Management, Environmental Change, and Public Involvement on Lake Sturgeon Population Dynamics.—The state of Wisconsin has recognized the importance of pro-active management of its lake sturgeon stocks since the late 1800s, and appears to have used, to the extent possible, the best scientific based information available at any time to make decisions on protection of sturgeon stocks and regulation of sturgeon fisheries. As a result of this management philosophy, and despite difficult limiting factors over the years including unknown or unforeseen impacts of dams on spawning rivers, pollution, and various political issues, Wisconsin has the best remaining stocks of lake sturgeon, and the greatest diversity of lake sturgeon fisheries left within the specie's North American range. Of all the suspected and known original lake sturgeon populations in Wisconsin, the Great Lakes populations were one of the few to suffer near extinction during their 25 year exploitation run to destruction before the state fisheries officials and politicians could develop and implement a program to conserve and more wisely manage the state's lake sturgeon resources. The creation of the Wisconsin Conservation Commission in 1915, following the period of Theodore Roosevelt resource

conservationism, lifted sturgeon protection in the state to a new level with ban on harvest on all waters of the state including the Winnebago System.

The population of lake sturgeon in the Winnebago System has been the crown jewel in the state's array of lake sturgeon populations since the demise of the Great Lakes stocks prior to 1915. Re-opening the winter spear fishery on Lake Winnebago in 1932 as part of economic relief legislation provided harvest opportunities for Wisconsin's citizens, which in turn provided the impetus for hiring the fisheries biologists needed to collect the data necessary to make informed management decisions about the Winnebago lake sturgeon stock. Dr. Edward Schneberger of the Wisconsin Conservation Department was the first biologist to work on the Winnebago lake sturgeon population initiating a creel census and collection of biological data during the February 1941 harvest season. Following his initial data collection, that included collection of otoliths for age estimation and viscera for determination of sex and food habits, Dr. Schneberger carried on almost a year long regular correspondence with Dr. William Harkness of the Toronto University, North America's leading lake sturgeon expert at the time (Harkness 1923), in an attempt to learn and improve his assessment techniques, especially as it concerned processing and estimating age from the otoliths (Schneberger and Harkness 1942). Both Schneberger and Harkness clearly understood the importance of determining the age and growth of lake sturgeon, especially from exploited populations.

After World War II, assessments of the Winnebago lake sturgeon population and fishery increased following the hiring of additional fisheries biologists and technicians who produced the first system-wide population estimates and did extensive work on age and growth. In the 1960's the 4.7% annual exploitation limit was adopted and became

the foundation of the program managing the sturgeon fishery from that time on. Dozens of rules and laws have been implemented over the decades since the 1960s to protect and effectively manage the Winnebago lake sturgeon population and harvest, all built upon the 4.7% exploitation limit foundation. Environmental changes within the lake system in the 1960s, primarily increased turbidity due to increased non-point pollution inputs, generally enhanced the effectiveness of harvest regulations during the 1960s-1980s by creating difficult spearing conditions in the winter. Widespread implementation of non-point controls in the late 1980s followed by improvement in winter water clarities in the 1990s, lead to significant increases in exploitation and enactment of another series of more restrictive harvest regulations.

The long term trends in the dynamics of the lake sturgeon population in the Winnebago System show a definite response to sturgeon harvest regulations and environmental conditions of the system. Firstly, the Wisconsin Conservation Commission's closure of the fishery in 1915 likely provided important protection to the Winnebago lake sturgeon population for the 17 years the ban was in effect, despite some unknown amount of illegal harvest that still undoubtedly took place during the period. The ban was, unfortunately, too little, too late for the Great Lakes populations, especially in Lake Michigan (Smith 1968), but no records have been found to indicate the level of commercialization for lake sturgeon present on the Great Lakes was present on the Winnebago System (Schmitt-Kline, et al. in press). Given what we now understand about lake sturgeon life history, a harvest ban for 17 years does not even span one generation, and would now be considered a minimal amount of time to expect recovery of a sturgeon stock following high exploitation. The status of the Lake Michigan

population provides testament to the long period of time necessary for a sturgeon stock driven near the point of extinction to begin to show signs of recovery. After nearly 100 years, the lake sturgeon stock in Lake Michigan is just beginning to show some signs of recovery in very limited areas (Holey et al. 2000). This supports the hypothesis that in 1915, the stock of lake sturgeon in the Winnebago System was still somewhat robust, or at least sufficiently stable to experience enough recovery prior to 1932 to support an annual harvest.

The first major concerns about overharvest expressed by biologists and game wardens in the late 1940s were about juvenile lake sturgeon being taken illegally in the legal set-line fishery on the Upriver Lakes, and adult lake sturgeon being taken illegally by poachers during the annual spawning runs on the Wolf and upper Fox Rivers (Personal communications, Tom Wirth, WI DNR Fisheries Research Biologist, Winnebago System, Oshkosh, retired; and Ken Corbett, WI DNR Game Warden, Wolf River, Clintonville, retired). These concerns led to closure of the set-line fishery for sturgeon in 1951 and increased enforcement activities during the spawning run beginning in the early 1950s. The long term data set on Winnebago lake sturgeon shows the significant impact of the illegal set line harvest. The size and age frequencies of lake sturgeon developed from various population and harvest assessments conducted in the 1950s and 1960s show a distinct group of fish missing from what we understand now (because of age validation) to be ages 20-28 from the 1927-1947 year classes. During 1932 to 1951 these missing fish would have been the predominant fish in the Upriver Lakes (where the set-line fishery took place – set-lines for sturgeon were not allowed on Lake Winnebago) as the Upriver Lakes are a nursery ground for sub-adult fish, 78-100

cm in total length, prior to recruitment to Lake Winnebago (R. Bruch, WI DNR, Oshkosh, and F.P. Binkowski, UW-Milwaukee WATER Institute, unpublished data). Sturgeon this size were targeted in the illegal harvest using legal set-lines in the Upriver Lakes (Figure 46) (Personal communication, Paul Mathwig, former Upriver Lakes sturgeon set-liner, Oshkosh). Priegel and Wirth (1975) noted the missing fish during their assessments in the 1950s and 1970s stating: "The catch curve is noted to have a depression that occurs between ages 17 and 24 [20 to 28 after correction from age validation]. Although no explanation for this depression was found, it may have been related to spawning behavior since male sturgeon reach maturity at an age close to 17 years and females first mature at about 25 years". After we finished age validation we recognized that the impact of the missing fish was felt until recently as the number of fish larger than 45 kg in the harvest dropped close to zero during 1985-2000, finally recovering to pre-1985 levels in the mid 2000s. A high minimum size limit of 114 cm in the fishery enacted in 1974 likely also contributed to the diminishing numbers of large fish from 1985-2000, due to the shift in exploitation to larger fish during this period, and an coincidental increase in exploitation during the same time brought on by more consistently clearer winter water conditions.

While the widespread occurrence of illegal harvest of adult lake sturgeon on the rivers during the spawning migration during the 1940s – 1970s is commonly accepted as fact, the actual extent or impact of the illegal harvest remains unknown. Game warden reports from this era chronicle extensive use of snag lines and large catches of sturgeon seized each year by enforcement authorities (Schmitt-Kline et al in press) (Figure 47). Although no density estimates were made in the late 1960s, we now know, using the

analysis from the present study, that the number of adult sturgeon in the Winnebago System were estimated to be at a low point in the mid 1960s following high spear harvests in the 1950s. Poaching of adults during the spring spawning migration could have also contributed to the low densities at this time as well. After several exceptionally poor harvests during spearing seasons in the late 1960s and early 1970s, Winnebago sturgeon spearers began to demand that the Wisconsin Conservation Department take more actions to protect and understand the lake sturgeon population in the Winnebago System. Poaching was blamed for apparent low densities and poor spearing success, and may have contributed to the apparent problems, but frequent turbid winter water conditions in the 1960s and 1970s also undoubtedly affected spear harvest rates during this time period.

Winter water clarity has a fairly close relationship to harvest rates – if spearers are unable to see the sturgeon down their spear holes, they are unable to spear them. There are other factors that could also affect success rate including fish movement patterns and weather, but water clarity appears to have the greatest impact. A log transformed exponential model explained 50% of the variability in SCAA model estimated instantaneous fishing mortality rates (F) and water clarity during the spearing season:

$$F = 0.0234 * e^{(0.503*WC)} * e^{\varepsilon}, \ (r^2 = 0.50, F = 28.04, df = 1,28, P = 1.24E\text{-}05),$$

where: F = instantaneous fishing mortality rate, WC = winter water clarity (secchi disc reading) in meters, and ε = stochastic error (Figure 48). Mean water clarity during the spearing season by decade and mean harvest by decade were closely correlated (86.1%) from the 1940s–2000s (Table 18, Figure 49). Mean harvest in the 1960s, 1970s, and 1980's during the period of poorest water clarities was significantly less than mean

harvests in the 1940s, 1990s, and 2000s (ANOVA and post-hoc Tukey Tests; $F=3.12$, df $= 6, 59$, $P = \leq 0.05$).

The diminished winter water clarity starting in the late 1960s occurred after wholesale loss of aquatic macrophytes throughout the Winnebago pool lakes (Lake Winnebago and the Upriver Lakes) in the late 1950s and early 1960s. While the specific cause or causes of the loss of macrophytes was not fully documented it was thought to be a result of long term changes due to impoundment of the pool lakes, and increases in non-point pollution inputs following changes in agricultural practices put in place after World War II (Kahl 1993).

The years of lowest winter water clarity coincide with the years of low sturgeon harvest rates, and with the most dramatic change in the lake sturgeon population in the Winnebago System over the last 55 years: the exponential increase in abundance between 1960 and 1990. SCAA model results indicate that recruitment of yearlings was at a high point in the 1950s and 1960s during the period of lowest adult stock densities. This surge of recruitment was noted by Folz and Meyers (1985) who felt than an estimated increase in total annual mortality (estimated from catch curves) between fish sampled during 1955-1967 and during 1975-1981 was due to an increase in recruitment and not because of an increase in mortality rates – they believed that more young fish in the sample increased the slope of the descending arm of the catch curve. The fish that Folz and Meyers (1985) noted were more abundant were estimated at the time to be age 15-19 [true estimated age of 17-22], placing them from the 1954-1964 year classes, within the period of peak recruitment identified by SCAA modeling. The surge of recruitment and lightly harvested adult stock during 1968-1989 combined to produce a lake sturgeon

population that was growing exponentially at a time when other important factors also came into play including the foundation of the citizens sturgeon advocacy group Sturgeon for Tomorrow in 1977 who funded the spring Sturgeon Guard program to protect spawning fish, the practical elimination of spring poaching following the implementation of the Sturgeon Guard program, and the institution of a $1500 fine for possession of an untagged sturgeon in 1985.

Other factors in this time period also likely had an impact on the sturgeon population, but not immediately, including a dramatic increase in the development of man-made sturgeon spawning sites on the Wolf River, and an increase in the minimum size limit in the spear fishery from 102 cm to 114 cm. The increase in spawning sites may have had an impact on recruitment, although SCAA modeling indicates that as the adult stock increased through the 1970s and 1980s, recruitment of yearlings was experiencing a concomitant decrease. The increase in the minimum size limit, as discussed earlier, contributed to increased exploitation of the largest fish in the population, primarily adult females.

During the period 1954-2007, thorough and consistent assessments of the lake sturgeon population and harvest were not conducted every year. As mentioned earlier, extensive assessments of the population and the harvest were conducted by Wisconsin Conservation Department fisheries staff beginning in the late 1940s through the mid 1960's. From 1964 through 1974 though only a minimal harvest data were collected; local taverns were paid $0.25 to $0.50 a fish to measure and weigh harvested fish, and collect recapture and spearer demographic data to meet the minimal legal requirements for mandatory registration of all harvested fish. This system of harvest data collection

continued until 1991, although rigorous assessments of spawning and legal stock began again in 1975 after Dan Folz became the biologist in Oshkosh responsible for sturgeon management. The assessment work accomplished, especially the tagging data collected, between 1975 and 1990 was critical, providing a link between the assessments of the 1950s and the expanded assessments of the 1990's and 2000's. Likely the most important management actions following the assessments initiated in the late 1970s was including sex and stage of maturity as metrics collected from harvested fish, and increasing effort to tag adults during spring spawning in 1991. These data, along with extensive annual age sampling during the harvests, provided the information necessary to complete a 60+ year view of and evaluate long term trends in the Winnebago lake sturgeon stock.

The expanded assessments of the 1990s also provided the data necessary to develop and implement the comprehensive series of new regulations and laws enacted between 1993 and 2006 to address the overharvest empirical tag return data indicated was occurring in the 1990s, specifically of adult female lake sturgeon. These data provided an opportunity to more accurately estimate adult sturgeon stock size by sex and set harvest caps to allow tighter control of exploitation by sex. An important component of the management program initiated early in this period was the WI Department of Natural Resource's creation of the Winnebago Citizen's Sturgeon Advisory Committee who worked jointly with fisheries staff to develop and recommend all the new sturgeon regulations and laws after 1992.

The density estimates developed through the 1990s consistently indicated the stock of adult lake sturgeon in the Winnebago System had increased four-fold from the

late 1950s to the 1990s. Long term density estimates developed from all three different models employed in the current study showed the increase, and also strongly indicate that the adult stock approached or reached carrying capacity in the 1990s (Figures 35 and 36). The steep downward trend in relative condition of lake sturgeon in the early to mid 1980s occurred at a time when adult densities were approaching a plateau, and at a time when the overall fish community in the Winnebago System was experiencing other historic changes.

Long term fish community monitoring found the 1982 year class of freshwater drum in Lake Winnebago the largest ever recorded (Kamke and Bruch 1992), which remains the dominant year class 25 years afterward (Davis-Foust et. al. in press). Drum are likely the most important competitor with lake sturgeon for the chironomid larvae (primarily *Chironomus plumosus*), the preferred prey item for both species (Priegel 1967b; Stelzer et al 2008). The simultaneous historic abundance of drum and lake sturgeon in the early 1980s could have caused a strain on forage resources for both species resulting in the dramatic decline in relative condition of lake sturgeon. The low relative condition of lake sturgeon persisted for several years until the late 1980s when, after a series of exceptionally warm winters, the population of gizzard shad (*Dorsoma cepedianum*), that throughout historic record to this point were present, but almost rare in the Winnebago System, exploded. The shad in the Winnebago System experienced a substantial winter die-off each year and the lake sturgeon immediately picked up the dead and dying shad as a seasonal forage item in the winter, almost immediately improving their relative condition (Stelzer et al. 2008) (Figure 27). From 1988 to 2008, lake sturgeon relative condition fluctuated almost annually depending on the abundance of

gizzard shad. The sturgeon in Lake Winnebago still continued to get 47% of their carbon from lakefly larvae but gizzard shad contributed 37% of the assimilated carbon (Stelzer et al. 2008). The decrease in relative condition of lake sturgeon in the 1980s and the highly variable recovery of relative condition following the exponential increase and widely fluctuating abundance of gizzard shad as a new seasonal sturgeon forage item, strongly suggests that the lake sturgeon stock in the Winnebago System has been at or near carrying capacity since the early 1990s.

The lake sturgeon population in the Winnebago System grew to a carrying capacity level of abundance in a relatively short time, a four-fold increase in adult stock in about 30 years, due to a combination of environmental conditions, management actions, and harvest regulations that resulted low exploitation rates for most of the 30 years. Low harvest rates during the 1960s–1970s resulted sufficient protection of adult lake sturgeon stocks in the Winnebago System to allow the estimated eggs per recruit ratio approach the 50% level recommended by Boreman et al. (1984) for recovery of shortnose sturgeon stocks in Atlantic coast rivers in the northeast United States. Ironically, negative environmental conditions, primarily turbid water brought on by anthropogenic factors, played a major role in allowing the lake sturgeon stock in the Winnebago System to recover from excessive legal and suspected illegal harvest during the 1930s-1960s. Good science, as well as solicited and sometimes unsolicited public input, shaped harvest regulations and management actions for at least half of the last century. Today, fisheries staff and Winnebago sturgeon public continue to work closely together to maintain a robust lake sturgeon population in the system and the tradition of the winter sturgeon spearing season.

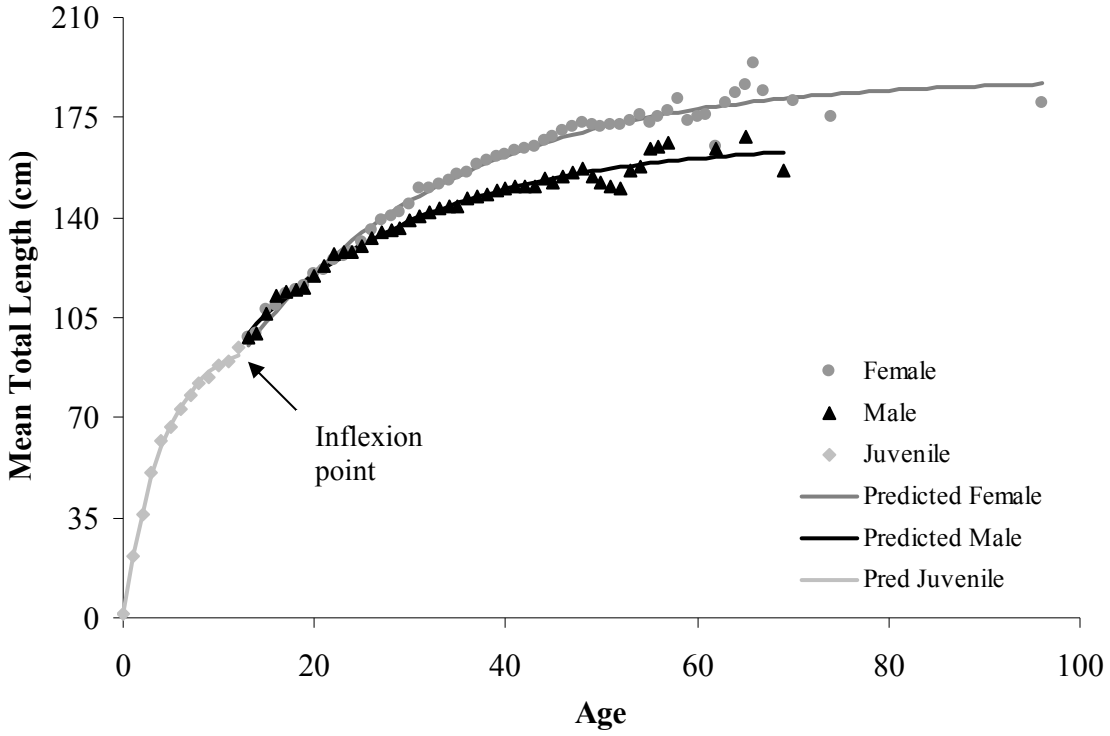

FIGURE 10.—Mean length at age of lake sturgeon, juveniles age 0-12, males age 13-69 and females age 13-96 in the Winnebago System, Wisconsin, 1953-2007. "Predicted" shows von Bertalanffy curves fit to each group. Original pectoral fins spine ages > 14 corrected with $TrueAge = EstAge^{1.054796}$.

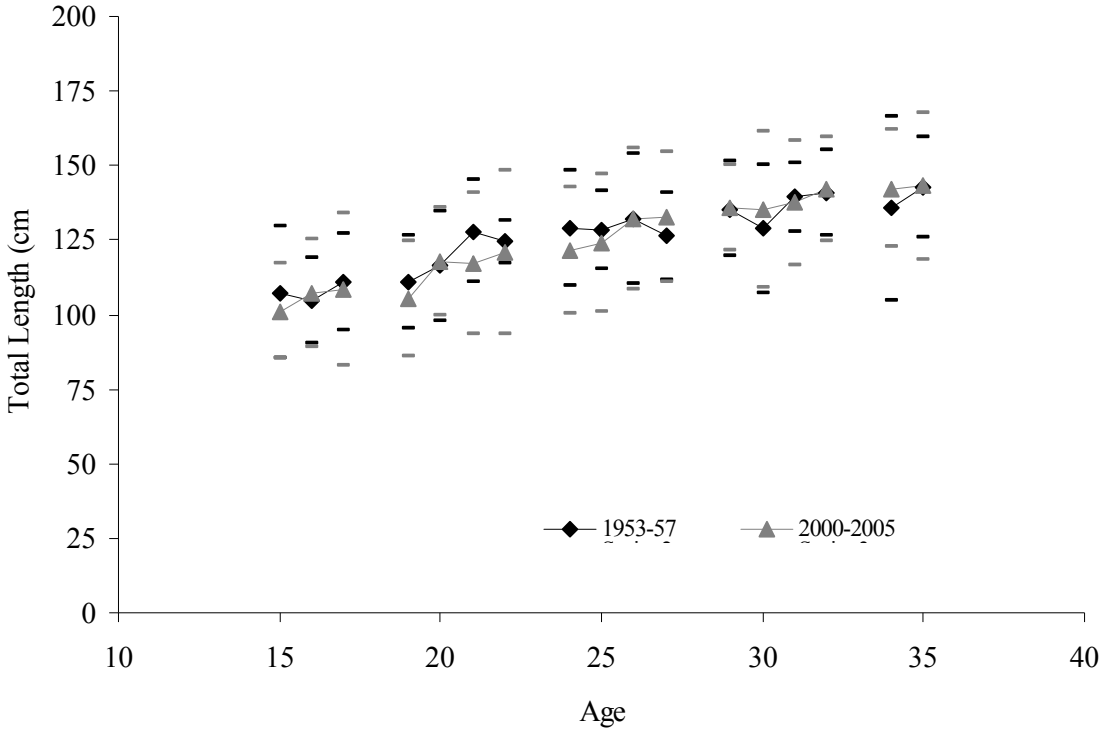

FIGURE 11.—Mean length at age 15-35 male lake sturgeon in spear harvest 1953-57 and 2000-2005, Upriver Lakes, Winnebago System, Wisconsin. Bars above and below each mean are respective upper and lower 95% confidence intervals around the mean. Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

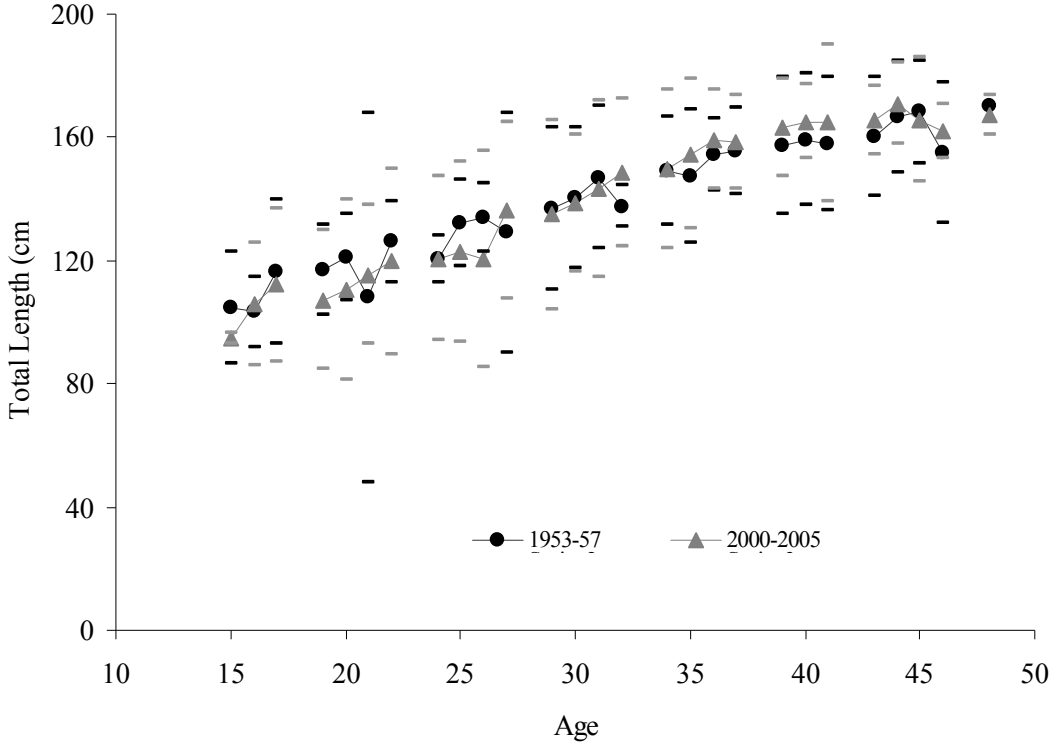

FIGURE 12.—Mean length at age 15-48 female lake sturgeon in spear harvest 1953-57 and 2000-2005, Upriver Lakes, Winnebago System, Wisconsin. Bars above and below each mean are respective upper and lower 95% confidence intervals around the mean. Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

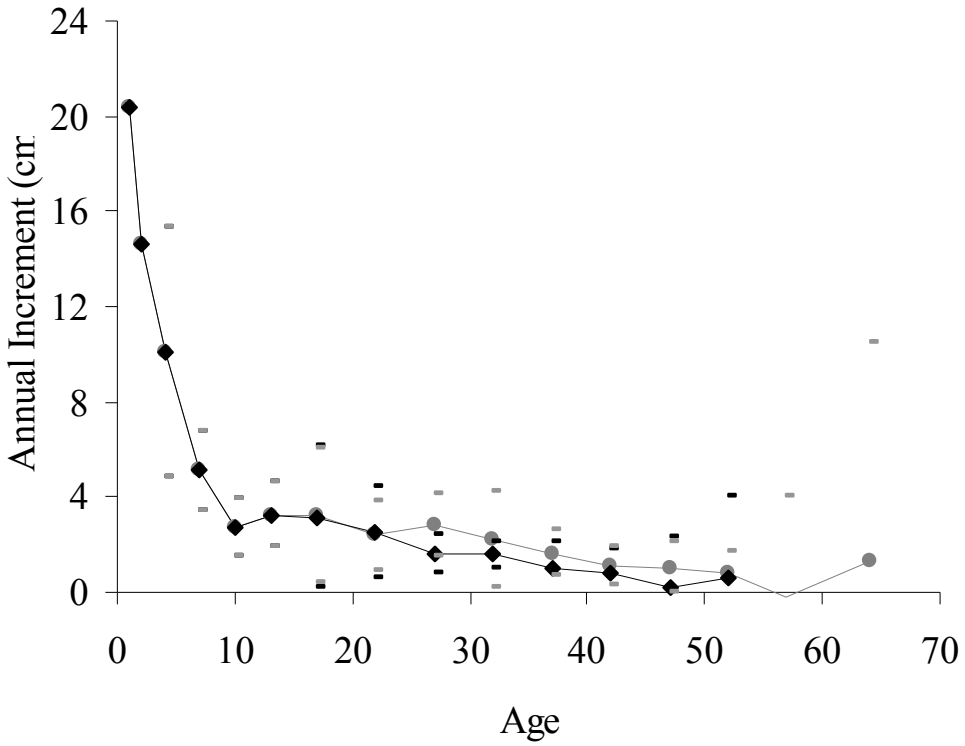

FIGURE 13.—Mean annual growth increments lake sturgeon, males age 0-54 (black diamonds; black bars ± 1 SD), and females age 0-70 (grey filled circles; grey bars ± 1 SD), 1953–2007, Winnebago System, Wisconsin. Growth increments calculated for age groups 0, 1, and 2; for groups of three successive age classes for ages 3 to 14; and for groups of 5 successive age classes for ages 15 and older. Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

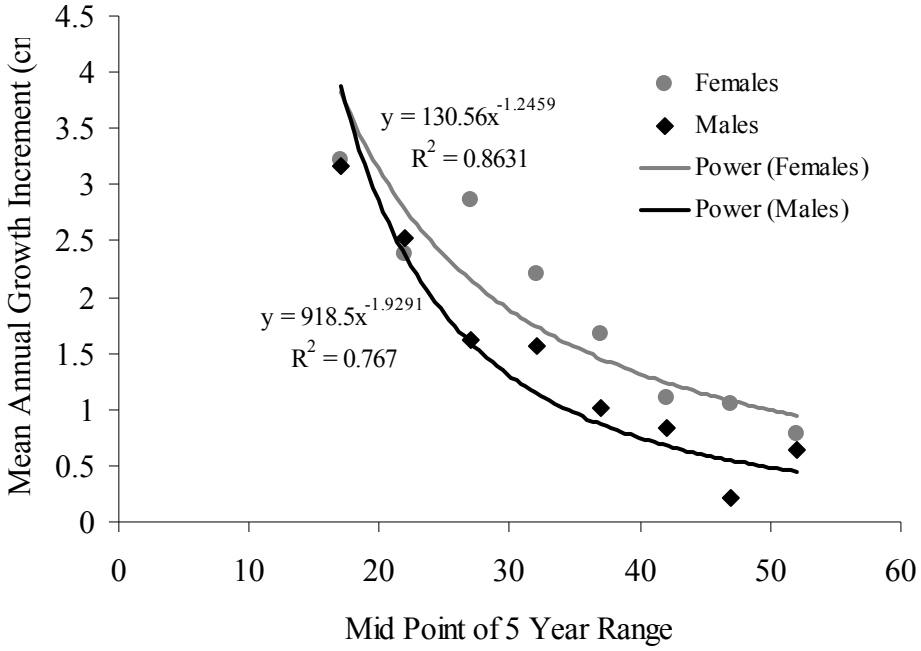

FIGURE 14.—Mean annual growth increments and power function relationships of male and female lake sturgeon ages 25-54, 1953–2007, Winnebago System, Wisconsin. Growth increments calculated on groups of 5 successive age classes. Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

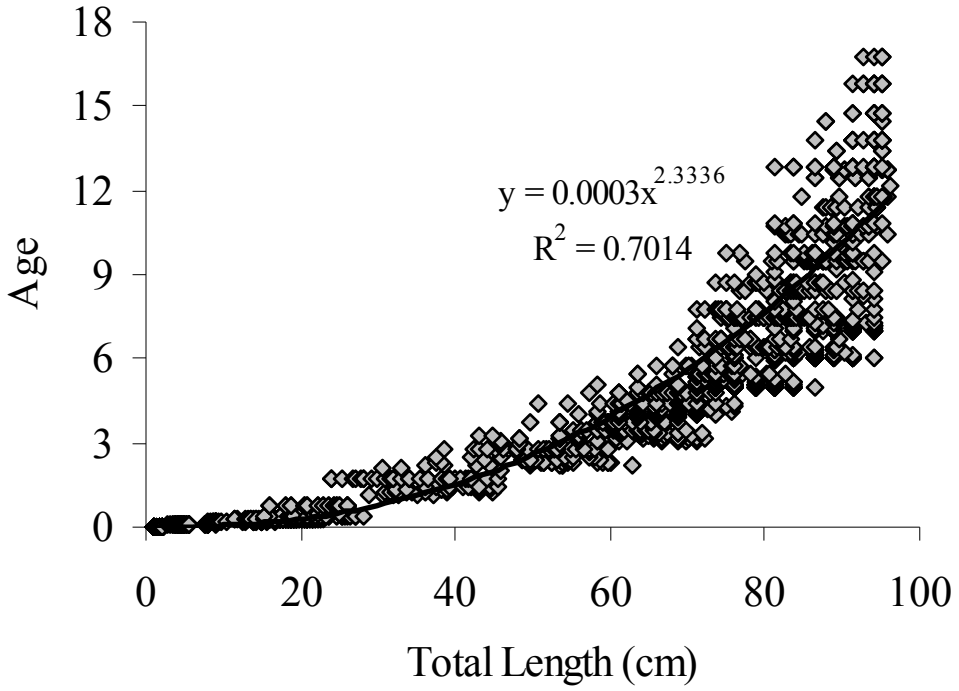

FIGURE 15.—Age at length of juvenile lake sturgeon, hatching to 96.25 cm, 1953–2007, Winnebago System, Wisconsin. Mean annual hatching date is May 5. Power function ($F = 3911.2$; $df = 1, 1665$; $P < 0.001$).

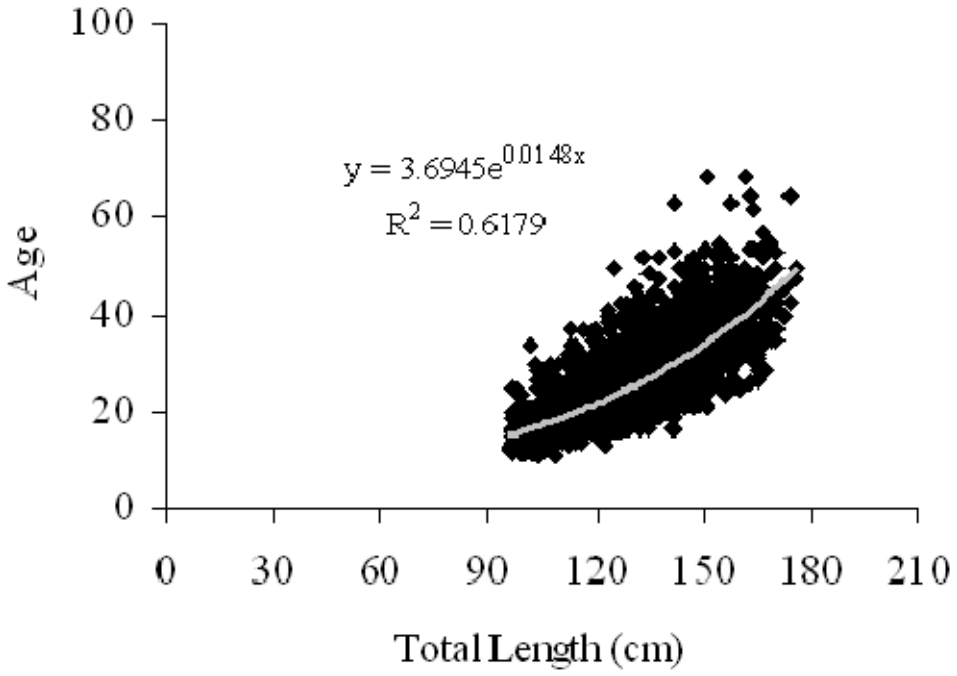

FIGURE 16.—Age at length of male lake sturgeon >96.25 cm, 1953–2007, Winnebago System, Wisconsin. Exponential function (F = 7381.8; df = 1, 4564; P < 0.001). Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

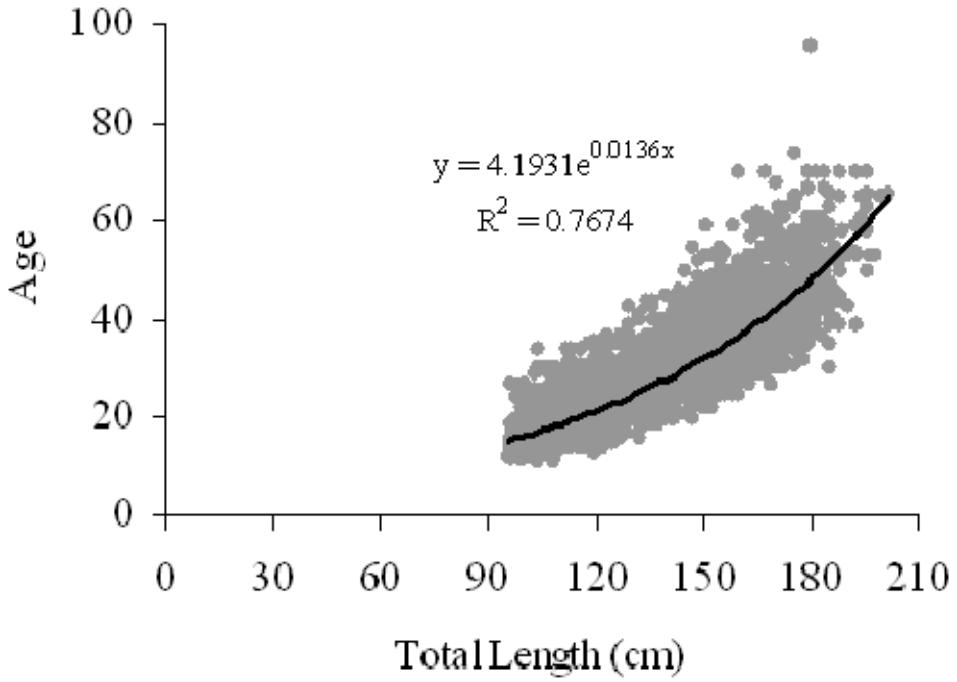

FIGURE 17.—Age at length of female lake sturgeon >96.25 cm, 1953–2007, Winnebago System, Wisconsin. Exponential function (F = 17768.1; df = 1, 5386; P = < 0.001). Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

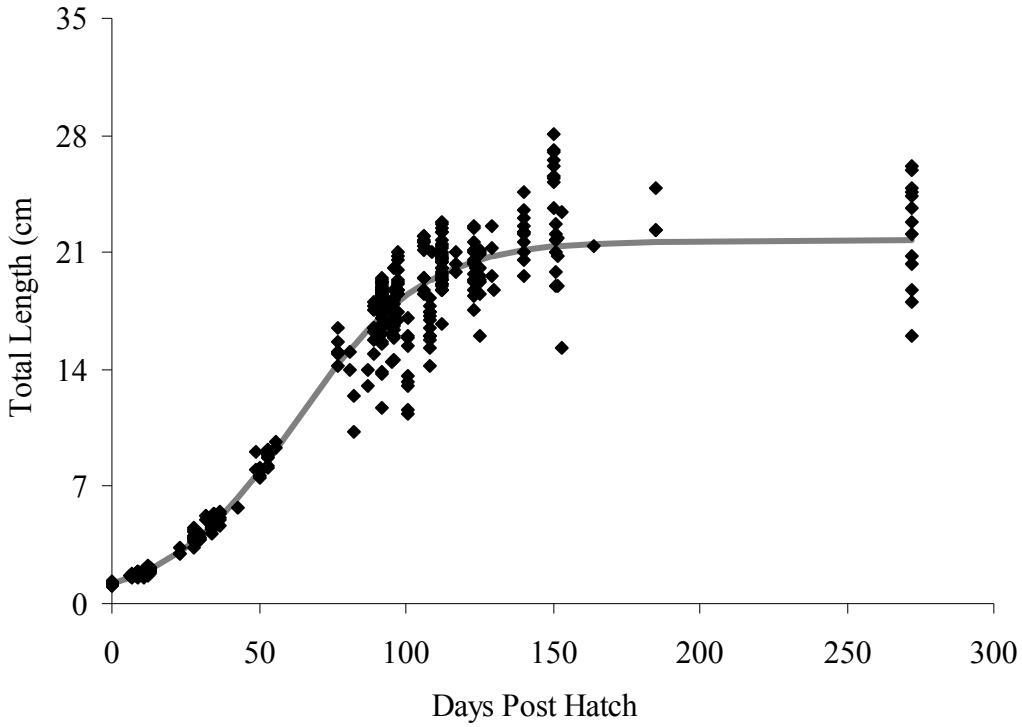

FIGURE 18.—Length at age of young of year lake sturgeon, from hatching to 272 days post hatch (mean annual hatching date is May 5), 1952–1992, Winnebago System, Wisconsin. Logistic model with parameters L_{max} = 21.7 cm, k = 16.7, and L_0 = 1.3 cm.

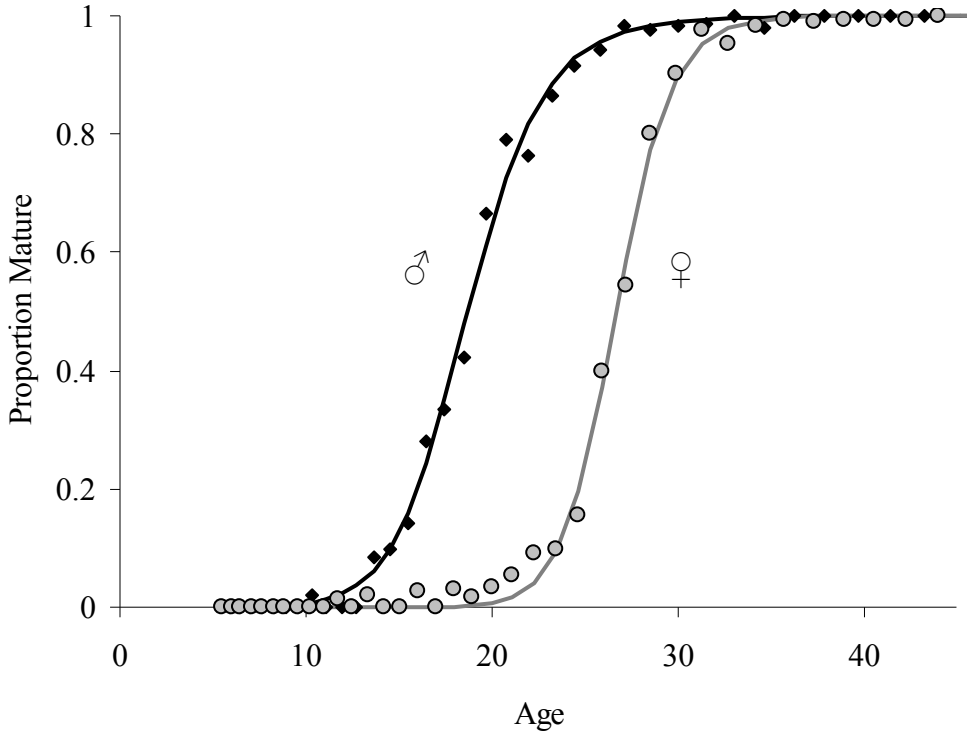

FIGURE 19.—Proportion of mature male (black points and line) and female (grey points and line) lake sturgeon by age in the Winnebago System, Wisconsin, 1991–2007. Ages estimated from total length: $Male\ EstAge = 0.000037 * (TL^{2.74})$; $Female\ EstAge = 0.000058 * (TL^{2.64})$.

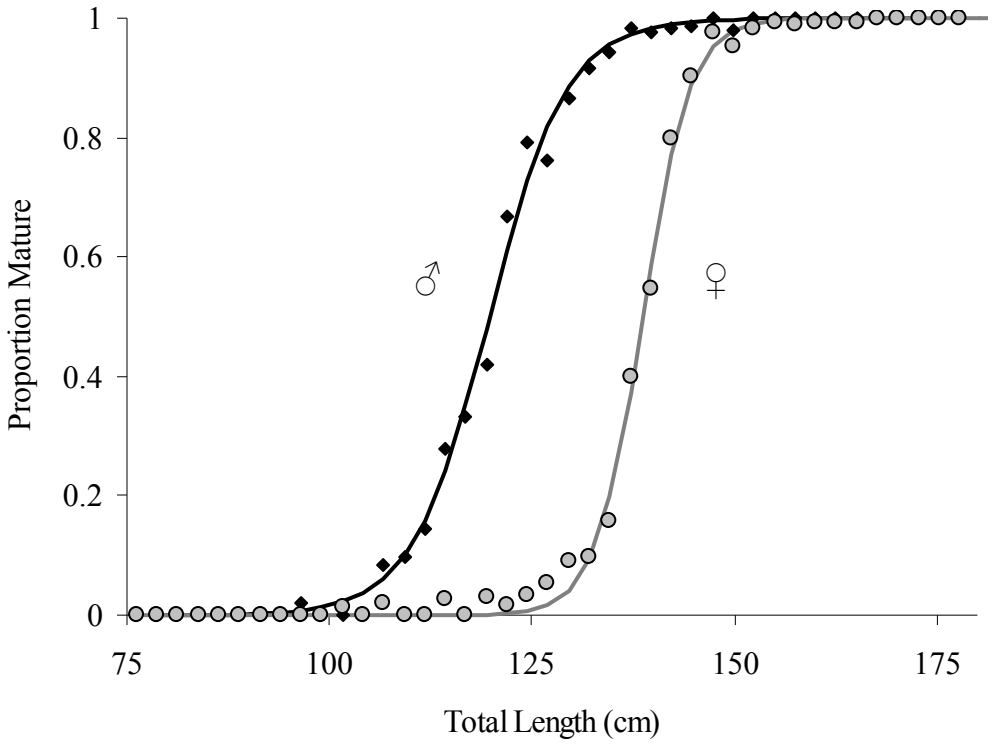

FIGURE 20.—Proportion of male (black points and line) and female (grey points and line) lake sturgeon by size in the Winnebago System, Wisconsin, 1991–2007. Logistic models developed from empirical length, sex and maturity data of harvested fish. males: $M = 1/(1+e^{(-0.209*(YL-119.775))})$; females $M = 1/(1+e^{(-0.345*(TL-138.69))})$.

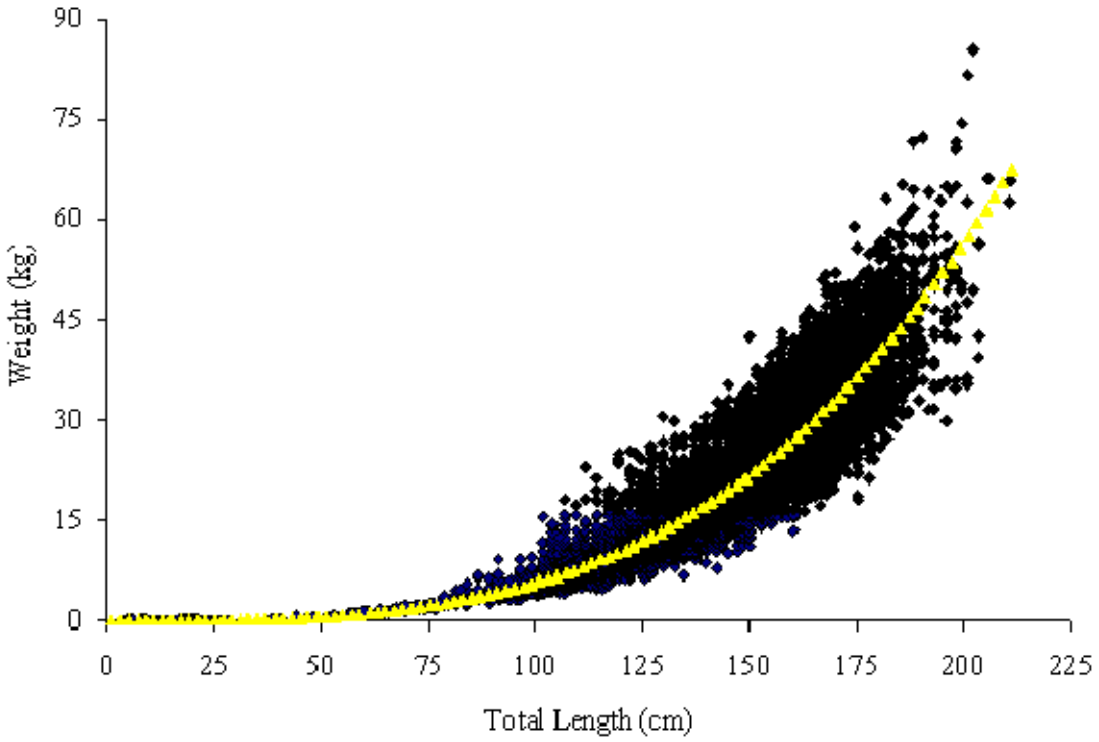

FIGURE 21.—General weight-length relationship of lake sturgeon, Winnebago System, Wisconsin, 1951–2007. Power function model parameters: $\alpha = 0.0000011396$, $\beta = 3.3065$ ($r^2 = 0.95$; F = 951927; df = 1, 50013; P = 0).

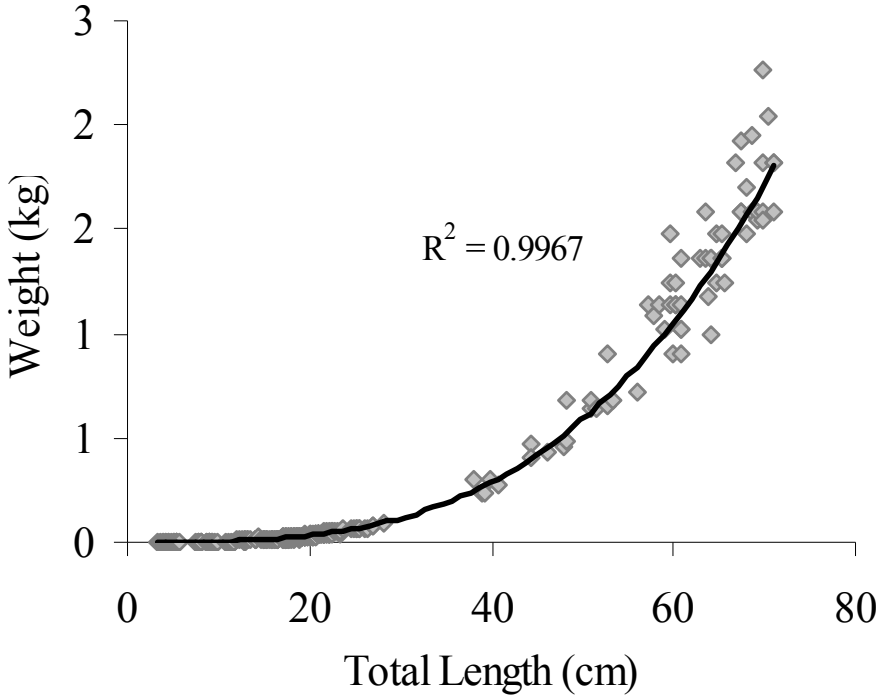

FIGURE 22.—Weight-length relationship of juvenile lake sturgeon < 71.1 cm, Winnebago System, Wisconsin, 1951–2007. Log10 power function $W = 0.000002258 * (L^{3.188})$, (F = 85415; df = 1, 287; P = 0).

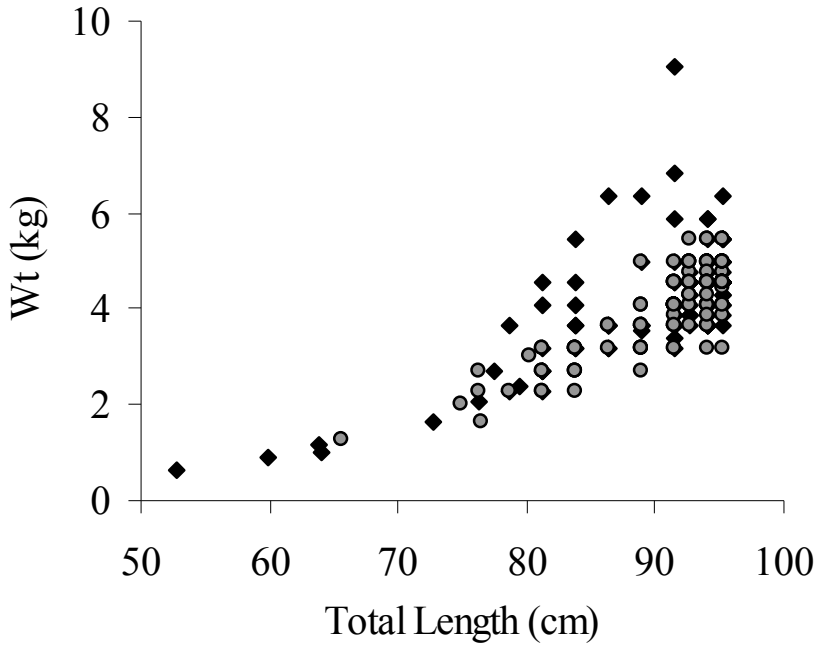

FIGURE 23.—Weight-length relationships of male (black diamonds) and female (grey diamonds) lake sturgeon 52-96 cm, Winnebago System, Wisconsin 1951–2007 showing divergence of relationships by sex after about 71 cm.

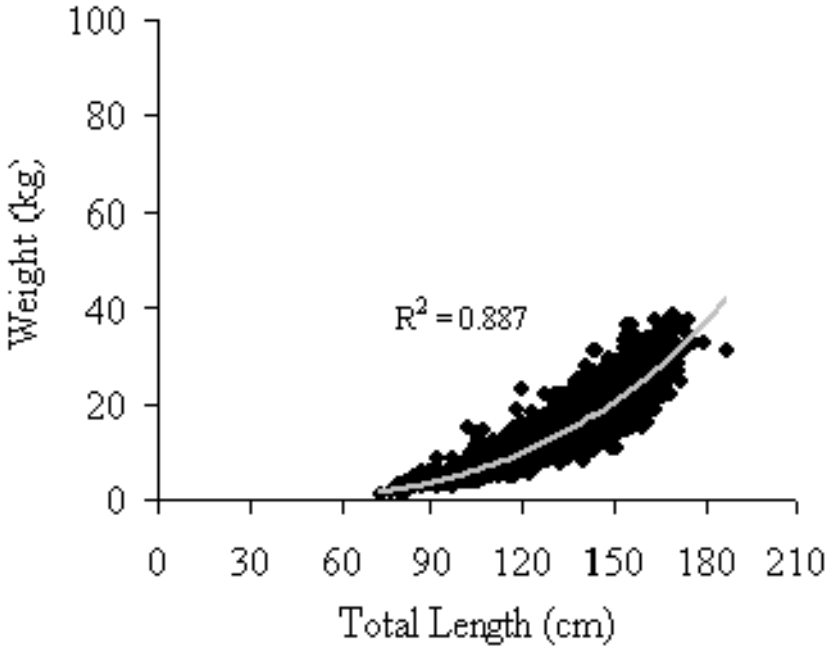

FIGURE 24.—Weight-length relationship for male lake sturgeon > 71 cm, Winnebago System, Wisconsin, 1951–2007. Log 10 power function $W = 0.00000180 * (L^{3.245})$, (F = 62804; df = 1, 7998; P = 0).

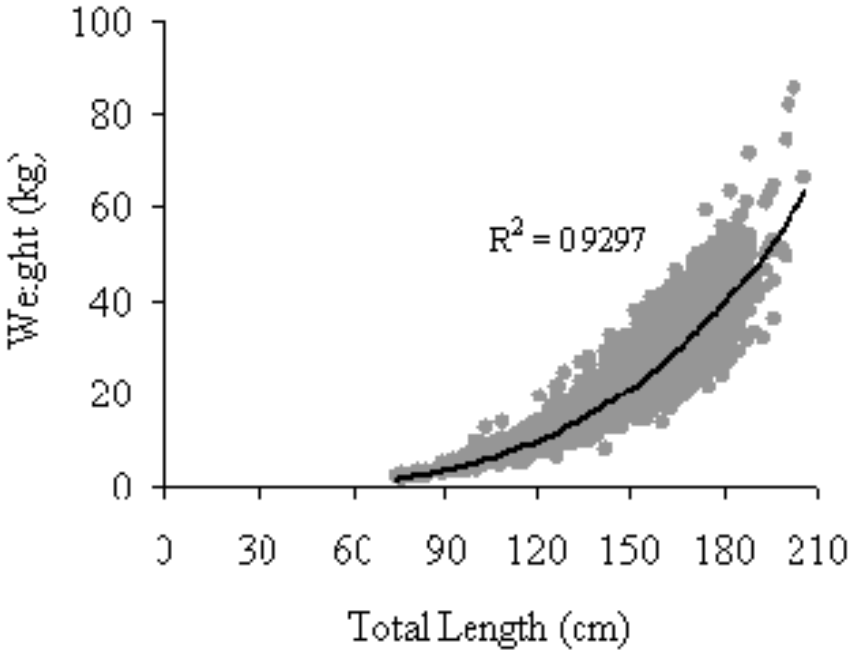

FIGURE 25.—Weight Length relationship for female lake sturgeon > 71 cm, Winnebago System, Wisconsin, 1951–2007. Log 10 power function $W = 0.00000076 * (TL^{3.422})$, (F = 122924; df = 1, 9292; P = 0).

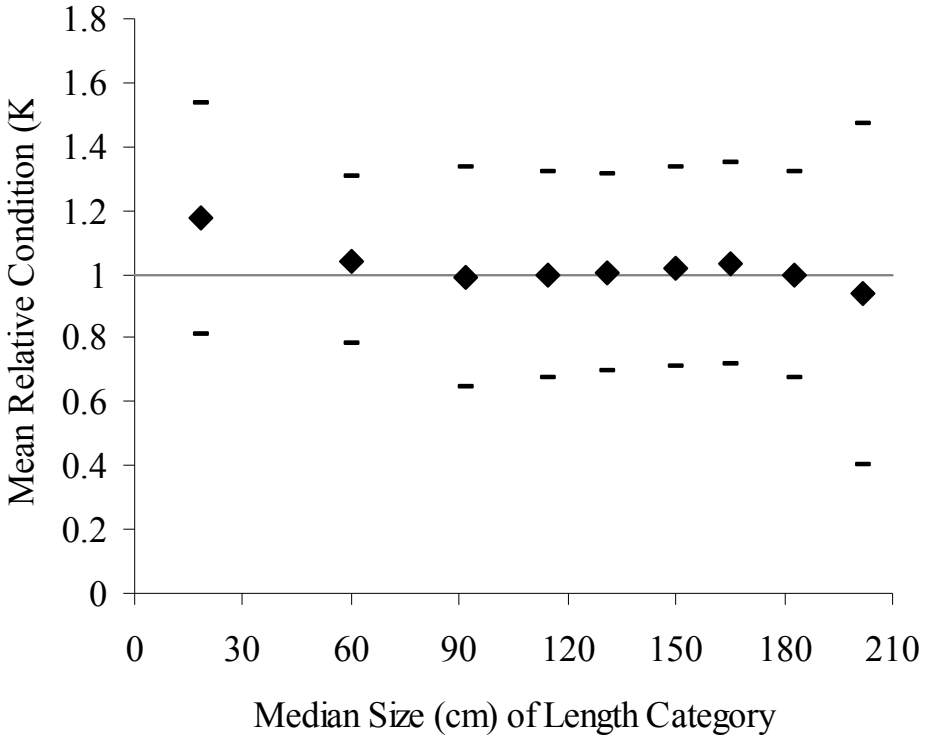

FIGURE 26.—Mean relative condition (K_n) of lake sturgeon by median length categories, without regard to sex or maturity stage, Winnebago System, Wisconsin during the period 1951–2007 ± standard deviation. Smallest length category fingerlings. Second length category contains fish 25 – 71 cm total length (first weight-length stanza minus fingerlings). Third length category (71-96 cm) ends at the break between the two length-age growth stanzas (96 cm).

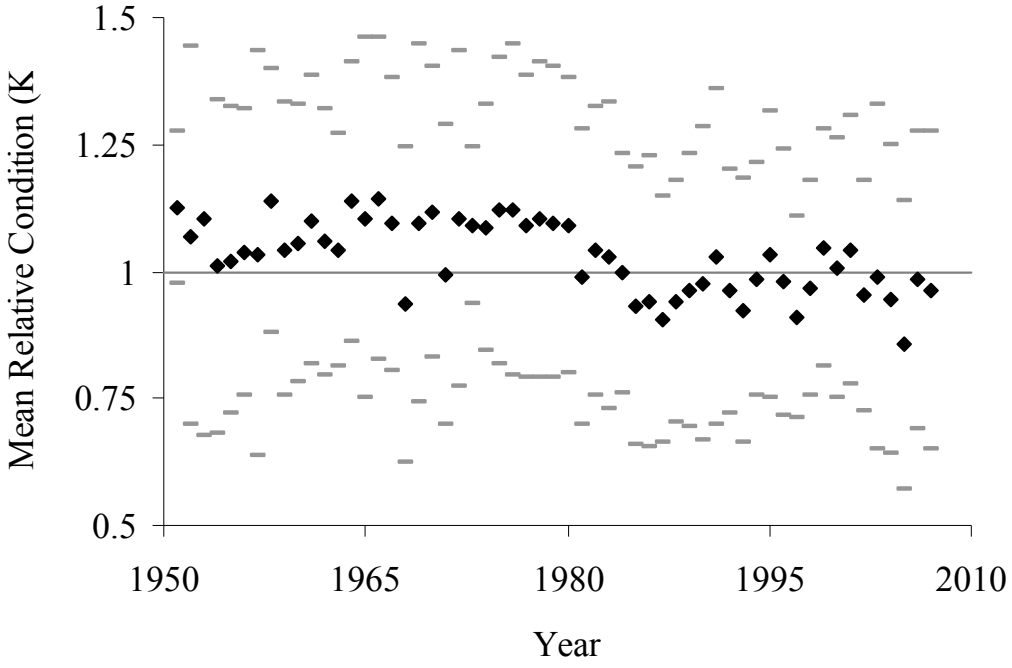

FIGURE 27.—Mean annual relative condition of lake sturgeon >114.2 cm in spear harvest 1952–2007, Winnebago System, Wisconsin. Bars are upper and lower 95% confidence intervals. Only fish ≥ 114.2 cm used to minimize bias of data collected under four minimum size limits ranging from 76.2 to 114.2 cm. Line depicting K = 1.0 illustrated.

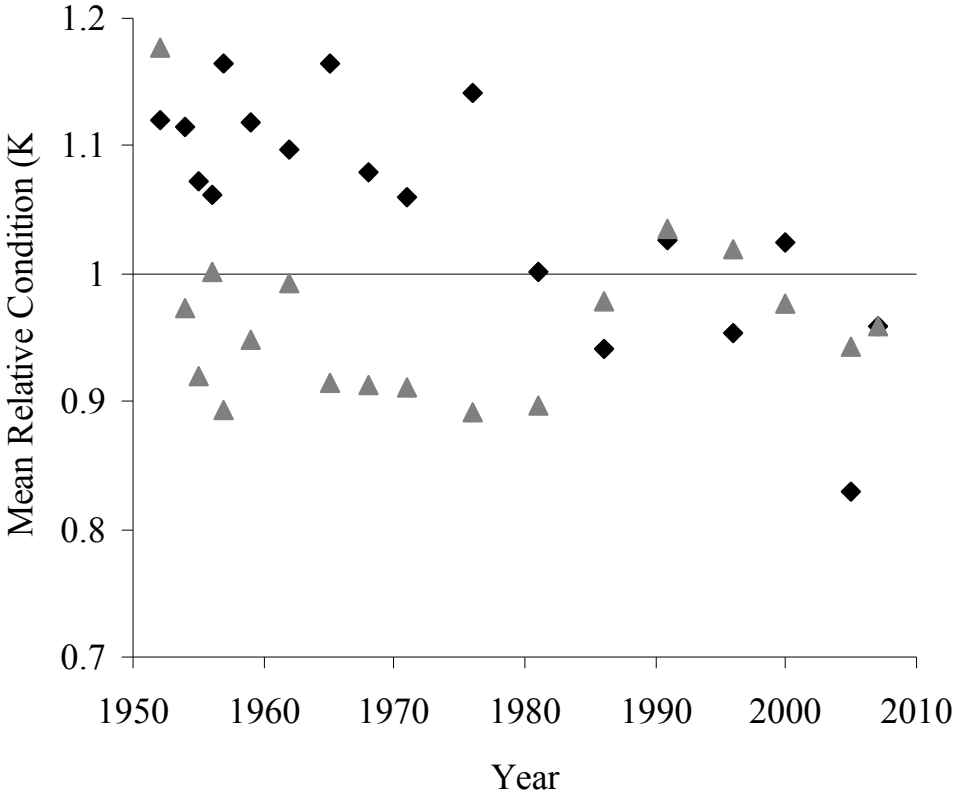

FIGURE 28.—Mean relative condition of lake sturgeon ≥ 76.2 cm from spear harvest 1952–2007 on the Upriver Lakes (grey triangles) vs. Lake Winnebago (black diamonds), Winnebago System, Wisconsin. Data from years when fisheries took place on both waters. Line depicting K = 1.0 illustrated.

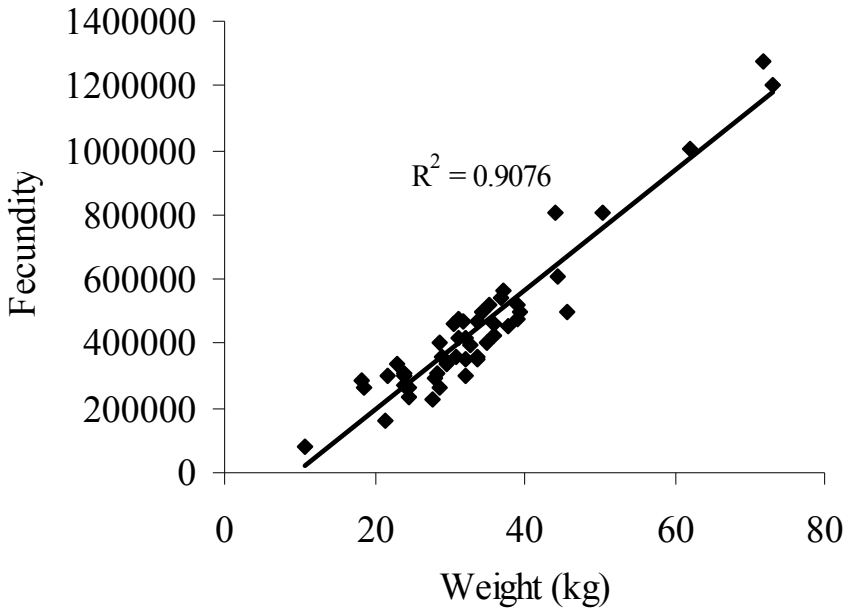

FIGURE 29.—Lake sturgeon fecundity vs. weight, Winnebago System, Wisconsin, 2005–2008. Linear function $Fecundity = (W * 18683.6) - 183527$, (F = 451.8; df = 1, 46; P < 0.001).

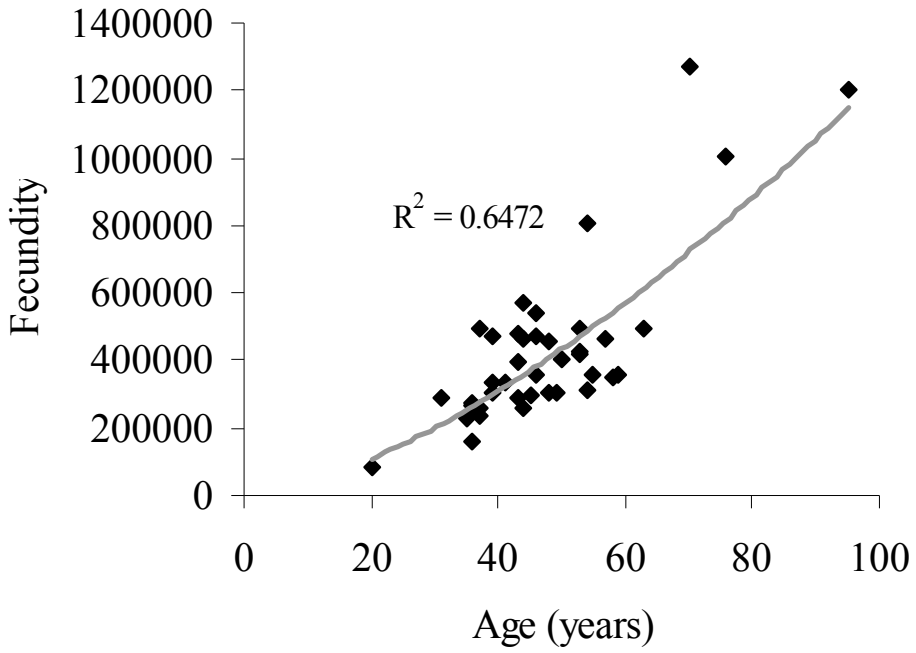

FIGURE 30.—Lake sturgeon fecundity at age Winnebago System, Wisconsin, 2005–2008. Power function $Fecundity = 1169.19 * (Age^{1.15124})$, (F = 69.7; df = 1, 38; P = < 0.001). Original pectoral fin spine ages corrected with $TrueAge = EstAge^{1.054796}$.

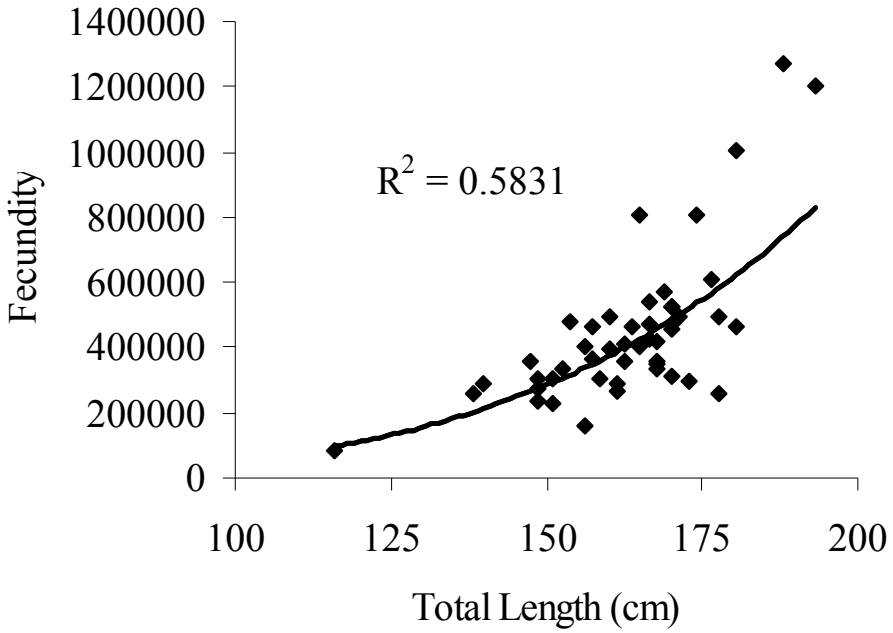

FIGURE 31.—Lake sturgeon fecundity at total length, Winnebago System, Wisconsin, 2005–2008. Power function $Fecundity = 0.000176 * (TL^{4.2315})$, ($r^2 = 0.58$; F = 64.3; df = 1, 46; P < 0.001).

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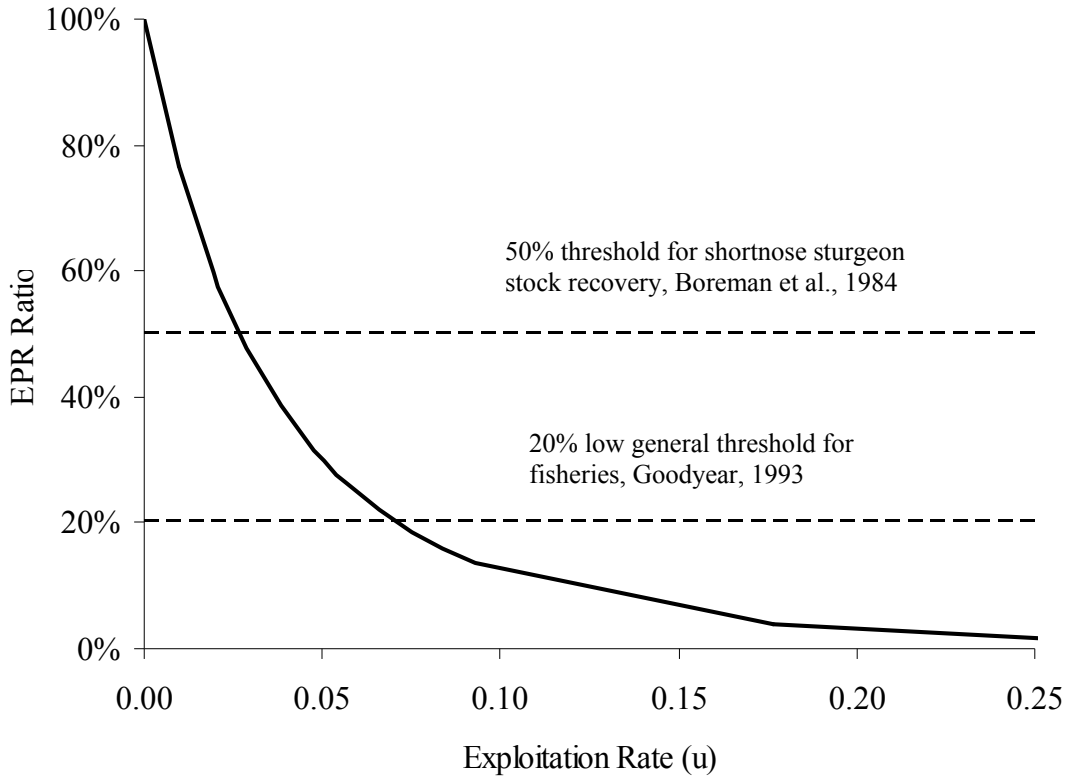

FIGURE 32.—Relationship between eggs per recruit ratio (EPR Ratio) and exploitation rate for lake sturgeon of the Winnebago System under a spear fishery with a 92.4 cm minimum size limit. EPR ratio compares the total estimated eggs a yearling female could produce in her lifetime at various levels of exploitation to the estimated number at zero exploitation (L_{max}). Based on 2005–2008 Winnebago System lake sturgeon fecundity at age data, an instantaneous natural mortality rate of 0.055, and a selectivity curve from a winter spear fishery with a 91.4 cm minimum size limit. General low threshold of 20% (Goodyear 1993) is lower dashed line. Threshold for shortnose sturgeon recovery, 50% (Boreman et al. 1984) is upper dashed line.

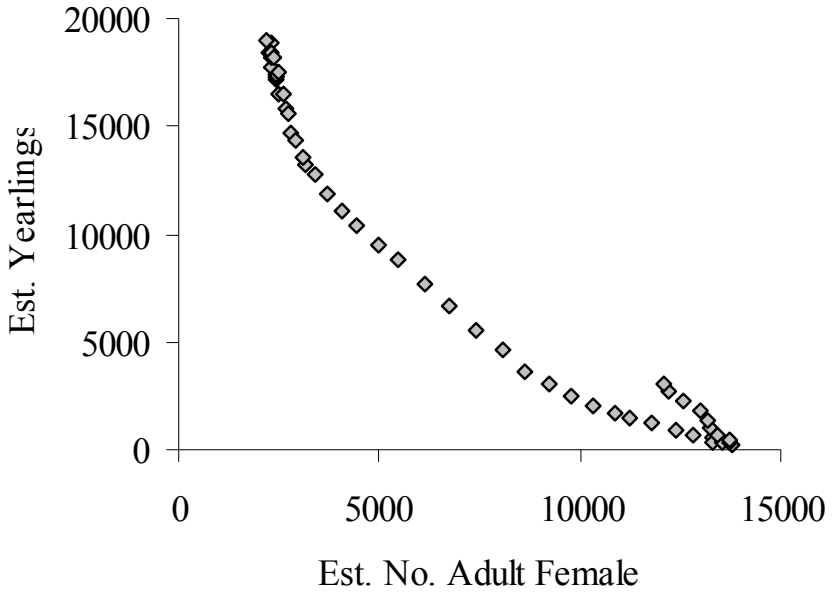

FIGURE 33.—Estimated stock-recruit relationship for lake sturgeon of the Winnebago System, Wisconsin, 1954–2007. Data are estimates of the number of adult females and number of yearling recruits derived from statistical catch at age model for lake sturgeon in the Winnebago System. Ricker model $R_i = 20.07706 * S * e\hat{}(-0.000445 * S) + \varepsilon$.

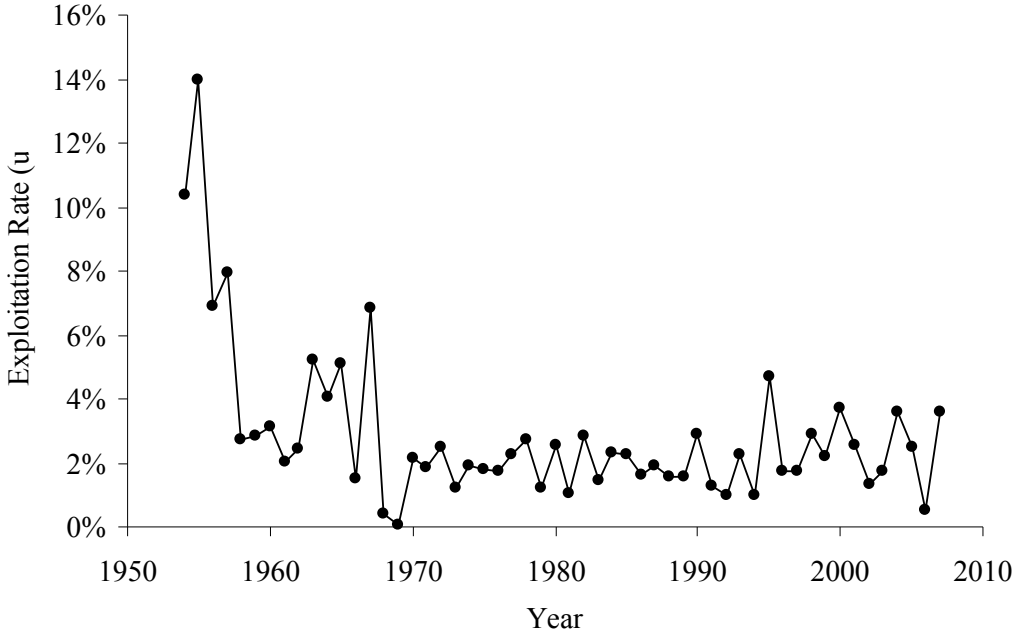

FIGURE 34.—Estimated exploitation rates of lake sturgeon in the winter spear fishery 1954–2007, Winnebago System, Wisconsin, from statistical catch at age model.

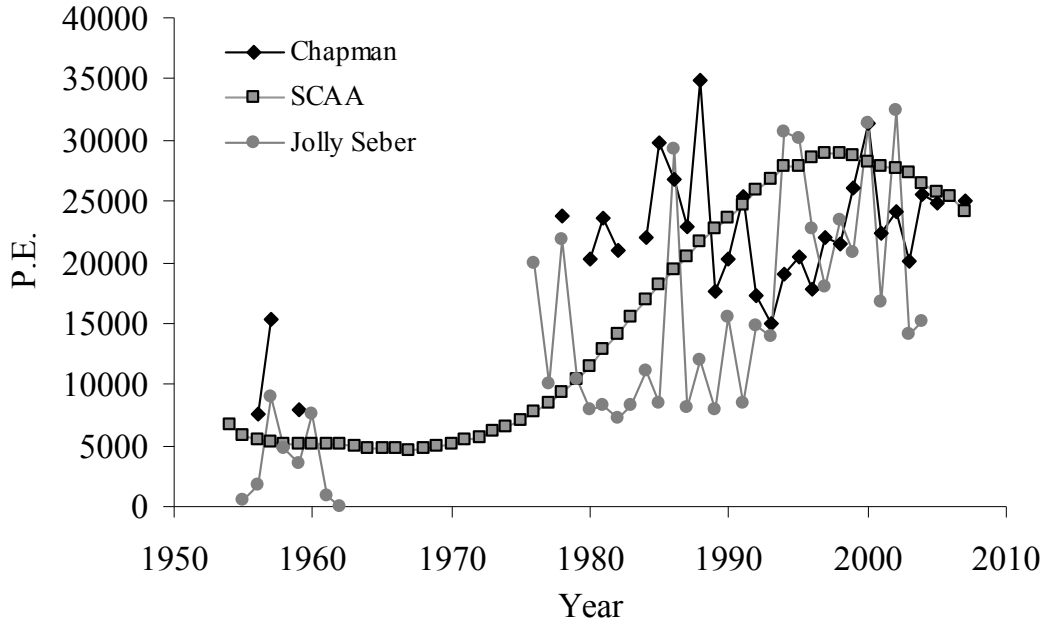

FIGURE 35.—Adult male lake sturgeon population estimates 1954–2007, Winnebago System, Wisconsin. Estimates developed from Chapman closed population, statistical catch at age (SCAA), and Jolly-Seber open population models. SCAA model estimated total abundance; adult male abundance (based on empirical data) is equivalent to 0.677 of all fish in population age 26 and older.

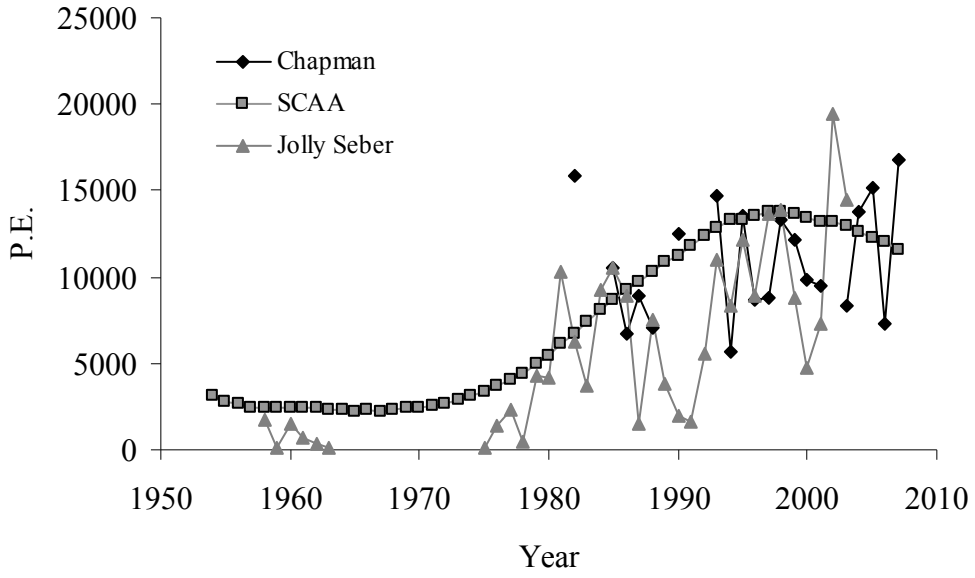

FIGURE 36.—Adult female lake sturgeon population estimates 1954–2007, Winnebago System, Wisconsin. Estimates developed from Chapman closed population, statistical catch at age (SCAA), and Jolly-Seber open population models. SCAA model estimated total abundance; adult male abundance (based on empirical data) is equivalent to 0.323 of all fish in population age 26 and older.

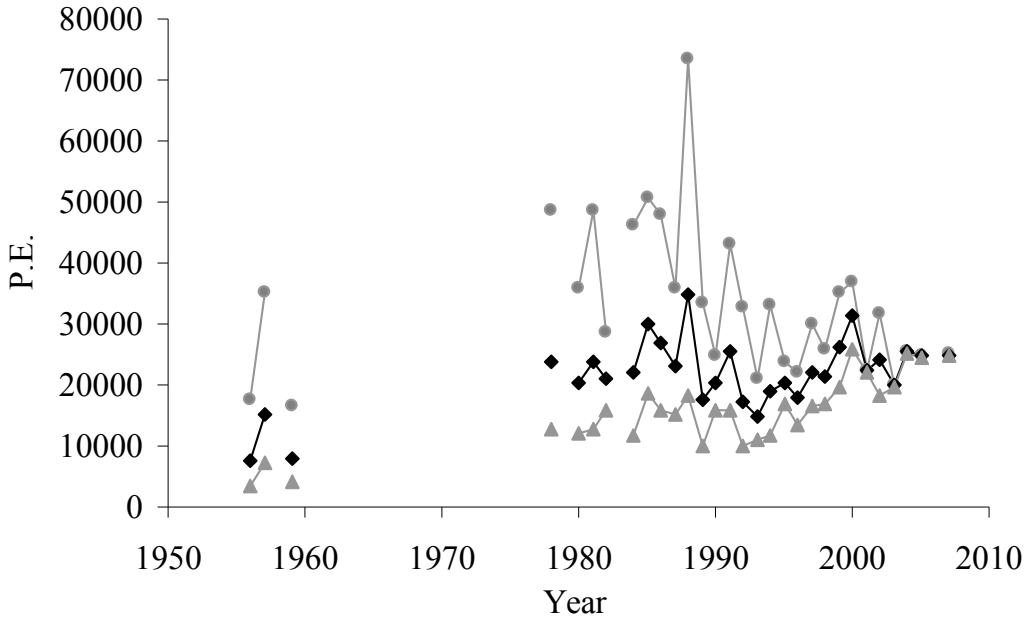

FIGURE 37.—Adult male lake sturgeon population estimates 1954–2007 and upper and lower 95% confidence intervals, Winnebago System, Wisconsin, developed with the Chapman modification of the Peterson estimator.

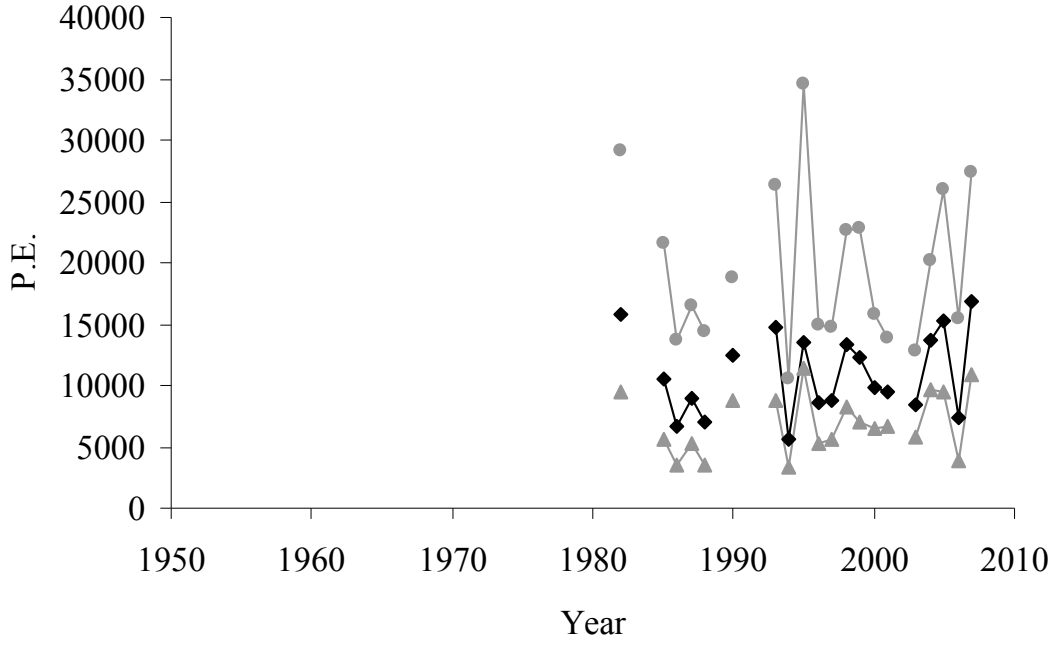

FIGURE 38.— Adult female lake sturgeon population estimates 1982–2007 and upper and lower 95% confidence intervals, Winnebago System, Wisconsin, developed with the Chapman modification of the Peterson estimator.

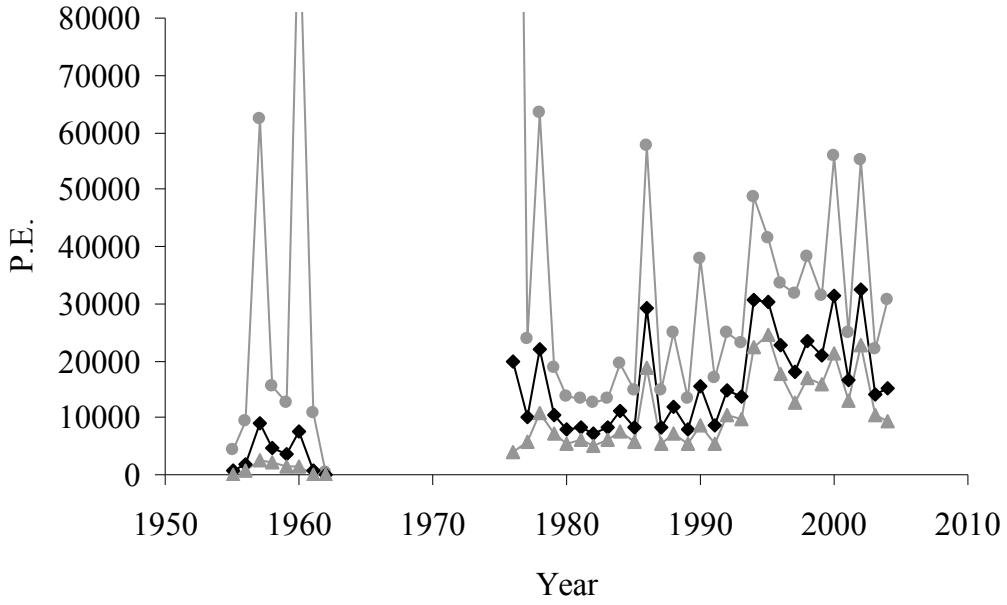

FIGURE 39.— Adult male lake sturgeon population estimates and 95% confidence intervals 1954-2007, Winnebago System, Wisconsin, developed with the Jolly-Seber estimator.

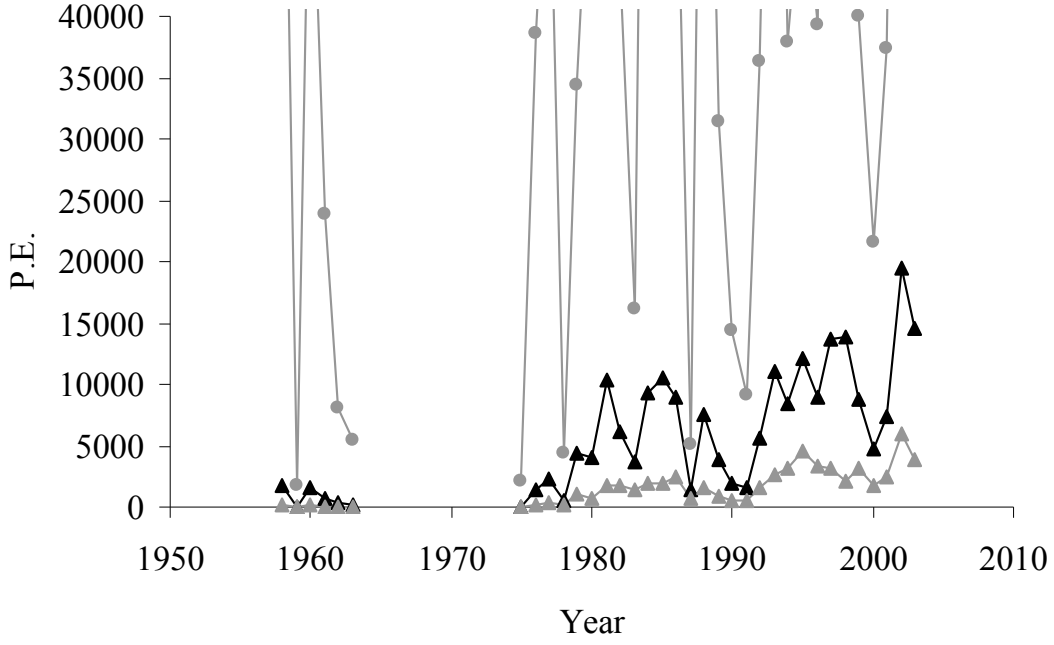

FIGURE 40.— Adult female lake sturgeon population estimates and 95% confidence intervals 1954-2007, Winnebago System, Wisconsin, developed with the Jolly-Seber estimator.

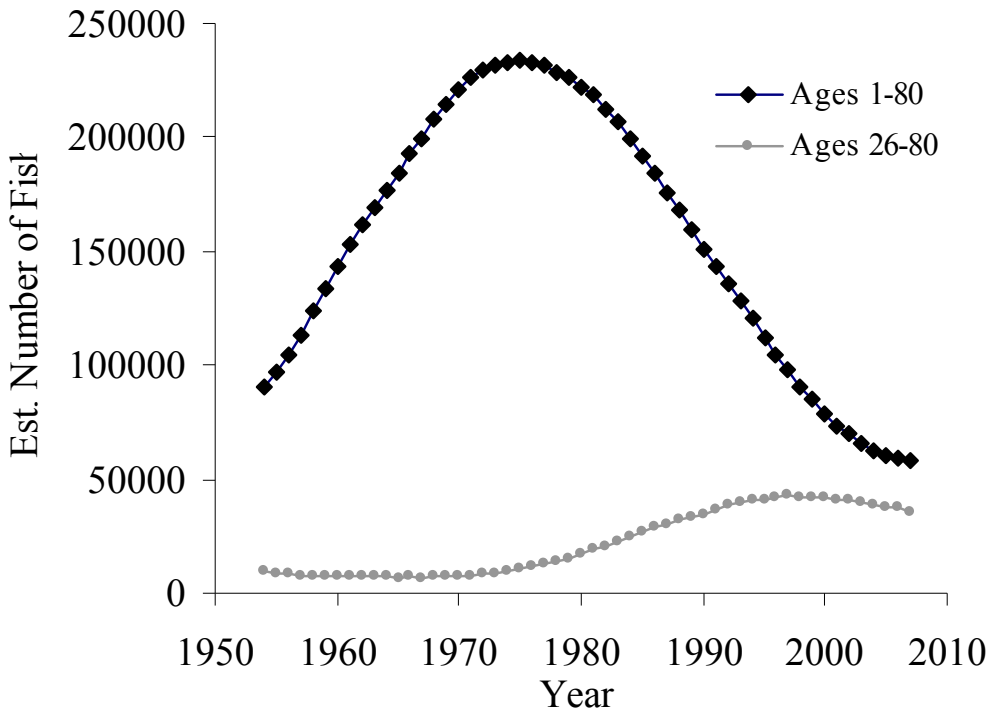

FIGURE 41.—Estimated lake sturgeon population abundance ages 1-80 and ages 26-80, 1954-2007, Winnebago System, Wisconsin. Estimates developed with a statistical catch at age model; M = 0.055.

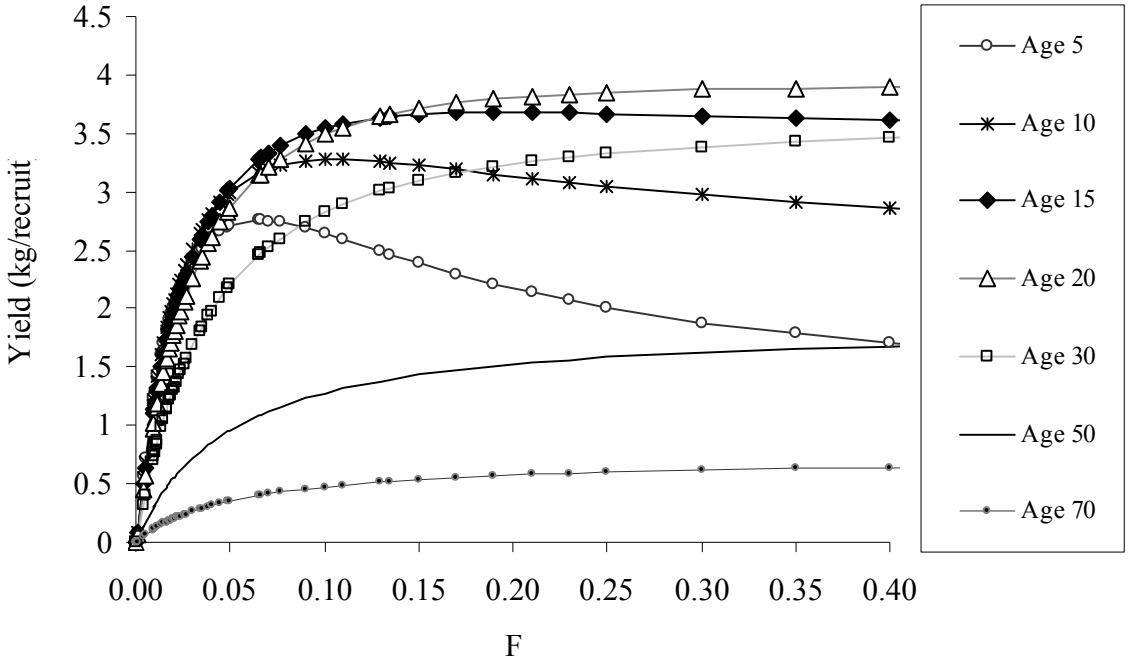

FIGURE 42.—Yield mortality curve, lake sturgeon spear fishery, 1954-2007, Winnebago System, Wisconsin.

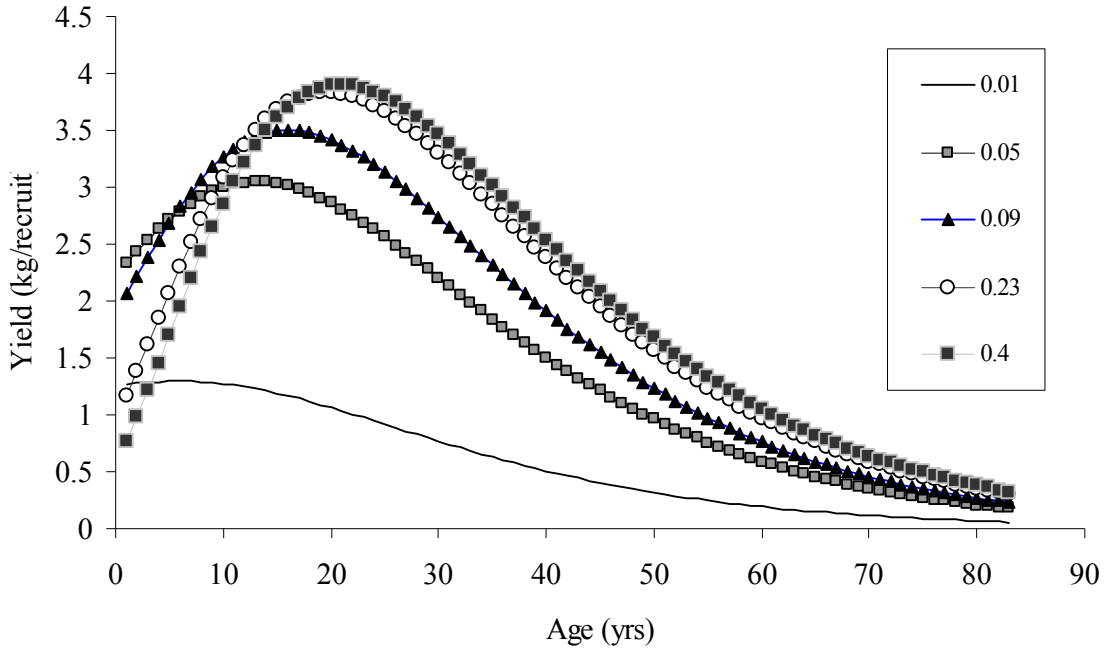

FIGURE 43.—Yield-age curve, lake sturgeon spear fishery 1954-2007, Winnebago System, Wisconsin at F = 0.01, 0.05, 0.09, 0.23, and 0.40. Annual exploitation limit of 4.7% is equivalent to an F of 0.05.

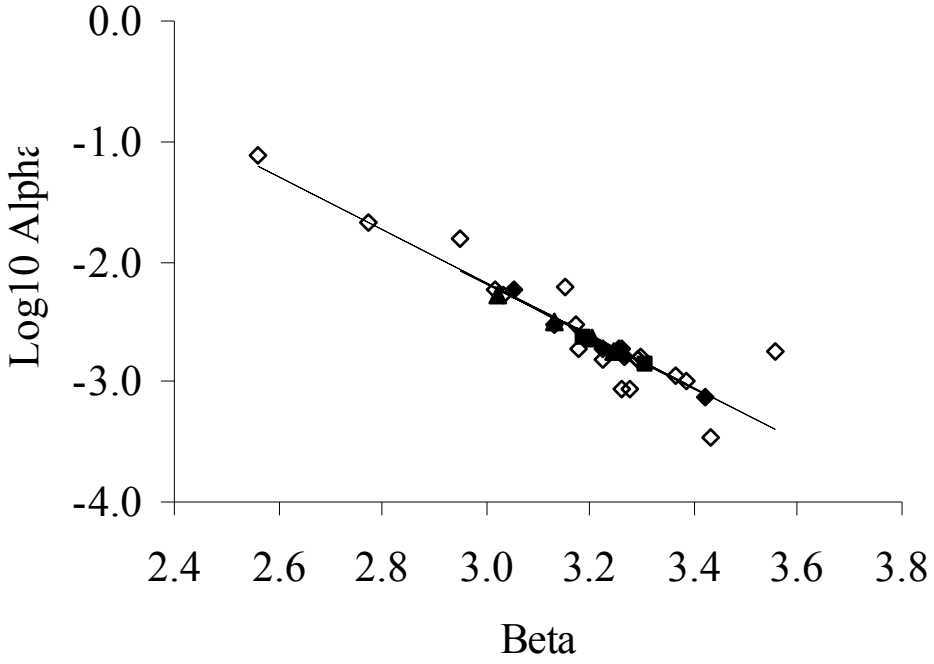

FIGURE 44.—Plot of log10α against β for 32 weight-length relationships of lake sturgeon. Open diamonds (◊) are non-Winnebago System lake sturgeon populations; black squares (■) are Winnebago lake sturgeon (unsexed); black triangles (▲) are Winnebago male lake sturgeon; and black diamonds (♦) are Winnebago female lake sturgeon. Regression line: Log10α = 4.403-2.195*β (r^2 = 0.85; F = 168.6; df = 1,29; P = < 0.001).

MSL 91 cm

Z **II** **XX** **ZZ** **00ZZZ**

90 cm 100 cm 110 cm 120 cm 130 cm 140 cm

Total Length

Z = size of initial recruitment (91 cm)
ZZ= size of 50% selectivity (115 cm)
ZZZ = size of 100% selectivity (138 cm)
II = size of knife-edge recruitment for maximum Y/R (98 cm)
XX = invariant model mean size of maximum yield for males (113 cm)
00 = invariant model mean size of maximum yield for females (137 cm)

FIGURE 45.—Sizes (total length in cm) of 0% (Z), 50% (ZZ), and 100% (ZZZ) selectivity in the winter spear fishery for lake sturgeon 1997-2007, Winnebago System, Wisconsin; size of knife-edge selectivity recommended by Y/R model for maximizing yield under a 4.7% annual exploitation limit (II); and mean size of maximum Y/R estimated from invariant models (Froese and Binohlan 2000) for male (XX) and female (00) lake sturgeon from the Winnebago System. MSL = minimum size limit.

FIGURE 46.—Sub-Adult lake sturgeon harvested illegally, in the set-line fishery, 1940s from the Upriver Lakes, Winnebago System, Wisconsin. Set-lines were legal for sturgeon September through October 1932-1951, with a season bag limit of five fish person and a minimum size limit of 30 inches (76 cm). All fish were required to be tagged with individual carcass tags upon harvest (usually around the caudal peduncle). Note that none of the fish in the photo have carcass tags attached to them. Wisconsin Department of Natural Resources photo.

FIGURE 47.—Wisconsin Conservation Wardens with catch of illegally harvested lake sturgeon taken with snag lines during the spring spawning migration, 1935, from the Wolf River, Winnebago System, Wisconsin.

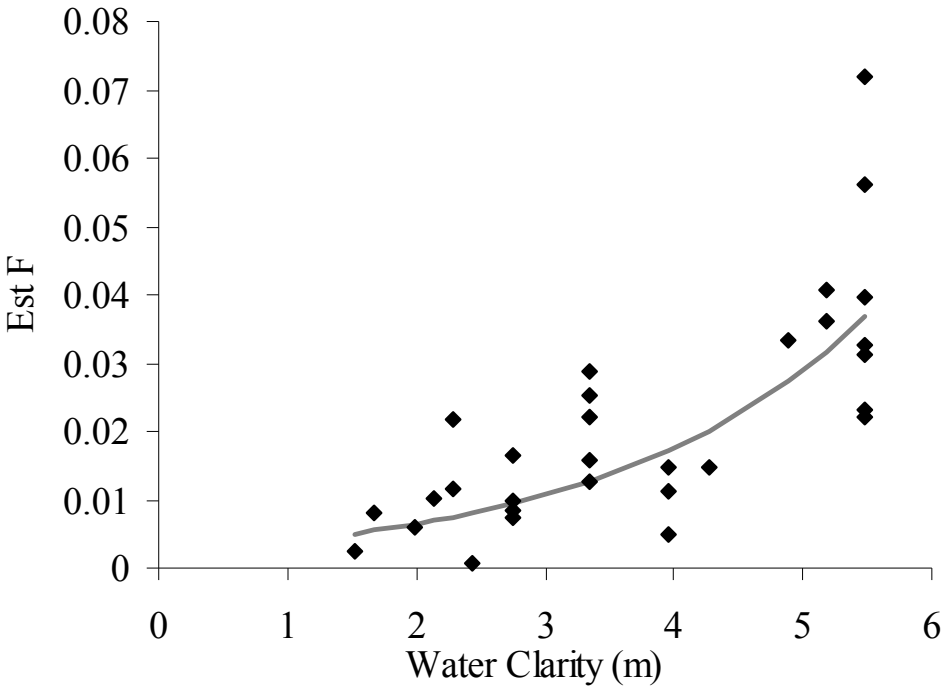

FIGURE 48.—Relationship between estimated instantaneous fishing mortality rates and winter water clarity in the lake sturgeon spear fishery, Lake Winnebago, Wisconsin, 1954-2007. Water clarity measured with a secchi disc at same location on Lake Winnebago each winter. Exponential function $F = 0.0234 * e^{(0.503*WC)} * e^{\varepsilon}$, ($r^2 = 0.50$; F = 28.04; df = 1, 28; P < 0.001). Fishing mortality rates estimated with a statistical catch at age model.

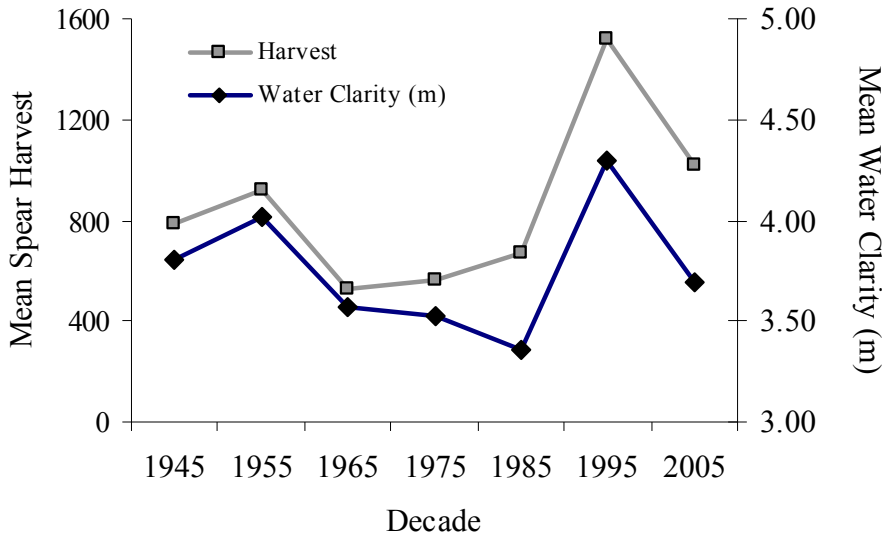

FIGURE 49.—Relationship between mean winter water clarity (m) and mean harvest in the lake sturgeon spear fishery by decade, Lake Winnebago, Wisconsin, 1940s-2000s. Water clarity measured with a secchi disc at same location on Lake Winnebago each winter during the spearing season.

TABLE 5.—Mean length at age, standard deviation, and sample size, male and female lake sturgeon, Winnebago System, Wisconsin, 1953–2007. Ages estimated from pectoral fin spines and corrected for error with model $TrueAge = EstAge^{1.054796}$. Age 0 is at time of hatching. Mean lengths of ages 18, 23, 28, 33, 38, 42, 47, 51, and 56 were derived through interpolation.

Unsexed				Male			Female		
Age	Mean TL (cm)	SD	N	Mean TL (cm)	SD	N	Mean TL (cm)	SD	N
0	1.2	0.03	50						
1	21.6	2.68	79						
2	36.3	5.96	53						
3	51.0	5.25	54						
4	62.0	4.38	78						
5	66.4	4.92	65						
6	73.3	3.95	51						
7	78.1	5.04	56						
8	81.7	6.19	62						
9	84.4	5.22	48						
10	88.4	6.12	43						
11	90.0	4.88	32						
12	94.7	5.22	32						
13	97.8	5.90	22						
14	99.7	6.41	26						
15				106.6	7.33	56	107.5	7.17	48
16				112.5	7.89	104	109.2	7.80	95
17				113.9	9.82	132	113.3	7.35	108
18				114.8			114.6		
19				115.6	9.01	143	115.9	8.58	127
20				119.5	8.64	189	120.0	10.03	151
21				123.3	9.61	261	121.6	10.27	168
22				127.4	9.76	222	125.4	10.03	172
23				127.8			126.6		
24				128.2	9.90	280	127.8	9.89	190
25				130.4	9.61	355	131.5	11.86	250
26				132.9	9.51	293	135.4	11.47	205
27				134.8	9.37	305	139.3	11.75	207
28				135.6			140.7		
29				136.3	8.95	295	142.1	11.26	287
30				138.8	9.54	248	144.4	12.34	216
31				140.6	9.44	257	150.0	10.69	317
32				141.7	8.33	161	150.4	10.50	255
33				143.0			151.8		
34				144.2	9.67	212	153.2	10.90	276
35				144.0	9.13	138	154.8	9.25	220
36				146.8	8.88	94	155.4	9.30	154
37				147.1	10.89	110	158.7	9.26	228

38	148.2			160.1		
39	149.3	9.98	73	161.5	8.95	191
40	150.4	9.44	68	162.0	9.97	157
41	151.2	10.06	58	163.7	9.27	177
42	151.1			164.2		
43	151.1	11.26	42	164.8	11.19	123
44	153.4	9.36	47	167.0	9.10	161
45	152.3	8.57	26	168.1	9.23	106
46	154.2	9.28	21	170.1	8.97	86
47	155.8			171.5		
48	157.4	9.40	13	172.9	7.97	81
49	154.5	12.62	6	172.2	8.46	54
50	152.0	12.85	13	171.8	9.79	40
51	151.0			172.3		
52	150.0	11.63	7	172.7	10.34	25
53	156.2	11.36	5	174.0	11.31	37
54	157.7	5.64	5	176.1	9.11	19
55	163.8	7.73	3	173.1	11.11	13
56	165.1			175.1		
57	166.4		1	177.1	6.45	13
58				181.4	8.23	13
59				174.1	14.11	11
60				174.9		
61				175.8	9.68	10
62	163.8		1	165.1		1
63				180.1	10.25	5
64				183.4		
65	168.3	8.08	2	186.7	10.66	5
66				194.3	8.33	3
67				184.2		1
68						
69	156.2	7.18	2			
70				181.1	12.18	8
71						
72						
73						
74				175.3		1
75						
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93		
94		
95		
96	180.3	1

TABLE 6.—Estimates of growth and maturity parameters for lake sturgeon juveniles age 0-12, males age 13-69 and females age 13-96, Winnebago System, Wisconsin, 1953–2007. Von Bertalanffy growth model; empirical data 1953-2007; invariate models of Pauley (1980), Froese and Binohlan (2000), Taylor (1958); logistic maturity models from present study.

Age Group & Sex	Parameter	vB	Empirical	Pauley (1980)	Froese & Binohlan (2000)	Taylor (1958)	Maturity Model
Juvenile age 0-12	L_∞	98.1					
	K	0.230					
	t_0	-0.070	-0.027				
Male age 13-69	L_{max}		185.4				
	L_∞	166.4		182.6			
	K	0.052			0.029	0.051	
	t_0	-4.527	-0.027				
	T_{max}		69		59.3		
	T_m						14
	$T_{50\%M}$						19
	$T_{100\%M}$						30
	L_m		97.9		93.6		96.5
	$L_{50\%M}$						119.8
	$L_{100\%M}$		139.7				142.2
Female age 13-96	L_{max}		213.4				
	L_∞	188.9		210.2			
	K	0.045			0.020	0.036	
	t_0	-2.485	-0.027				
	T_{max}		96		83.1		
	T_m						21
	$T_{50\%M}$						27
	$T_{100\%M}$						39
	L_m		121.9		121.1		127.0
	$L_{50\%M}$						138.7
	$L_{100\%M}$		157.5				160.0

TABLE 7.—Length at age t-test comparisons of male lake sturgeon age 15-35, Upriver Lakes winter spear harvest, Winnebago System, Wisconsin, 1953–57 vs. 2000–2005. Mean total length at age (cm), standard deviation, t value, critical t value, degrees of freedom, and P values.

Age	1953-1957 Mean TL	SD	2000-2005 Mean TL	SD	t statistic	critical t	df	P
15	107.5	11.2	101.1	8.0	1.52	2.08	21	0.14
16	104.5	7.2	107.1	9.3	-0.99	2.02	38	0.33
17	111.1	8.2	108.3	12.9	0.94	2.00	51	0.35
19	110.7	7.9	105.2	9.8	1.61	2.05	27	0.12
20	116.3	9.4	117.7	9.3	-0.44	2.03	36	0.66
21	127.8	8.7	117.2	12.1	2.38	2.05	29	0.02
22	124.5	3.6	120.7	14.0	0.37	2.06	24	0.71
24	128.9	9.8	121.7	10.8	1.69	2.04	30	0.10
25	128.3	6.7	124.0	11.8	0.70	2.03	37	0.49
26	132.1	11.1	132.1	12.1	-0.01	2.03	35	0.99
27	126.4	7.5	132.8	11.1	-1.89	2.02	43	0.06
29	135.5	8.0	135.8	7.2	-0.12	2.05	28	0.90
30	128.8	11.0	135.2	13.3	-1.43	2.03	42	0.16
31	139.3	5.8	137.5	10.8	0.60	2.03	37	0.55
32	140.8	7.2	142.0	8.8	-0.35	2.06	24	0.73
34	135.6	15.8	142.2	10.0	-1.33	2.06	26	0.19
35	142.7	8.7	143.2	12.6	-0.07	2.13	15	0.94

TABLE 8.—Length at age t-test comparisons of female lake sturgeon age 15-48, Upriver Lakes winter spear harvest, Winnebago System, Wisconsin, 1953–57 vs. 2000–2005. Mean total length at age (cm), standard deviation, t value, critical t value, degrees of freedom, and P values.

Age	1953-1957 Mean TL	SD	2000-2005 Mean TL	SD	t statistic	critical t	df	P
15	104.6	9.2	94.6	0.9	1.47	2.29	10	0.16
16	103.3	5.9	105.8	10.2	-0.94	2.03	34	0.35
17	116.5	12.0	112.1	12.8	0.82	2.06	26	.042
19	117.0	7.4	107.2	11.5	2.81	2.04	32	0.01
20	121.2	7.2	110.5	14.8	2.16	2.09	20	0.04
21	108.0	30.5	115.4	11.5	-0.78	2.07	23	0.45
22	126.2	6.7	119.7	15.4	0.98	2.11	17	0.34
24	120.2	3.9	120.7	14.9	0.85	2.03	35	0.95
25	132.1	7.2	123.0	14.9	0.85	2.03	35	0.40
26	134.0	5.6	120.4	17.8	1.78	2.17	12	0.17
27	129.0	19.8	136.3	14.6	-0.87	2.11	17	0.40
29	137.0	13.5	135.0	15.7	0.33	2.07	23	0.74
30	140.3	11.7	138.6	11.3	0.40	2.05	28	0.69
31	146.9	11.9	143.1	14.7	0.83	2.04	32	0.41
32	136.7	3.3	148.3	12.2	-1.90	2.08	21	0.07
34	149.1	9.0	149.9	13.1	-0.20	2.03	35	0.84
35	147.2	11.0	154.7	12.3	-1.83	2.04	31	0.08
36	154.4	5.9	159.0	8.2	-1.92	2.03	31	0.06
37	155.4	7.0	158.7	7.7	-1.34	2.03	36	0.19
39	157.3	11.5	163.2	8.2	-1.76	2.03	33	0.09
40	159.3	11.0	165.1	6.0	-1.34	2.11	17	0.19
41	158.0	11.0	164.7	13.0	-1.10	2.14	14	0.29
43	160.0	9.8	165.6	5.7	-1.44	2.14	14	0.17
44	166.7	9.2	171.0	6.6	-1.13	2.13	15	0.28
45	167.4	8.5	165.6	10.3	0.51	2.28	10	0.62
46	154.9	11.5	161.9	4.5	-0.77	2.78	4	0.48
48	170.2	0	167.2	3.2	1.24	3.18	3	0.30

TABLE 9.—Mean annual growth increments, male and female lake sturgeon, Winnebago System, Wisconsin, 1953-2007; increments age 0 to 1, through 50 to 54. Unsexed sample used for ages 0-14 assuming no sexual differentiation in growth.

	Male		**Female**	
Age	**Mean Increment**	**SD**	**Mean Increment**	**SD**
1	20.41		20.41	
2	14.66		14.66	
3-5	10.06	5.23	10.06	5.23
6-8	5.10	1.69	5.10	1.69
9-11	2.75	1.21	2.75	1.21
12-14	3.26	1.37	3.26	1.37
15-19	3.17	2.95	3.23	2.80
20-25	2.52	1.95	2.39	1.44
26-30	1.63	0.81	2.86	1.30
31-35	1.57	0.56	2.21	1.98
36-40	1.02	1.12	1.66	0.99
41-45	0.83	1.01	1.10	0.78
46-50	0.22	2.11	1.05	1.03
50-54	0.64	3.41	0.79	0.97

TABLE 10.—Lake sturgeon weight-length Log10 power function regression parameters and characteristics (TL in cm, Wt in kg), Winnebago System, Wisconsin, 1953-2007. Pattern: A = allometric, I = isometric. Model was considered isometric if the 95% confidence intervals of β included the value 3.0. Multiplicative error in all models.

Model	Pattern	r^2	α	β	F	df	P value
General W-L	A	.950	0.00000140	3.3065	951927.0	1, 50013	0
Juvenile ≤71 cm	A	.998	0.00000226	3.1875	85415.4	1, 287	0
Male > 71 cm	A	.887	0.00000180	3.2453	62804.4	1, 7998	0
Mv	I	.904	0.00000538	3.0198	6404.5	1, 680	0
M1	A	.853	0.00000312	3.1301	33032.8	1, 5711	0
M2	A	.827	0.00000236	3.2026	7252.1	1, 1519	0
Female > 71 cm	A	.930	0.00000076	3.4223	122924.1	1, 9292	0
Fv	A	.907	0.00000190	3.2240	15068.9	1, 1550	0
F1	A	.891	0.00000163	3.2662	46453.6	1, 5703	0
F2	A	.782	0.00000184	3.2628	3873.5	1, 1082	0
F4	I	.762	0.00000576	3.0530	1727.3	1, 540	2.26E-170
F6	I	.661	0.00000294	3.1330	718.7	1, 368	1.51E-88

TABLE 11.—Mean relative condition and standards deviations of female and male lake sturgeon the Winnebago System, Wisconsin, winter spear harvests 1952–1954, 1956, 1991, 1996–2007. Within year comparisons: t value, critical t value, degrees of freedom, and P values. Years with significant differences between sexes in mean relative condition are bolded.

Year	Female Mean K_n	SD	Male Mean K_n	SD	t statistic	critical t	df	P
1952	1.10	0.26	1.19	0.29	-1.51	1.98	99	0.13
1954	0.96	0.16	0.97	0.18	-1.13	1.96	485	0.26
1956	1.03	0.11	1.01	0.15	0.37	2.06	25	0.72
1991	**1.07**	**0.17**	**1.00**	**0.15**	**2.68**	**1.97**	**164**	**0.01**
1996	**1.00**	**0.14**	**0.95**	**0.12**	**5.78**	**1.96**	**1197**	**9.3E-09**
1997	**0.92**	**0.10**	**0.90**	**0.09**	**4.89**	**1.96**	**1286**	**1.7E-06**
1998	**0.98**	**0.11**	**0.96**	**0.10**	**3.15**	**1.96**	**2203**	**2.0E-03**
1999	**1.05**	**0.19**	**1.03**	**0.12**	**3.57**	**1.96**	**1481**	**3.7E-04**
2000	**0.99**	**0.14**	**0.97**	**0.12**	**3.23**	**1.96**	**2509**	**1.3E-03**
2001	1.04	0.14	1.03	0.14	1.48	1.96	1588	0.14
2002	**0.96**	**0.12**	**0.94**	**0.11**	**2.33**	**1.96**	**845**	**0.02**
2003	0.99	0.16	0.99	0.18	0.51	1.96	900	0.61
2004	0.95	0.16	0.94	0.15	1.75	1.96	1851	0.08
2005	0.86	0.15	0.86	0.14	-0.31	1.96	1236	0.75
2006	0.99	0.15	0.98	0.19	0.43	1.97	223	0.67
2007	0.96	0.16	0.95	0.16	1.05	1.96	1357	0.29

TABLE 12.—Mean annual yearling lake sturgeon recruits by decade, 1954–2007, Winnebago System, Wisconsin. Based on output from statistical catch at age analysis.

Decade	Mean Yearling Recruits	St. Dev
1954-1959	14892	2039.290
1960-1969	17986	693.186
1970-1979	14190	2713.176
1980-1989	5393	2656.706
1990-1999	762	523.479
2000-2007	1682	958.881

TABLE 13.—Mean instantaneous fishing mortality and exploitation rates by decade and minimum size limit, lake sturgeon spear fishery, Winnebago System, Wisconsin, 1954–2007; estimated from statistical catch at age (SCAA) model and empirical tag return data. Standard deviations for each mean in parenthesis in italics.

Year	Mini -mum Size Limit (cm)	SCAA F	Empir -ical Total F	Empir -ical F Adult ♂	Empir -ical F Adult ♀	SCAA u	Empir -ical Total u	Empir -ical u Adult ♂	Empir -ical u Adult ♀
1954	76.2	0.100				10.35%			
1955-	101.6	0.049				5.13%			
1964		*(0.036)*				*(0.037)*			
1965-	101.6	0.023				2.40%			
1973		*(0.021)*				*(0.022)*			
1974-	114.3	0.019	0.016	0.015	0.024	1.99%	1.50%	1.41%	2.32%
1984		*(0.006)*	*(0.016)*	*(0.015)*	*(0.022)*	*(0.006)*	*(0.015)*	*(0.015)*	*(0.021)*
1985-	114.3	0.019	0.029	0.027	0.042	1.98%	2.78%	2.52%	4.02%
1996		*(0.010)*	*(0.026)*	*(0.027)*	*(0.026)*	*(0.010)*	*(0.025)*	*(0.026)*	*(0.025)*
1997-	91.4	0.022	0.029	0.027	0.038	2.39%	2.70%	2.53%	3.58%
2007		*(0.010)*	*(0.013)*	*(0.013)*	*(0.017)*	*(0.010)*	*(0.012)*	*(0.013)*	*(0.017)*

TABLE 14.—Estimated intrinsic (r) and discrete (λ) rates of increase of adult male and female lake sturgeon, Winnebago System, Wisconsin 1954–2007.

	Adult Male r	Adult Male λ	Adult Female r	Adult Female λ	Combined Adult r	Combined Adult λ
Chapman	0.138	1.148	0.016	1.016	0.138	1.148
Jolly Seber	0.089	1.093	0.086	1.090	0.089	1.093
SCAA	0.049	1.050	0.049	1.050	0.049	1.050

TABLE 15.—Chronology of management policies and actions, regulations, significant known environmental changes, and public involvement affecting lake sturgeon on the Winnebago System, Wisconsin 1874–2008.

Year(s)	Sturgeon management actions, harvests, regulations and laws, significant environmental events, and public involvement on the Winnebago System.
1874	Wisconsin Fisheries Commission created by state legislature to survey the status of declining fisheries in the state.
1878	Spearing fish outlawed statewide on inland waters, except for mullet, suckers, bill fish, and dog fish.
1881	A. Cooley of Ripon becomes Wisconsin's second fish warden, patrolling Fond du Lac and Green Lake Counties.
1887	Spearing made legal on Lake Winnebago for sturgeon only.
1897	Ice shanties outlawed statewide; set lines outlawed statewide on inland waters.
1899	Lake Winnebago granted an exemption to ice shanty prohibition; setlines legal for sturgeon in Lakes Winnebago, Butte des Morts, Winneconne, and Poygan, and the Fox River; required set-line license (for $1.00) and a metal tag for each 100 yards of setline (25¢ per tag).
1903	March 1 to May 25 closed season on sturgeon in the Winnebago System.
1905	Sturgeon classified as a gamefish; 8 lb (3.6 kg) minimum size limit statewide on lake sturgeon.
1913	May 14 to April 31 open season, 20 lb (9.1 kg) round weight minimum size limit.
1915	All sturgeon harvest in state is banned.
1932	First regulated spearing season on Lake Winnebago, January 1-March 1, 30 " (76.2 cm) minimum size limit, 5 bag limit per person per season, tags $.05 each, fishing license required.
1932	Set line fishery opened on the Upriver Lakes, September 5 to October 31, 30" (76.2 cm) size limit, 5 bag limit per person per season (spear and set line fisheries combined), tags $.05 each, set line license required.
1935	Wolf River hook and line season opened (Waupaca and Winnebago Counties), September 5 to October 31, no minimum size limit, 5 bag limit per person per season (spear, set line and hook & line combined), tags $.05 each, fishing license required.
1937	Wolf River hook and line season expanded to include Shawano County. Final increase in head of Lake Winnebago Pool lakes (6 inches) to bring overall increase since initial impoundment in the 1850s to 3 feet.
1939	Hook and line season on Wolf River shortened by two weeks, September 5 to October 15.

1940	Hook and line 30" (76.2 cm) minimum size limit initiated, and bag limit modified to allow only 1 fish per day. (maintaining 5 per season limit).
1941	Hook and line season closed on Wolf River.
1941	Lake Winnebago spearing season reduced to one month, February 1 through March 1.
1941	First assessment conducted on the sturgeon spearing harvest by Wisconsin Conservation Department Fisheries Biologists Edward "Doc" Schneberger and Lowell Woodbury.
1944	Hook and Line season reopened on Wolf River but in Winnebago County only.
1946	Hook and line season opened on all portions of Wolf River (now including Outagamie County), retaining previous season length of September 5 to October 15, 30" (76.2 cm) size limit, bag limit of 5 per season, and $.05 tags.
1949-1953	Wisconsin Conservation Department Fisheries Biologists Tom Wirth, Robert Probst, Edwin Cooper, and Vern Hacker conduct first comprehensive biological assessment on the Winnebago lake sturgeon population.
1940s	Average annual sturgeon spear harvest through the 1940's: 691.
1950	Hook and line, and spearing sturgeon tag fees increased to $1.00 each.
1952	Set line season on Upriver Lakes eliminated.
1952	"Experimental" spearing season conducted on the Upriver Lakes, 16 days February 15 through March 1, 30" (76.2 cm) minimum size limit, seasonal bag limit of three, (Lake Winnebago retained the Feb 1 -March 1 season and the bag limit of 5).
1953	Hook and line seasonal bag limit on Wolf River reduced to 3.
1953	Upriver Lakes spearing season reduced to 14 days .
1953	Record sturgeon harvested on Lake Winnebago: 180 pound, 79" fish speared by Elroy Schroeder of Appleton.
1953	Record sturgeon harvest (Winnebago and Upriver lakes combined) of 2828 fish taken during seasons of 29 days on Lake Winnebago and 14 days on the Upriver Lakes.
1953	First serious concern about overharvest of the sturgeon population since harvest ban enacted in 1915.
1954	Spearing seasonal bag limit on Lake Winnebago reduced to 3.
1954	First biological assessment conducted on the sturgeon spawning stock by WCD Fisheries Biologists Tom Wirth, Gordon Priegel and Clarence Cline (conducted annually until 1964).
1955	Minimum size limit for spear fishery (Lake Winnebago and Upriver Lakes) increased from 30" (76.2 cm) to 40" (101.6 cm).
1955	First year of mandatory registration of all sturgeon harvested in spear fishery (Lake Winnebago and Upriver Lakes); fish must be registered on same day speared by 6:00 pm.

1956	Spearing, and hook and line seasonal bag limit reduced to 2 fish.
1956	Upriver Lakes spearing season reduced to 9 days.
1956	Lake Winnebago spearing season reduced to 2nd Saturday in February through March 1.
1957	Spearing seasonal bag limit on the Upriver Lakes reduced to 1 fish (2 fish limit retained on Lake Winnebago).
1957	Upriver Lakes season length reduced to 5 days.
1958	Spearing seasonal bag limit on Lake Winnebago reduced to 1 fish .
1958	Spear fishery closed on Upriver Lakes.
1959	Upriver Lakes spearing season reopened for one year for three days (On both Lake Winnebago and the Upriver Lakes at this point there was a 40" (101.6 cm) minimum size limit and a seasonal bag limit of 1).
1959	Hook and Line season on the Wolf River closed.
1955-1959	First estimates of the number of "legal sized" sturgeon in the Winnebago System developed. Average abundance 1955-59, of legal sized sturgeon in the Winnebago population estimated to be 11,320.
1950s	Average annual sturgeon spear harvest through the 1950's: 1225.
1960s	Beginning of a three decade period of persistent cloudy water in Lake Winnebago in most winters during the spearing season causing harvest rates to drastically decline from the rates experienced in the 1950's. (Cloudy water due to impact of accelerated run-off of non-point pollution and other changes occurring in the Winnebago Pool lakes).
1960	Separate sturgeon spearing license is required at a cost of $2.50; only persons age 14 and over could buy a spearing license, and persons age 16 and over were also required to possess a fishing license; a license could be purchased before, or at anytime during the spearing season.
1962	Upriver Lakes new spearing season format implemented: 2 day season once every three years.
1968	All transported sturgeon must be "openly exposed", i.e. they must be visible in the transporting vehicle, to a person in a passing vehicle.
1969	Winnebago spear fishery produces new record low harvest of 8 sturgeon over a 22 day season.
1960s	Average annual sturgeon spear harvest through the 1960's: 590.
1971	Upriver Lakes spearing season format reconfigured again to a 2 day season once every five years (Upriver Lakes population of lake sturgeon considered at this time to be distinct from the population in Lake Winnebago).
1973	Winnebago spear fishery ties the record for low harvest of 8 sturgeon over a 27 day season.

1974	Minimum size limit increased from 40" (101.6 cm) to 45" (114.3 cm) in another attempt to protect sturgeon from harvest until after they are big enough to spawn.
Mid 1970s	Spearers demand action by Wisconsin Department of Natural Resources to "restore" sturgeon stock in Lake Winnebago. Agency biologists disagree that the sturgeon stock is depleted but have no recent data to substantiate their opinions.
1975	Dan Folz appointed by the Wisconsin DNR as Oshkosh Area Fisheries Supervisor and re-establishes annual assessments of spawning stock on the Wolf and upper Fox Rivers and spear harvest assessments on Lake Winnebago and the Upriver Lakes. (No assessments had been conducted during 1964 to 1974 except for total annual sturgeon harvest from mandatory registration.) Assessment work initiated in 1975 lays the foundation for future sturgeon management program.
1977	The "Main Chapter" of Sturgeon for Tomorrow formed by local sturgeon spearers Bill Casper, Dan Groeschel, Bob Blanck, Vic Schneider and Lloyd Lemke, based out of Malone, WI, as a private sturgeon conservation organization to provide financial and political support for sturgeon management, artificial reproduction and other activities.
1977	"Sturgeon Patrol" initiated in the spring using volunteers (citizens, students, DNR staff, etc) to guard sturgeon spawning sites on the Wolf River 24 hours a day during the spawning period; funded by Sturgeon for Tomorrow.
1979	First successful efforts to collect lake sturgeon eggs and propagate young sturgeon in North America conducted on the Wolf River, the DNR Wild Rose Fish Hatchery and at the University of Wisconsin-Milwaukee Center for Great Lakes Studies by Don Czeskleba (WI DNR) and Fred Binkowski (UW-Milwaukee).
1970s	Significant increase in sturgeon spawning sites due to increased riprapping activity on the Wolf River by property owners attempting to protect their eroding shorelines from the wakes of increasing motorboat traffic on the river.
1970s	Average annual sturgeon spear harvest through the 1970's: 596.
1975-1979	Average abundance of "legal sized" portion of the Winnebago sturgeon population estimated to be 20,900 fish.
1980	Spearing license fee increased to $5.50; license has to be purchased prior to season.
1980	"Southwest Chapter" of Sturgeon for Tomorrow formed by Fritz Wendt, Lee Patt, Glenn Ninneman, Mike Schrage, Mike Wendt and Jerry Dombraski, based out of Fond du Lac, WI.
1982	New record spear harvest of 2238 fish; largest harvest since the 1950's – first crystal clear water spearing season since the 1950s.
1982	"Northern Half Chapter" of Sturgeon for Tomorrow formed by Wayne Hoelzel, Bob Schroeder, Louie Hemauer, Tom Burr, Darlene and Bob Holmann, Donny Peterson, Steve Karow, Arnie Landsverk and Don Mielke, based out of Appleton, WI.
1983	Spearing license fee increased to $7.10. Largest year class for freshwater drum ever recorded [*in 2008 the 1982 hatch of drum remains the most dominant year class in the Winnebago System drum population*].

1981-1983	Average abundance of "legal sized" portion of the Winnebago sturgeon population estimated to be 31,133 fish.
1985	$1,500 minimum fine established for possession of illegal sturgeon.
1986	Sturgeon registration hours extended to 7:00 pm during the spearing season.
1986	In response to loss of habitat, poor water quality, and other fish and wildlife resource issues on the Winnebago System, the Department of Natural Resources initiates project to develop and implement long term plan for comprehensive management and balanced use of Winnebago fish, wildlife and water resources. Ron Bruch is appointed as the Winnebago System Biologist to facilitate development and implementation of this plan.
1988	"West Central Chapter" of Sturgeon for Tomorrow formed by Dick and Pat Braasch, Jim Jensen, Donny Payne, Ron Harrison, Ron Jungwirth, Jim Gibson, Bruce Schoenberger, and Bill McAloon, based out of Oshkosh, WI.
1988	Fish migration barrier is installed at Rapid Croche dam on the lower Fox River and the locks at the dam are closed and sealed to protect Winnebago fish populations from sea lamprey (and other exotic species) threatening invasion from Green Bay.
1989	"Winnebago Comprehensive Management Plan" is completed and implemented. Implementation of sweeping actions begins immediately addressing habitat and water quality issues in the Winnebago Pool Lakes to improve Winnebago water quality and clarity. Plan addresses wide range of fish and wildlife resource use issues, recommends a fishway be constructed at the Eureka Dam on the upper Fox River to allow sturgeon, walleye and other species access to upstream traditional spawning and nursery grounds, and recommends continuing protection and development of sturgeon spawning sites on the Wolf and upper Fox Rivers.
1989	Eureka Fishway is constructed at the Eureka Dam on the upper Fox River.
1980s	Riprapping projects on Wolf and upper Fox Rivers expands number of sturgeon spawning sites from approximately 20 sites to 50 sites by the end of the decade.
1980s	Average annual sturgeon spear harvest through the 1980's: 679.
Late 1980s	Gizzard shad population explodes in the Winnebago System. [Gizzard shad, an excellent forage fish, had been found in Winnebago System waters for decades but warm winters in the late 1980's are suspected to have allowed shad numbers to increase exponentially between 1988-1990. Shad experience a winter die off in Lake Winnebago and concentrate in the southern part of Lake Winnebago as well as in the Upriver Lakes. Sturgeon readily adapted to utilizing dead and dying shad as a forage item with many sturgeon sampled in the spear harvest found to have 2 gallons or more of shad in their foreguts.]
1990	New record spear harvest of 2908 sturgeon during a 20 day season raises serious concerns about overharvest of the stock.
1990	Ron Bruch appointed to fill the Oshkosh Area Fisheries Supervisor position following the retirement of Dan Folz. Art Techlow hired as new Winnebago System Biologist to replace Bruch and continue driving implementation of the Winnebago Comprehensive Management Plan.

1990	Lake sturgeon utilize the newly constructed fishway at Eureka dam on the upper Fox River for upstream migration to historic spawning sites and as a new spawning site.
1991	Expanded harvest and population assessments are initiated on Lake Winnebago, the Upriver Lakes and the Wolf and upper Fox Rivers. Harvested fish are checked for sex and maturity in addition to traditional length and weight measurements. New harvest assessment data estimate adult females were harvested in 1990 at a rate of 9.6% - twice the recommended level of 5%.
1990	Adult female sturgeon comprise 46% of all harvested fish. High minimum size limit of 45" enacted in 1974 suspected cause of the high proportion of adult female sturgeon in the harvest. Harvest data also show the proportion of sturgeon > 100 lbs (all adult females) in the harvest is significantly lower (5x) than the proportion observed in annual harvests from 1950-1985.
1992	Sturgeon spearing license fee increased to $10.00.
1992	Winnebago Citizens Sturgeon Advisory Committee, comprised of representatives of 30 sturgeon spearing and conservation organizations from the Winnebago region, established to work with DNR fisheries and law enforcement staff in the development and implementation of regulations and management actions.
1992-1993	Construction of "Eureka Rapids" at the Eureka Dam on the upper Fox River. Project led by Walleyes for Tomorrow with substantial financial support from Sturgeon for Tomorrow provides in-river spawning and nursery habitat for sturgeon, walleye and a wide range of other fish species.
1993	Angling through a sturgeon spearing ice hole prohibited (due to serious illegal hooking problems during the 1992 spearing season).
1990-1994	Average annual abundance of adult female sturgeon in the Winnebago stock estimated to be 10523 fish. Average abundance of adult males estimated to be 25288.
1995	New record season harvest total of 3173 sturgeon registered in a 19 day season. Serious concerns about overharvest of adult females prompts discussions between biologists and spearers about major changes in Winnebago sturgeon spearing regulations.
1996	Emergency rule reduces Lake Winnebago spearing season to nine days with the possibility of extension if the average water clarity on the 3rd day of the season is less than 10 feet (Average water clarity was >12 ft, therefore the season ran only nine days).
By 1997	Clear water in Lake Winnebago in the winter is becoming more common as opposed to a once a decade phenomena resulting in significant increases in spear harvest success and increases in spearing effort. (Thought to be due, at least in part, to sweeping non-point and point pollution controls implemented following the completion of the Winnebago Comprehensive Management Plan.)
1997	Series of new rules went into effect as the 1st phase of developing a new Safe Harvest Management System for Winnebago sturgeon: • The Lake Winnebago spearing season length is reduced to 16 days, beginning the second Saturday in February (no change in the Upriver Lakes season format);

	• The minimum size limit is reduced from 45" to 36" (91.4 cm); • Successful spearers are required to accompany their fish to a registration station, and to stay within a specific road boundary around the lake until their fish is registered; • The covering of large ice holes (spearing holes) with shanties is prohibited during periods other than 48 hours before and continuing through the open spearing season; • Hours of sturgeon spear harvest registration are reduced by one hour to close at 6:00 pm.
1998	2051 fish harvested through a 12 day season. Season was cut short after ice went out early on Lake Winnebago on February 26.
1998	Sturgeon for Tomorrow and Otter Street Fishing Club purchase and donate to DNR Fisheries, Oshkosh, state of the art $30,000 electrofishing boat to assist with sturgeon population assessments on the Winnebago System.
1998	First zebra mussels (exotic mussel originally from the Caspian Sea) found in Winnebago System waters on a buoy marking one of the outlet channels from Lake Winnebago at Neenah-Menasha.
1999	Harvest cap system instituted via emergency rule to manage the Winnebago System sturgeon spear harvest. Under the rule, the season is closed 24 hours after reaching 80% of the total allowable annual harvest of adult females, juvenile females or males. Cap levels set at 400 for adult females, 400 for juvenile females and 2150 for males.
1999	Lake Winnebago spearing season under new harvest cap rule lasts just three days and produces a sturgeon harvest of 1484 fish.
1999	"Night spearing" with lights starting at midnight gains popularity with spearers attempting to maximize their spearing time in the "race horse" harvest cap fishery.
1990s	Average annual sturgeon spear harvest through the 1990's: 1583.
2000	Harvest cap system instituted via permanent rule to manage the Winnebago System sturgeon spear harvest. Under the rule, the season is closed 24 hours after reaching 80% of the total allowable annual harvest of adult females, juvenile females or males. Cap levels set at 400 for adult females, 400 for juvenile females and 2150 for males.
2000	Two day spearing season on Upriver Lakes produces 2169 sturgeon – a new record for the Upriver Lakes fishery and the first time since the 1950's the Upriver Lakes harvest resulted in overharvest problems.
2000	Spearing season on Lake Winnebago lasted just two days and produced a harvest of 347 fish.
2001	Another two day season (due to the harvest cap controls) results in harvest of 1590 sturgeon. Cap levels set at 400 for adult females, 400 for juvenile females and 2150 for males.
2002	Emergency rule passed reducing sturgeon spearing hours to 6:30 am to 12:30 pm. Spearers had until 1:30 pm to register their fish the same day it was speared. Cap levels set at 400 for adult females, 400 for juvenile females and 1300 for males.

2002	Permanent rule changes approved for the 2002 season: • No night spearing- "unlawful to use any artificial lights as an aid in sturgeon spearing"; • Hole or holes size per shanty are limited to no more than 48 square feet – spearers are allowed to have more than one hole per shanty or shelter no matter how big the shelter is, but the total area of all the holes in that one shelter can not exceed 48 square feet.
2002	Shortened spearing day, along with poor ice conditions and only fair water clarity, resulted in a full 16 day season and a total harvest of 847 fish.
2002	"Upper Fox River Sturgeon Rehabilitation Project" launched by Wisconsin DNR, University of Wisconsin-Milwaukee Great lakes WATER Institute and Sturgeon for Tomorrow – a 25 year project with the goal of increasing the productivity of the sturgeon spawning run in the upper Fox River through habitat improvement, stocking and sturgeon migration studies.
2002	Zebra mussel population peaks in Lake Winnebago Pool Lakes. Lake fly (Chironomid) hatches much diminished in Lake Winnebago.
2003	Permanent rule passed reducing sturgeon spearing hours to 6:30 am to 12:30 pm. Spearers had until 1:30 pm to register their fish the same day it was speared. Cap levels set at 400 for adult females, 400 for juvenile females and 1300 for males.
2003	The Winnebago Citizens Sturgeon Advisory Committee worked with Senator Carol Roessler (Oshkosh) and Representative Dean Kaufert (Neenah) to pass new state statutes which: • Required spearers to buy their sturgeon spearing license by October 31 in order to participate in the following February's Winnebago sturgeon spearing season. An exception was included for Wisconsin residents who turned 14 between November 1 and the last day of the following spearing season, and for Wisconsin residents serving in the Armed Forces and home on leave during the following spearing season; • Increased the sturgeon spearing license fee from $10 to $20 for Wisconsin residents and to $50 for non-residents; • Removed the sturgeon spearing tag from the Conservation Patron license; • Eliminated the requirement that a spearer first purchase a fishing license before they were allowed to purchase a sturgeon spearing license; • Required that all the sturgeon spearing license revenues be used only to fund the Winnebago Sturgeon Management Program.
By 2004	Estimated exploitation rates of adult female sturgeon in the Winnebago system reduced and sustained at annual levels close to recommended 5% from high levels experienced in early to mid 1990's.
By 2004	Proportion of sturgeon > 100 lbs in the harvest increasing - close to historic levels seen prior to 1985.
2004	First year that the Conservation Patron tag did not include a sturgeon spearing tag. 8798 resident and 114 non-resident sturgeon spearing licenses sold for the 2004 season.
2004	Harvest caps increased to 425 for adult females and 425 for juvenile females, and maintained at 1300 for males.

2004	High concentrations of sturgeon in the south end of Lake Winnebago draw large numbers of spearers resulting in an extremely high harvest rate, a short two day season and a total harvest of 1854 fish. 89% of the harvest is taken from the southern 14% of the lake area. The highest one-day harvest of sturgeon ever – 1,303 on opening day. The shortest season ever, lasting just 12 hours (6 hours each day).
2004	Largest fish ever registered in the history of the 73 years of sturgeon spear fishing on Lake Winnebago: 188 pounds, 79.5 inches in total length, registered by David Piechowski of Redgranite.
2004	Winnebago Citizens Sturgeon Advisory Committee, DNR staff and the general public, out of concern over short 2004 season and potential for overharvest in future seasons, initiate discussions on harvest and effort management alternatives to maintain acceptable harvests, maintain the open fishery, while at the same time significantly extending the length of the spearing season.
2004	Zebra mussel population found to be significantly reduced from levels observed in 2003. Sturgeon (as well as drum, carp, perch and other species found to be feeding on zebra mussels). Few lake fly larvae found in sturgeon stomachs during the spearing season. Poor to no lake fly hatch observed in May although small but significant hatch observed in August. Sturgeon sampled in August – October found to be foraging heavily on lake fly larvae.
2005	Permanent rule implemented limiting the 2005 Upriver Lakes spearing season to one day (6:30 am to 12:30 pm) in an effort to avoid overharvest as was experienced there in the 2000 season. Harvest cap levels increased to 500 for adult females, 500 for juvenile females and 2000 for males.
2005	Emergency rule passed giving the Department of Natural Resources the authority to close the spearing season at the end of a spearing day if 100% of one of the three harvest caps (adult females, juvenile females, males) is exceeded that day. Former permanent harvest cap trigger still remains in force – season would close 24 hours after harvest total reaches 80-99% of any one of the three caps by the end of a fishing day.
2005	Spearers are required to purchase either a spearing license for Lake Winnebago or the Upriver Lakes. For the first time spearers are not be able to fish both water bodies in the same season. A total of 10,634 sturgeon spearing licenses sold for the 2005 season – 6465 for Lake Winnebago, and 4169 for the Upriver Lakes.
2005	Legislature increases out of state sturgeon spearing license from $50 to $65.
2006	"Fast Start" Season 100% Closure Trigger implemented. Beginning in 2006, the Winnebago sturgeon spearing season would be closed at the end of the spearing day in which 100% of any one of the three harvest caps (juvenile females, adult females, males) is reached or exceeded that day. "Slow Finish" Season 90% Closure Trigger implemented. Beginning in 2006, the general season 24 hour closure trigger was changed to 90% (an increase from the previous trigger of 80%). Harvest cap levels maintained at 500 for adult females, 500 for juvenile females and 2000 for males.
2007	Upriver Lakes Lottery fishery implemented. An annual lottery sturgeon spear fishery to be held annually on the Upriver Lakes beginning in 2007. Spearers required to apply for an Upriver Lakes sturgeon lottery tag by August 1 and notified by October 1 if they were successful in receiving authorization to

	purchase an Upriver Lakes sturgeon spearing tag. Group lottery applications of up to four persons accepted. Sales for both Lake Winnebago and Upriver Lakes sturgeon spearing licenses end October 31. The Upriver Lakes sturgeon lottery fishery limited participation to 500 tags in 2007 (numbers of tags in future seasons may vary) and received an allocation of the overall Winnebago System sturgeon harvest cap of 20% of the juvenile females, 10% of the adult females, and 20% of the males.
2007	Harvest cap levels increased to 556 for adult females, 556 for juvenile females, and decreased to 1000 for males.
2008	Harvest cap levels maintained at 556 for adult females, 556 for juvenile females, and 1000 for males.
2008	IMAX film *Mysteries of the Great Lakes* (Science North production, Sudbury, Ontario, Canada) featuring the Winnebago System lake sturgeon population and the DNR Upper Fox-Wolf Fisheries Work Unit staff debuts in theatres in US and Canada.
2008	Upper Lakes Chapter of Sturgeon for Tomorrow founded by Matt Woods, John Buttke, Sally Gilson, Dana Woods, Todd Gilson, Dave Lamers, Brian Loker, Craig Reinert, Pauline Reinert, and Mike Will.
2009	Harvest caps are modified to reflect new population estimates developed through Statistical Catch at Age modeling: 630 for adult females, 350 for juvenile females, and 1000 for males.

TABLE 16.—Mean fecundity (number of eggs), number of fish examined, mean weight, and mean number of eggs per kg for lake sturgeon, North America.

Study	Origin	Estimated Mean Fecundity	Number of Fish examined	Mean Fish Weight (kg)	Mean Number of Eggs per kg of Fish
Cuerrier (1949)	Lake St. Peter, Ontario, Canada	295573	9	23.9	12264
Dubreuil and Cuerrier (1950)	Ottawa River, Canada	118205	4	9.0	11467
Harkness and Dymond (1961), and von Bayer (1910)*	Lake Erie	583661	3	65.6	8744
Sandilands (1987)	Kenogami River, Ontario, Canada	120998	2	13.3	8797
Present Study (2008)	Lake Winnebago System, Wisconsin, USA	445703	48	33.68	12767

* Harkness and Dymond used von Bayer's reporting of lake sturgeon egg diameter of 2.6 mm to volumetrically estimate the number of eggs in three Lake Erie fish whose roe was processed for caviar.

TABLE 17.—Ranked form factors for lake sturgeon populations, US and Canada, along with reference, water, sampling season and sample type (unsexed, sexed, maturity staged). Lower form factor denotes skinny or thin body shape fish; higher form factor denotes fatter or heavier body shape fish (Froese 2006), Sex and maturity stage in Sample Type column after Bruch et al. (2001).

Reference	Water	Sampling Season	Sample Type	Form Factor	Body Shape
Dumont, et al 1987	upper St. Lawrence R, Quebec	spring, summer, fall	Unsexed	0.003024	skinny
Ecologistics Ltd 1987	Kenogami River, Ontario	spring, summer, fall	Unsexed	0.003213	
Sandilands 1987	Kenogami River, Ontario	spring, summer, fall	Unsexed	0.003504	
Dumont, et al 1987	lower St. Lawrence R, Quebec		Unsexed	0.004655	
Threader and Brousseau 1986	Moose R, Ontario	summer, fall	Unsexed	0.004839	
Present Study	Winnebago System	winter	F6	0.005749	
Present Study	Winnebago System	all seasons	Unsexed Juveniles	0.005825	
Present Study	Winnebago System	winter	Fv	0.005894	
Present Study	Winnebago System	winter	Mv	0.005946	
Present Study	Winnebago System	winter	M1	0.006022	
Adams et al. 2006	Rainy Lake, Ontario	spring, summer, fall	Unsexed	0.006059	
Priegel 1973	Menominee River, WI	summer	Unsexed	0.006203	
Present Study	Winnebago System	all seasons	Male >71 cm	0.006208	
Present Study	Winnebago System	winter	F1	0.006258	
Present Study	Winnebago System	all seasons	Female >71 cm	0.006423	
Present Study	Winnebago System	winter	M2	0.006570	
Present Study	Winnebago System	all seasons	Unsexed	0.006571	
Probst and Cooper 1954	Winnebago System	all seasons	Unsexed	0.006710	
Larson 1988	Wisconsin River	spring	Unsexed	0.006710	
Smith and Baker 2005	Black R, MI	spring	male	0.006746	
Craig et al. 2005	St. Clair R, MI	spring, summer	male	0.006753	
Present Study	Winnebago System	winter	F2	0.006944	
Craig et al. 2005	St. Clair R, MI	spring, summer	Unsexed	0.007017	
Lallaman et al 2008	Manistee River MI,	Spring	Unsexed	0.007131	
Craig et al. 2005	St. Clair R, MI	spring, summer	female	0.007262	
Smith and Baker 2005	Black R, MI	spring	Unsexed	0.007305	
Present Study	Winnebago System	winter	F4	0.007529	
Smith and Baker 2005	Black R, MI	spring	female	0.008266	
McDonald 1998	Nelson R	spring	Unsexed	0.011744	
Nowak 1987	Groundhog and Mattagami R, Ontario	spring, summer	Unsexed	0.012913	
Hughes et al 2005	Lower Niagara River, NY	All seasons	Unsexed	0.029965	fat

TABLE 18.—Mean winter water clarities and mean lake sturgeon spear harvests, standard deviations, and coefficients of variation by decade, 1940s–2000s, Lake Winnebago, Wisconsin. Water clarities in meters, measured annually during the sturgeon spearing season with a secchi disc at the same location on Lake Winnebago.

Period	Mean WC (m)	Yrs Sampled	SD	CV	Mean Harvest	Yrs Sampled	SD	CV
1940s	3.81	2	1.08	0.28	790	7	553	0.70
1950s	4.01	6	0.59	0.15	924	10	567	0.61
1960s	3.57	10	0.99	0.28	528	10	444	0.84
1970s	3.52	10	0.87	0.25	565	10	455	0.81
1980s	3.35	10	1.01	0.30	670	10	604	0.90
1990s	4.30	10	1.37	0.32	1519	10	943	0.62
2000s	3.69	9	1.44	0.39	1023	9	549	0.54

CHAPTER 3

Long-Term Sustainability of the Lake Sturgeon Population in the Winnebago System

Introduction

Simulation models have been used to predict an animal population's future or sustainability and to integrate and assess information such as birth, death, immigration and emigration rates, and how environmental and ecological factors affect these rates through time. Individual rates of birth and death are estimated using population data and population dynamics models. Immigration and emigration rates can be derived from population dynamics models, field telemetry data, or knowledge of the population's habitat requirements and life history. Simulation models can be used to examine the risk of extinction of an animal population and provide insight into the factors that contribute greatest to the risk.

Simulation modeling can be a useful tool to examine alternative strategies for recovery plans for species threatened by human activities. Simulation modeling was used to assess extinction risk of Lake Superior lake trout and affirmed acceptable commercial and recreational fishing mortality rates that minimized the risk of extinction in the face of sea lamprey mortality (Nieland 2006). The extinction risk for threeridge mussels, a relatively slow growth animal, under pressure from zebra mussel (*Dreissena polymorpha*) competition and commercial over-harvest in the Mississippi River was estimated with a simulation model (Hart et al. 2004).

While simulation modeling can be used to predict a sturgeon population's sustainability and assess extinction risk from alternative management strategies, sufficient long term sturgeon population data are often not available to allow estimation of model parameters with confidence. Thirty years of sturgeon catch data from the lower Danube River in Serbia were used to predict the extinction of the beluga sturgeon (*Huso huso*) in 450 years, and Russian sturgeon (*Acipenser gueldenstaedtii*) in 50 years (Lenhardt et al. 2006). Twenty-four years of demographic population assessment data were used to predict the extinction in 30 years of the endangered white sturgeon in Kootenai River, Idaho, USA (Paragamian and Beamesderfer 2004).

The population and harvest of lake sturgeon in the Lake Winnebago System in east-central Wisconsin has been consistently monitored since the early 1940s (Schneberger and Woodbury 1946; Probst and Cooper 1954; Priegel and Wirth 1975, 1978; Folz and Meyers 1985; Bruch 1999) and provides a unique long-term time-series of data that can be used to develop a population simulation model.

Historically, sturgeon management actions and regulations have been implemented on the Winnebago System in a trial and error manner over many years, and potential risks posed to the lake sturgeon population have been assessed by the local sturgeon biologist's knowledge of lake sturgeon life history, historic harvest trends, and professional opinion about the potential effectiveness of a new proposal. An iterative process, and the review of historic trends are valuable tools for assessing the impact of past management decisions, but simulation modeling can provide an additional tool that may help provide a more complete picture of potential future impacts of management options.

Since the mid 1960s, the lake sturgeon in the Winnebago System have been managed to sustain robust levels by limiting annual exploitation to ≤ 5% (Priegel and Wirth 1975). This exploitation limit appears to have withstood the test of time and has been established as a limit for all of Wisconsin's lake sturgeon fisheries (WI Dept. of Natural Resources 1998), but has never been thoroughly evaluated. Evaluating the 5% annual exploitation limit in a simulation modeling exercise allows examination of the limit's flexibility, sensitivity to mortality rates and recruitment, and long-term effectiveness in sustaining lake sturgeon populations. Results from the simulation modeling will provide guidance for management of the lake sturgeon fishery in the Winnebago System, and for development of management plans and harvest limits for other sturgeon fisheries.

Methods

I built a time series simulation model in Excel with VBA (Virtual Basic for Applications) code to predict lake sturgeon abundance in the Lake Winnebago System in future years (Figure 50). I used estimates of demographic parameters from the statistical catch at age model for lake sturgeon in the Winnebago System to parameterize the simulation model, and to estimate annual abundance at age, year specific average adult female abundance, and year-specific total annual mortality at annual levels of exploitation in the winter spear fishery from 0 to 38%.

I derived initial abundance N_{ij} at age j for year $i = 0$ for the simulation model from age-specific lake sturgeon abundance estimates from the SCAA model for the year 2007. In each simulation, age-specific abundance estimates from 2007 were inputs for year zero and used to predict abundance at age for the next year using the formula:

$$N_{i+1,j+1} = N_{ij} e^{-Z_{ij}},$$

where: $N_{i+1,j+1}$ = the number of lake sturgeon surviving in each age class *j* and year *i* to the next age class $j+1$ and year $i+1$; N_{ij} = the number of lake sturgeon in age class *j* in year *i*; and Z_{ij} = the total instantaneous mortality rate for each age class *j* in year *i* (Haddon 2001; Quinn and Deriso 1999; Hilborn and Walters 1992).

The total instantaneous mortality rate Z_{ij} for each age class *j* and year *i* was equal to the sum of the total instantaneous natural mortality rate *M* and the total instantaneous fishing mortality rate F_{ij} for age class *j* in year *i*:

$$Z_{ij} = M + F_{ij}.$$

I used an estimate of 0.055 for instantaneous natural mortality rate (*M*), derived from a sensitivity analysis designed to estimate M from the SCAA model, as a constant in the simulation model.

I maintained instantaneous fishing mortality F_{ij} of age *j* lake sturgeon in year *i* as a constant input in the model for all ages and years as the primary independent variable. I used the age-specific selectivity (S_j) curve for a 91.4 cm minimum size limit in the winter spear fishery on the Winnebago System to adjust *F* for ages of sturgeon unrecruited to those fully recruited to the fishery:

$$S_j = 1/1 + e^{-Ln(19)*((j-j_{50})/(j_{95}-j_{50}))}$$

where s_j = relative selectivity of the spear fishery for age class *j* (Haddon 2001).

I predicted the number of recruits with a Ricker (1954) stock-recruit model:

$$R = \alpha * S * e^{-\beta * S} + \varepsilon ,$$

where: R = the estimated number of yearling recruits; α = parameter that describes the recruitment rate at low adult abundance (density independent parameter); S = estimated number of adult females in the stock; β = density dependent parameter; ε = stochastic error.

I tested exploitation rates in the simulation model as a function of F, Z and A:

$$u = (F * A) / Z ,$$

where: u = exploitation rate; F = instantaneous fishing mortality rate; A = total annual mortality rate; and Z = instantaneous total annual mortality rate.

I ran the model 1,000 times for 500 years in separate runs testing 40 different levels of exploitation from 0% to 38% and calculated average adult female lake sturgeon abundance from year 50 to year 500 for each simulation. I used initial abundance at year 50 as a starting point to allow the model to stabilize before using output. Mean abundances also included predicted abundances of zero. Adult female abundance, derived from empirical data from harvest and population assessments 1954-2007, was estimated to be 30.305% of all fish in population 26 years and older.

I built stochasticity into the model through the recruitment estimates for each simulation year by:

1) using the coefficient of variation of recruitment estimated by the SCAA model for the years 1955-2007 in the calculation of recruits with the LOGINV and RAND functions in Excel that together randomly selects a value for recruitment from a log normal distribution of possible recruitment values with a mean of zero and a standard deviation

equal to the coefficient of variation of the SCAA estimated recruitment from 1955-2007; and,

2) through variance estimated for each recruitment model parameter (alpha and beta) using: 1000 pairs of alphas and betas I created through a Monte Carlo bootstrapping exercise, where a separate pair of parameters is used in the recruitment calculation in each of the 1000 simulations for each model run of 500 years.

I tested a range of exploitation rates that included the current recommended annual exploitation limit of 5% and the instantaneous fishing mortality rate predicted by the yield per recruit model (Chapter 2) that produced maximum yield, F = 0.40, u = 32.1% (F_{max}).

For each simulated fishing mortality rate, I calculated the total annual mortality rate (*A*) as:

$$A = 1 - e^{-Z_{ij}} .$$

I used predicted average adult female lake sturgeon abundance, probability of extinction, and time to extinction as the metrics to evaluate sustainability of total instantaneous fishing mortality and total annual mortality rates; and considered a population extinct in the first year when adult female abundance equaled zero.

I calculated 95% confidence intervals for mean adult female lake sturgeon abundance as:

$$\bar{x} \pm s * 1.96 ,$$

where $\bar{x}$ = average adult female lake sturgeon abundance and *s* = the respective standard deviation of adult female lake sturgeon abundance for the sample.

I calculated the probability of extinction as the proportion of 1,000 simulations when the adult female lake sturgeon abundance declined to zero, and the 95% confidence intervals for the probability of extinction using the exact upper and lower 95% confidence limits for a binomial proportion (Zar 1999).

I defined time to extinction as the median number of years until adult female lake sturgeon abundance declined to zero (Nieland 2006); and assigned an extinction time of 500 years to simulations that did not result in an extinction event. I calculated the 95% confidence interval for the time to extinction as the 2.5-percentile and the 97.5-percentile of the time to extinction for the 1,000 simulations.

I evaluated the model through sensitivity analysis; a method commonly used to quantify uncertainty in simulation models and to determine which model parameters have the most influence on model predictions (McCarthy et al. 1996; Cross and Beissinger 2001; Ellner and Fieberg 2003; Essington 2003). I performed the sensitivity analysis by holding each parameter at a constant value while changing one parameter at a time by ±10% (Table 19). I evaluated the sensitivity of each parameter by comparing the mean adult female lake sturgeon abundance from all simulations when the parameter was changed to the mean abundance when all parameters were set at their 2007 estimates from the SCAA model, and at a constant instantaneous fishing mortality rate of 0.50. I considered parameters that caused the mean adult female abundance to deviate more than 10% highly sensitive; those that caused the mean abundance to deviate by 10% linearly sensitive; and those that caused the mean abundance by less than 10% insensitive (Essington 2003). I ran the model 1000 simulations for 500 years for each parameter deviation.

Results

At the average annual exploitation rate experienced by the lake sturgeon population during 1997-2007, 3.2%, and an SCAA estimated constant annual conditional natural mortality rate of 5.4%, the long term abundance of adult female lake sturgeon in the Winnebago System out to the year 2507 based on 1000 simulations in the stochastic simulation model is estimated to average 8147 (95% CI's: 7342 – 8951). The inverse relationship between adult female stock and number of yearling recruits results in a sign wave pattern of abundance of adult females with a peak in abundance an average of every 57 years (SD 7.1 years) (one random simulation) of 12651 adult female sturgeon (SD 2450), and a low point in abundance approximately 28 years after each peak at an average rate of every 57 years (SD 4.3 years) of 2494 adult female sturgeon (SD 575) (Figure 51).

Average long term abundance of adult females dropped consistently with increases in annual exploitation above zero. For example, the sustained adult female population, at an annual exploitation rate of 3.2% (the empirical 1997-2007 rate), of 8147 (SD 410.5) was 28.3% less than the estimated abundance of the stock with 0% exploitation, 11369 (SD 725.6). At an annual rate of 4.7%, the current recommended exploitation limit, the long term stock estimate was 6751 (SD 273.6), 40.6% less than the average stock estimated to be present in the absence of exploitation (Figure 52).

Adult female lake sturgeon dropped to very low levels of average long term abundance of less than 2000 fish at exploitation rates 16% and higher, and went extinct as exploitation exceeded 20%. Extinction probabilities rose rapidly from 0.026 at 20% exploitation, to 0.999 at 22% exploitation (Figure 53). The median years to extinction at

an exploitation rate of 20.8% was 470 (95%CI 241-501), 237 years (95%CI 164-362) at 22% exploitation, 36.1 years (95%CI 34-38) at 37.1% exploitation, and 13 years (95%CI 13-13) at 38% exploitation (Figure 54).

The sensitivity analysis indicated that long-term mean adult female lake sturgeon abundance was relatively insensitive to deviations in all model parameters except natural mortality and β the stock-recruit model density dependent parameter (Table 20). Natural mortality and β were both highly sensitive to 10% decreases in their value resulting in 10.4% and 11.0% increases respectively in long term mean abundance of adult females. Parameters of the selectivity model were the most insensitive to deviations resulting in mean differences in adult female abundance of <4%.

Discussion

Based on results from stochastic simulation modeling, the lake sturgeon population in the Winnebago System can be maintained at stable levels capable of supporting the annual winter spear fishery at exploitation rates up to the current limit of 4.7%. Annual exploitation maintained at an average of 3.2%, the average rate from 1997-2007, would result in a robust stock of adult females, but at a level 28.3% less than the estimated abundance of the stock with 0% exploitation. With a Ricker stock-recruit relationship, and an annual conditional natural mortality rate of 5.4%, adult females are predicted to cycle every 28 years from high abundance to low abundance; with the average level of abundance over the long-term dependent upon the level of exploitation. The model indicates recruitment is currently increasing, but that the adult stock is currently moving towards the next low point in the abundance cycle predicted to occur in approximately the year 2034, followed by a high point of abundance approximately in the year 2062. If

the model is accurate, annual adult population estimates should reflect the long term changes, and harvest caps in the winter spear fishery will need to be adjusted to maintain exploitation at or below 4.7%.

The recreational sturgeon spear fishery on the Winnebago System is managed first to sustain a viable and robust lake sturgeon population, and second to sustain a viable lake sturgeon spear fishery with annual recreation and harvest opportunities. All fisheries with an exploitation component are managed towards some harvest objective, typically a sustained yield, and policies are developed and put in place with the hopes of meeting the objectives. Common policies include constant catch, constant fishing mortality rate, and constant escapement. The 4.7% exploitation limit in place since the 1960s as a harvest control goal for lake sturgeon in the Winnebago System is a constant fishing mortality rate policy. Constant fishing mortality rate policies were the most effective at minimizing the risk of overharvest when applied to fish stocks for which error in stock size estimates is determined (Deroba and Benson 2008). The harvest cap system in place on the Winnebago System since 1997 utilizes population estimates (with error) to set harvest caps at 5% of estimated stock size for adult females and males. Harvest caps have traditionally been set for the third component of the harvest, juvenile females, at the same level as the adult females since prior to the SCAA model, there were no juvenile females estimates available. While the harvest cap system has worked quite well since its implementation to maintain exploitation at an acceptable level, it has exhibited implementation error as the mean annual exploitation rate since 1997 has been 3.2%, substantially below the 4.7% limit. This error though places the fishery on the

conservative side of exploitation, a much more preferable side to be on with a species like sturgeon that have a high vulnerability to overharvest.

My simulation model supports the common belief that sturgeon are very susceptible to overharvest and provides some insight into possible dynamics of stocks exploited at various levels. A modest increase in total annual mortality from 16% to 20% was predicted to cause the Gulf sturgeon population to decline (Pine et al. 2001). Shovelnose sturgeon (*Scaphirhynchus platorynchus*) in the Missouri River System were found to be much more sensitive to low levels of exploitation than previously thought (Quist et al. 2002). The simulation model for lake sturgeon of the Winnebago System predicted a decline in adult stocks to lower and lower levels as exploitation increased from zero, although, despite being at lower levels the populations appeared to be relatively stable until the number of adult females dropped below 300 and exploitation persisted at 20% or more. If exploitation increased beyond 20%, the population went extinct.

The time to extinction of the Winnebago lake sturgeon population predicted by the simulation model also provides insight into the sensitivity of sturgeon to overexploitation. The Winnebago model predicted that even at the relatively high exploitation rate of 20% extinction took a long time, hundreds of years, but once exploitation increased beyond 20% that extinction came much more rapidly. At 30% exploitation, median years to extinction were estimated at 42. At 37% exploitation, median years to extinction were predicted to be 36, and at 38% exploitation the model predicts the population would be extinct in 13 years. The lake sturgeon populations in the Great Lakes were nearly decimated between 1879 and 1910; a period of 31 years

(Smith 1968). Although the gear selectivity of the Great Lakes fisheries in the late 1800s for lake sturgeon has not been quantitatively defined, it is possible that it may not have been too different from the selectivity of the Winnebago spear fishery where fish are initially recruited into the fishery at 91 cm. If the gear selectivity was at all similar, the Winnebago model suggests that the Great Lakes lake sturgeon populations experienced annual exploitation rates in the range of 35%-38% in the late 1800s to cause the total collapse of the Great Lakes stocks by 1910. Holzkamm and McCarthy (1988) used records of isinglass returns from the Hudson Bay Company, Canada, to estimate the production and collapse of the lake sturgeon fishery on Lake of the Woods between Ontario, Canada and Minnesota, USA during 1888 and 1908. The 20 year period between the initiation of the fishery and its collapse indicates annual exploitation was likely in excess of 35-38%. Taghavi (2001) in his assessment of the status of Beluga sturgeon stocks in the Caspian Sea estimated that adult female and male Beluga were being exploited in the 1990s at rates of 35.8% and 27.5%, and called for a complete closure of the Caspian Beluga sturgeon fishery.

The results of the sensitivity analysis indicate that long-term mean abundance of lake sturgeon in the Winnebago System under a spear fishery with a constant annual exploitation rate of 4.7%, would potentially respond positively to decreases in density dependent factors or natural mortality. A decrease in density dependence would result in an increased overall population including increased numbers of adult females. With a constant annual fishing mortality rate, a decrease in natural mortality would decrease total annual mortality resulting in more adult females over time.

Since the mid 1960s, the Winnebago System lake sturgeon population and fishery have been managed to sustain robust levels by limiting annual exploitation to ≤4.7%. This exploitation limit appeared to have withstood the test of time and was established by the Wisconsin Department of Natural Resources as a limit for all of Wisconsin's lake sturgeon fisheries (Wisconsin Department of Natural Resources 1998), and has now been evaluated. The Winnebago lake sturgeon simulation model has allowed evaluation of high and low exploitation rates and their long-term impact on the sustainability of the lake sturgeon stock in the Winnebago System. While the model predicts that the 4.7% harvest limit allows the lake sturgeon population in the Winnebago System to maintain itself at a viable level, environmental factors and regulations maintained actual mean annual exploitation of the stock since the mid 1960s at 3.4%, substantially less than 4.7%. At the lower exploitation rate the population has been able to grow and approach carrying capacity in the relatively short time of 30 years. If the Ricker style stock-recruit relationship predicted by statistical catch at age modeling proves to be reality over time, the inverse relationship between adult stock density and recruits will need to be factored into management decisions for healthy stocks that are at or approaching carrying capacity. I recommend that the 4.7% exploitation limit be retained as a management guideline for exploited populations and model results be used to assist in the development of harvest management objectives for other sturgeon populations.

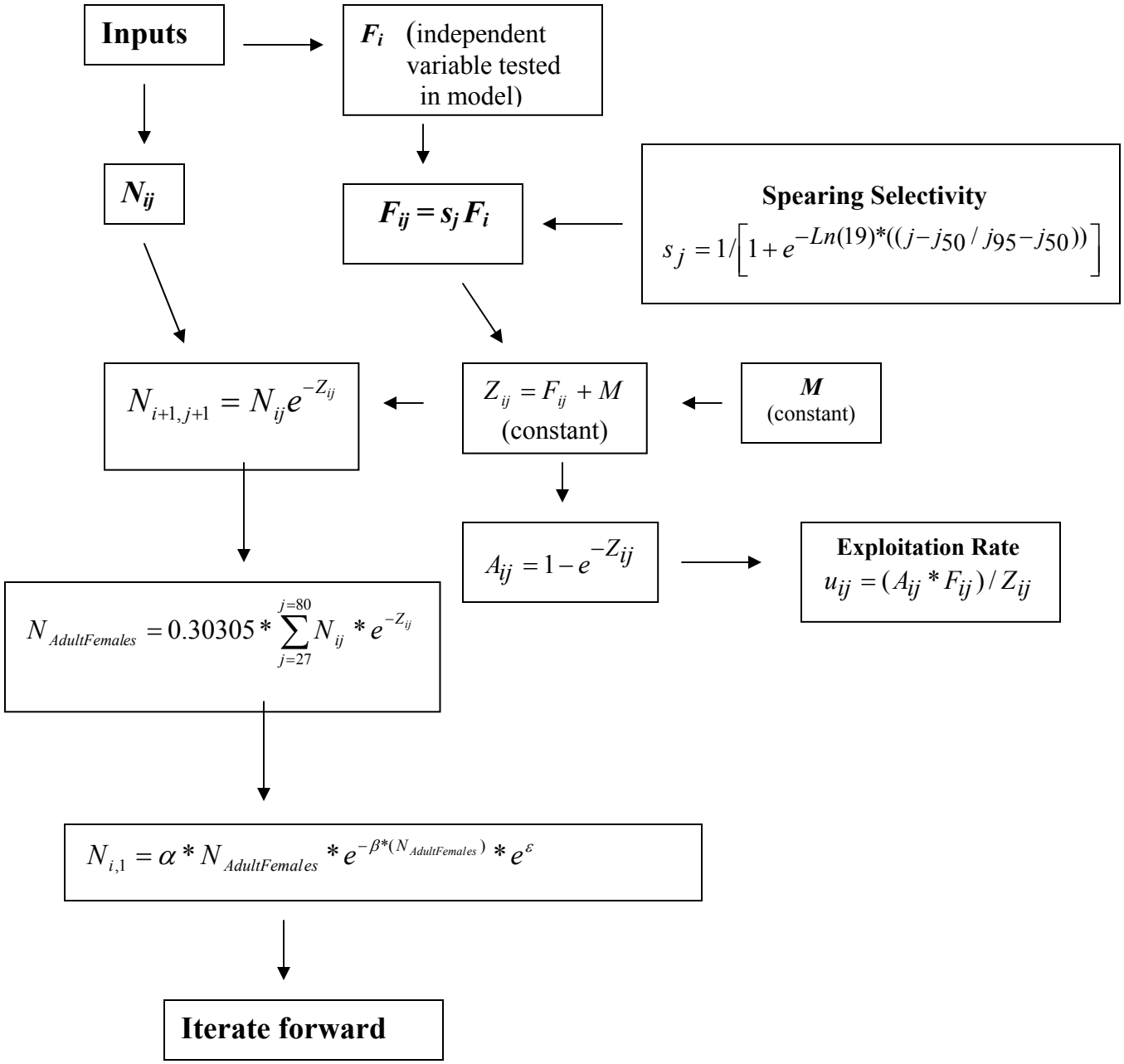

FIGURE 50.—A schematic diagram of a lake sturgeon population simulation model, Winnebago System, Wisconsin, where *i* is year and *j* is age, and the inputs are total instantaneous fishing mortality F_i, natural mortality M, and the initial abundance in the year *i* for age *j*. Model projects population abundance using a Ricker stock-recruitment model to predict the number of age 1 recruits produced from the estimated number of adult females in the stock the year before.

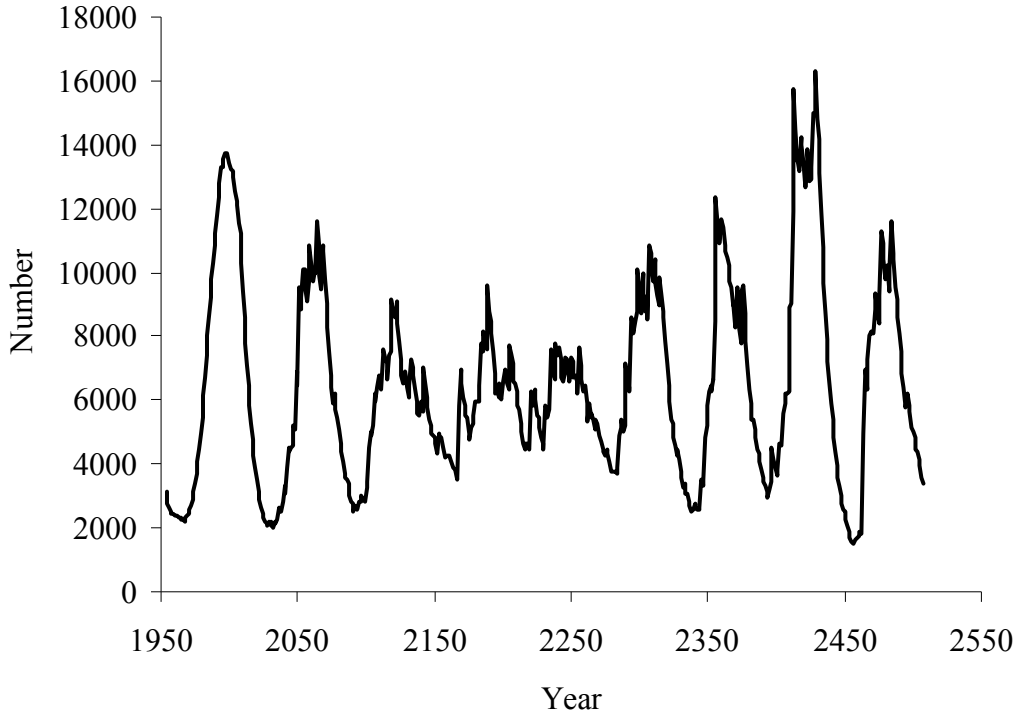

FIGURE 51.—Estimated adult female lake sturgeon abundance, 1954-2507, Winnebago System, Wisconsin, with annual exploitation rate of 4.7%; instantaneous natural mortality rate constant at 0.055. Estimates for 1954-2007 from statistical catch at age model, estimates for 2008-2507 from one run of simulation model out of 500 ran for each exploitation rate tested.

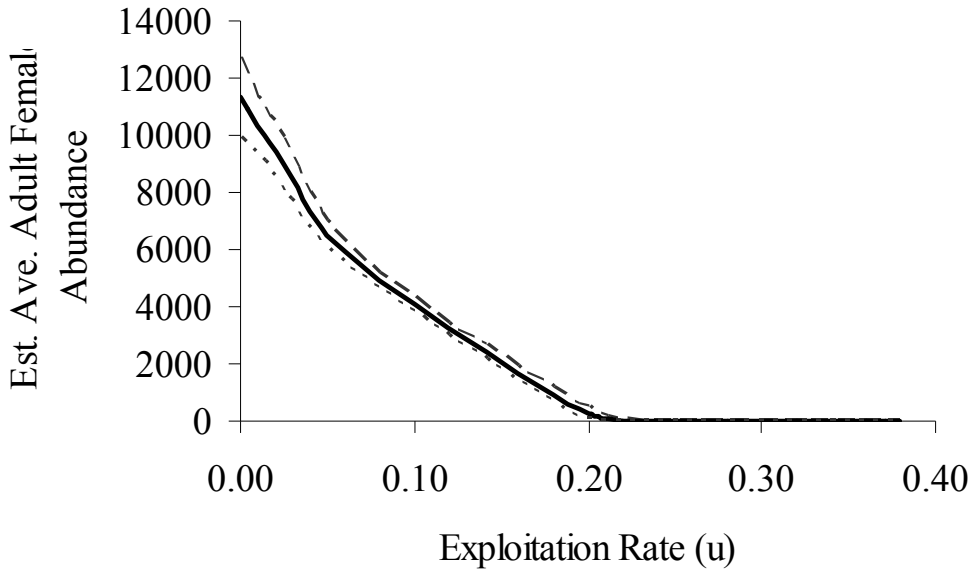

FIGURE 52.—Long-term average of estimated number of adult females in lake sturgeon population 2059-2507 Winnebago System, Wisconsin, as a function of average annual exploitation in the winter spear fishery; dashed lines are upper and lower 95% confidence intervals around means.

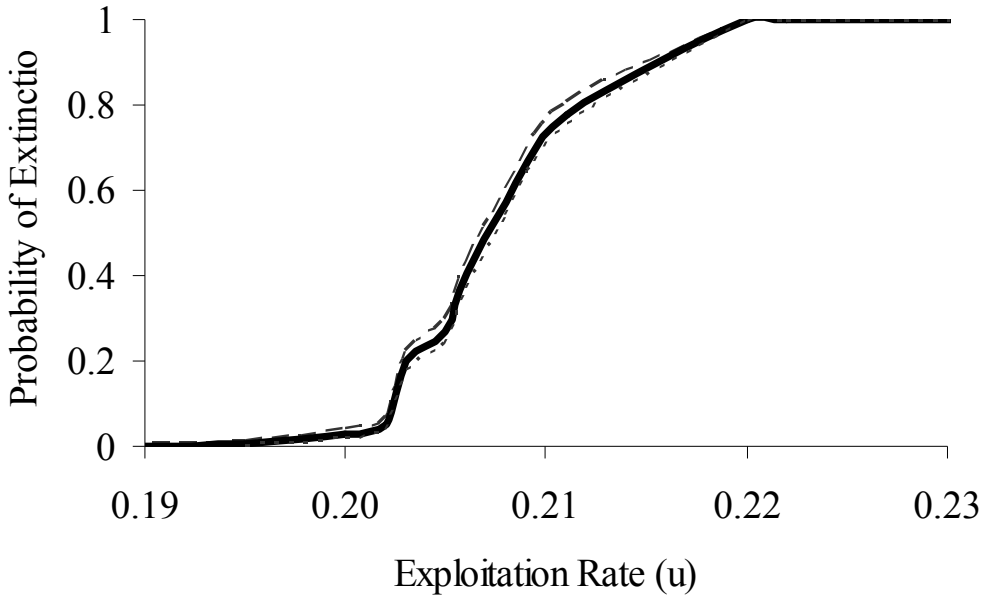

FIGURE 53.—Estimated probability of extinction of adult female lake sturgeon in the Winnebago System, Wisconsin at exploitation rates from 19% to 23% in the winter spear fishery; dashed lines are upper and lower 95% confidence intervals around means.

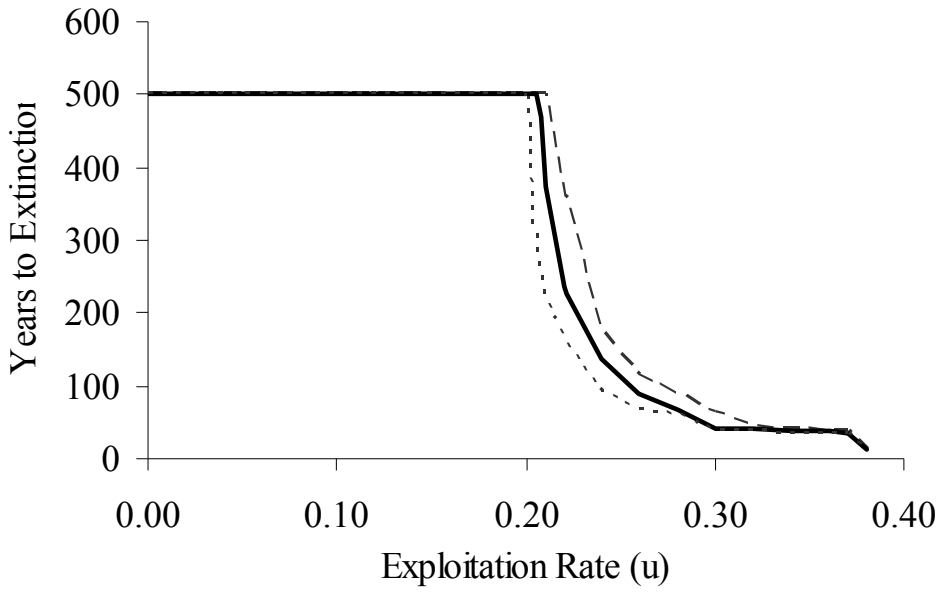

FIGURE 54.—Average estimated median years to extinction and 95% confidence intervals (based on the 2.5 and 97.5 percentiles) of the adult female lake sturgeon population in the Winnebago System, Wisconsin, at exploitation rate of 0% to 38% in the winter spear fishery based on output from stochastic simulation model with F constant in each model run of 1000 simulations, and M = 0.055.

TABLE 19.—Parameters tested in a sensitivity analysis of a lake sturgeon simulation model for the Winnebago System, Wisconsin.

Parameter	Parameter Description
Baseline	The baseline run for the sensitivity analysis with a constant instantaneous fishing mortality rate of 0.05
M	The natural mortality value.
S-R alpha	The density-independent parameter in the Ricker stock-recruitment curve.
S-R beta	The density-dependent parameter in the Ricker stock-recruitment curve.
S-R Error	The error term for the Ricker stock-recruit rate.
a50	The parameter of the selectivity curve that describes the age of 50 % selectivity to the winter spear fishery with a 91.4 cm minimum size limit.
a95	The parameter of the selectivity curve that describes the age of 95 % selectivity to the winter spear fishery with a 91.4 cm minimum size limit.

TABLE 20.—Parameter tested, deviation tested, mean abundance of adult females, standard deviation of the mean, lower and upper 95% of mean abundance, and percent difference between the baseline mean and the mean for the parameter deviated for a lake sturgeon simulation model for the Winnebago System, Wisconsin. The model was run for 1,000 simulations and 500 years for each simulation at a constant instantaneous fishing mortality rate of 0.05. Parameter deviations listed in descending order of mean difference.

Parameter	Deviation	Mean	SD	Lower 95%	Upper 95%	Mean % Difference	Sensitivity
Baseline	-	6751.4	273.6	6,215	7,288	–	–
S-R β	-10%	7497.1	297.0	6,915	8,079	11.04%	High
M	-10%	7453.0	328.9	6,808	8,098	10.39%	High
S-R β	10%	6153.1	239.3	5,684	6,622	-8.86%	Insensitive
M	10%	6167.9	210.3	5,756	6,580	-8.64%	Insensitive
S-R α	-10%	6366.2	222.8	5,930	6,803	-5.71%	Insensitive
S-R α	10%	7135.7	301.4	6,545	7,726	5.69%	Insensitive
S-R Error	10%	7056.6	346.2	6,378	7,735	4.52%	Insensitive
a50	10%	7017.3	296.2	6,437	7,598	3.94%	Insensitive
S-R Error	-10%	6497.2	207.7	6,090	6,904	-3.77%	Insensitive
a50	-10%	6501.2	241.3	6,028	6,974	-3.71%	Insensitive
a95	-10%	6742.0	267.5	6,218	7,266	-0.14%	Insensitive
a95	10%	6753.6	269.7	6,225	7,282	0.03%	Insensitive

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Education

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- M.S. Zoology, December 1986. University of Wisconsin-Milwaukee. Thesis topic: Age and growth, mortality, reproductive cycle, and fecundity of the deepwater sculpin, *Myoxocephalus thompsoni* (Girard), in Lake Michigan.

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Positions

Senior Fisheries Biologist/Work Unit Supervisor, 1990 -Present. WI DNR Oshkosh.
Winnebago System Biologist/Planner, 1986-90. WI DNR Oshkosh.
Fisheries Biologist-Great Lakes, Lake Michigan, 1984-86. WI DNR Milwaukee.
Fisheries Technician-Operations and Coldwater Habitat Improvement, 1981-84. WI DNR Eagle.
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Fisheries Project Biologist-Oconto River Restoration Project, 1978-80. WI DNR Oconto Falls.
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Professional

Serve on Editorial Board of the Journal of Applied Ichthyology
Member of the Scientific Committee for the 6th Intl Symposium on Sturgeon (Wuhan, China, Oct 2009)
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Co-Chaired the 4th International Symposium on Sturgeon (Oshkosh, WI, USA 2001)
Served on the Scientific Committee of the 3rd International Symposium on Sturgeon (Piacenza, Italy 1997)
Member of the World Sturgeon Conservation Society (Founding Committee and current Treasurer)
Chair of the Executive Committee of the North American Chapter of the World Sturgeon Conservation Society
Member of the American Fisheries Society
Member of the Wisconsin Chapter of the American Fisheries Society

Selected Publications

Bruch, R.M., S.E. Campana, S.L. Davis-Foust, M.J. Hansen, and J. Janssen. In press. Age validation of lake sturgeon using bomb radiocarbon and known age fish. Transactions of the American Fisheries Society.

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